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M. C. F. Proctor

N. K. B. Robson

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THE GROWTH OF *EUPHRASIA* IN CULTIVATION

By P. F. YEO

University Botanic Garden, Cambridge

ABSTRACT

Previous workers found that *Euphrasia* could be brought to maturity in cultivation whether supplied with a host-plant or not (though better growth was obtained with a host than without), and found also that a wide variety of annual and perennial herbs could act as hosts. The present paper describes chiefly cultures in clay pots, into which the *Euphrasias* were transplanted as seedlings. Usually growth was better when a host was provided than when it was not, but growth without a host was better than that obtained by previous workers. The development of some plants without a host was much affected by a difference of soil composition. A spurt of growth some weeks after planting with a host was taken to indicate parasitic establishment on the host, and the shorter the distance between the *Euphrasia* and its host the sooner establishment occurred. *Euphrasias* grown with certain *Leguminosae* were particularly vigorous and showed symptoms of a good nitrogen supply. Some severely retarded *Euphrasia* plants were probably being parasitized by their neighbours.

Euphrasias sometimes flowered very early, beginning at a very low node; this appeared to be caused by unusually high temperatures. The early-flowering species were particularly frequently affected in this way, which made it difficult to raise normal plants of these species.

Deaths of young *Euphrasia* plants took place chiefly in cold, dull weather, but were reduced by watering sparingly.

Cultures of various *Euphrasia* species with various hosts showed that certain hosts were good, and that others were bad or probably bad. There were indications of a difference between *E. pseudokernerii* and *E. anglica* in their growth on the same hosts. Different populations of the same *Euphrasia* species sometimes differed in their host-reactions. The host affected percentage establishment, mortality and vigour of the *Euphrasias*.

For cultivation in the open ground *Euphrasia* plants and hosts were planted in bituminized paper pots, which were embedded in the ground. Very vigorous growth was obtained in this way, using *Plantago lanceolata* as a host-plant.

The parasitic habit is probably not responsible for the taxonomic complexity of *Euphrasia*, but may be connected with its gregariousness in nature.

PREVIOUS WORK

The possibility of cultivating haustoria-forming Scrophulariaceae was demonstrated at the end of the last century. The behaviour in cultivation of the three semi-parasitic genera, *Rhinanthus*, *Odontites* and *Euphrasia*, was first studied by Ludwig Koch. His first paper dealt with *Rhinanthus*, and the second (1891) with *Euphrasia officinalis* L. He found that seedlings which germinated in pots grew much as wild ones do, if the pots contained old tufts of grass or grass seed sown at the same time as the *Euphrasia* seed (*i.e.* autumn). In *Rhinanthus minor*, however, Koch had found that simultaneous sowing of host and parasite gave retarded growth. He attributed this to the more rapid growth and earlier maturity of *Rhinanthus* placing a big demand on the host plants while they were still relatively young. Koch also sowed grass seed in pots with *Euphrasia* seedlings which were 3 cm tall (possibly an error for 3 mm tall). The effect of this was similar to that of simultaneous sowing with *Rhinanthus*, but worse from the point of view of the *Euphrasia* plants, which died off after 3 to 4 weeks. *Euphrasias* with no host-plant grew about as weakly as those with host seed sown after germination; if the seedlings were thinly and evenly distributed, they appeared starved and died off from mid-June onwards; in thick, uneven distributions some plants grew faster than the rest and were found to be attached to their neighbours by haustoria. These plants died if surrounded by few others, but if surrounded by enough others they occasionally flowered. They were prevented from fruiting by being dug up for investigation of the roots. Koch concluded that, for *Euphrasia* and *Rhinanthus*, parasitism on an autotrophic host was essential and not merely facultative.

Wettstein (1896) at first came to the same conclusion. He reported that seedlings of *E. rostkoviana* germinating in troughs in the open, in which grass seed had been sown the previous year, produced quite vigorous plants which flowered and had numerous haustoria. With no hosts the plants were dwarf, produced up to ten pairs of leaves, formed no flowers and had no haustoria. Later, however, among many seedlings grown together in pots or pricked out singly in pots after germination, he brought a few plants to the stage of flowering or fruiting (Wettstein 1897). Some of them were without haustoria, while others had haustoria on the roots of other *Euphrasias*. Wettstein now concluded that, though parasitism on an autotrophic host is necessary for vigorous development, individuals can flower and fruit, either alone or when behaving autoparasitically.

Heinricher's four papers on 'The Green Semiparasites', describe a lot of work on *Euphrasia*. It is first necessary, however, to describe an experiment with *Odontites odontites* (*O. verna*) (Heinricher 1898a). Seed was sown in a pot on 2 March 1895, and the largest plants were 2.5 to 3 cm tall by 27 April. On 29 April, it was found that seedlings of a closely-sown group had haustorial initials at the points where their roots were in contact. Two other cultures, thickly-sown, gave the following results: in one there were 36 plants on 2 August, with from 3 to 12 pairs of leaves; two plants had flower buds and branch initials. On 20 September the strongest plant was 20 cm tall, had produced 20 flowers, and its lowest capsules were ripe. In the other thickly-sown culture the plants, on 3 August, were from 2 cm tall, with four leaf-pairs, to 7-8 cm tall, with 2-3 flowers. The plants did not grow much more, and produced up to two or three fruits each. The wide individual variation of the first culture is attributed to a long period of germination, enabling some plants to get ahead by parasitizing others; the uniformity of the second is attributed to germination taking place over a short period. These results are similar to those obtained by Koch with uneven and even sowings respectively, using *Euphrasia* seed.

In addition to *Odontites*, Heinricher (1898a) got *Euphrasia stricta* Lehm. to flower with no host in a thickly-sown pot or garden soil. Germination began on 17 March 1896, and 70 plants were present on 15 May. Some plants that were surrounded by many others grew more strongly, and the strongest one started to flower on 8 August when 32 mm tall. Eight more were in flower on 13 September. The smallest flowering plants had stems 7-10 mm tall, their leaves were scarcely half the area of those of the largest, and their flowers were a half to a third the size. In two other pots, with 30 and 36 seedlings respectively, no plants came into flower.

Later, experiments were carried out with *E. rostkoviana* (Heinricher 1898b). In one pot the seedlings were abundant, and in places dense, on 17 March; flower buds appeared in May but none opened; more were formed in July, and the plants produced up to 20 leaf-pairs, but only one eventually flowered, although 80-90 had germinated. In each of five further pots, one seedling came up; these died one by one, from May to August, all without flowering.

The growth of a third species, *E. minima* Lam., in the absence of a host plant, was also investigated (Heinricher 1898b). In one pot 27 seedlings were present in June 1898, but they were mostly chlorotic and were attacked by aphides, and none flowered. A similar number of seedlings appeared in this pot in 1899, and six dwarf plants flowered in May. *E. minima* was also sown outdoors on a plot of gravelly, stony soil. Most plants flowered in June; three examples which were growing 2 cm apart from one another but isolated from other plants were illustrated; they were about 2 cm tall and began flowering at the third node. Another similar small isolated plant was found and its roots examined. Lateral roots had penetrated and formed many branchlets in rotting wood-fragments in the ground; root hairs were plentiful in places, but no haustoria were found.

These dwarf plants of *E. minima*, and also those of *E. stricta* mentioned earlier, resembled wild plants of *E. minima* seen in late August at Hühnerspiel, Brenner, growing on stony ground at a distance from other plants.

Heinricher concluded that *E. rostkoviana*, with one out of 90 plants flowering with no host, was the most advanced parasite, *E. stricta*, with nine out of 70 flowering with no

host, was less advanced, and *E. minima* was the least advanced. In fact, Heinricher did not grow approximately similar numbers of plants per pot of each species in the same year and with the same soil. Nor was there any duplication of pots, and his conclusions, though possibly correct, have little foundation. In any case, such a comparison would be very difficult to make because the three species probably have different optimal soil conditions. The occurrence of wild populations of *E. minima* with no apparent access to hosts, which Heinricher reports, does, however, indicate that this species is sometimes autotrophic in nature. Heinricher (1898*b*) states that, in having plenty of root hairs and in being relatively independent, *E. minima* resembles *Odontites odontites* (*O. verna*).

Heinricher also raised *Euphrasia* to the flowering and fruiting stages with host-plants, finding that the parasites were more vigorous with hosts than without, and more of them flowered. Pot cultures on indoor window-ledges suffered from unsatisfactory conditions, the best results being obtained with *E. stricta*. About 100 seeds of *E. stricta* were sown in a large pot of garden soil with seed of *Trisetum flavescens* on 27 February 1896 (Heinricher 1898*a*). *Stellaria*, *Capsella* and *Polygonum* came up as weeds, and most *Euphrasia* plants were closer to weeds than to *Trisetum*. Some plants evidently became established; the number of flower initials formed ranged from 1 to 16. The weakest plants were weaker than the strongest in the cultures with no host.

Better results were obtained outdoors by sowing seed in autumn on plots planted with tufts of *Carex*, *Luzula* and Gramineae (Heinricher 1898*a*). At a suitable time *Euphrasia*s and hosts were dug up and haustoria were found on the host roots. Seedlings of *E. salisburgensis* were abundant on all plots on 14 April 1897 and flowering reached its peak at the end of June. Haustoria were found on:

Carex alba Scop.

Luzula spadicea (All.) Lam. & DC.

Carex firma Host

Trisetum distichophyllum (Vill.) Beauv.

Carex sempervirens Vill.

Sesleria caerulea Scop.

Carex brachystachys Schrank & Moll.

Poa alpina was also used, but it was not investigated for haustoria. It was found that the hosts tended to shade out the *Euphrasia*s, while vigorous development occurred when the *Euphrasia*s were not shaded but were within reach of the host roots. Under the conditions of this experiment, the host species therefore varied in suitability as hosts according to their habit, caespitose species with short leaves being best.

The following results were obtained with weeds acting as hosts:

extraordinarily vigorous growth on *Capsella bursa-pastoris*;

vigorous growth on *Trifolium pratense*;

better growth on young seedlings than on larger plants of *Dipsacus fullonum*;

giant plant on *Senecio vulgaris*, similar to result with *Capsella*;

one plant vigorous on *Sonchus oleraceus*, lower parts shaded by host rosette and etiolated, upper parts normal;

very vigorous development on *Veronica peregrina* and *V. persica*.

In some cases a *Euphrasia* plant was found to have attachments to more than one host-plant simultaneously—in one case, for example, to *Carex alba*, *Poa annua* and *Trifolium pratense*.

Sowings of *E. rostkoviana* and *E. minima* were made under similar conditions, and gave very similar results.

Heinricher (1910) concluded that cultivation of *Euphrasia* was easy, provided the seed was sown in summer or autumn, the density of growth of the host-plant restricted, and good illumination ensured; a wide range of species could be used as hosts.

Euphrasia rostkoviana was also grown by Neidhardt (1947). The numbers of plants per pot were not given, but numbers of seeds sown were, and germination was up to 40%. Neidhardt tried one, two, five or 100 seeds per pot with no host, one, 100 and over 100 with

Poa annua, and over 100 with *P. nemoralis* and *Agrostis tenuis*. With no host, no *Euphrasia*s flowered; when there were 100 in a pot some grew more strongly if in a group of several close together; with one per pot, plants attained a height of 1 to 3 cm and were chlorotic; with two and five per pot they were similar but reached 5 to 6 cm. With host-plants present and many seedlings in a pot, the *Euphrasia*s became more vigorous after 4 weeks. If the host was regularly cut back, plants reached 25 cm and began to flower at the beginning of August. If it was not cut back, the *Euphrasia*s developed slowly, and died in June without flowering. With one seedling per pot and *Poa annua* the *Euphrasia*s were vigorous, much-branched and up to 15 cm tall, and they began to flower at the beginning of August.

Neidhardt also got *E. rostkoviana* to grow in grass in the garden of the Hamburg-Fuhlsbüttel school, in a part of Germany where the species is not native. Germination took place in April, plants were similar to those of pot cultures and they flowered at the beginning of August. Success was not achieved in all cases, and Neidhardt states that the ground should not be too solid and should be as moist as possible, and that the hosts should be as low-growing as possible and not too dense.

Recently Wilkins (1963) has given comparisons of dry weights of *Euphrasia* grown with four hosts and no host. All the *Euphrasia* samples reacted in much the same way to the hosts, and all hosts gave superior growth to no host, the difference being marked for all except one of the *Euphrasia*s. Successful cultivation was achieved at least once with seven other hosts. Many of the potted plants were planted out in the garden when the roots had bound the soil together sufficiently. Establishment on the host was estimated by measuring the span of the largest leaf-pair; with *Trifolium repens* the time required for establishment was about 7–10 weeks.

METHODS OF CULTIVATION

The simplest method of growing *Euphrasia*, in my experience, is to dig up turf in which the plants are growing and plant it in pots.

In 1952, I collected plants of many species by this method from early May until mid-September. In the great majority of samples collected in this way some of the *Euphrasia*s continued to grow and flower. In another instance a turf was dug up in November, and *Euphrasia*s germinated and flowered in it the following year. In such cultures the host-plants have to be cut back to prevent them smothering the *Euphrasia*s; this is chiefly necessary in the early stages, as the host-plants later become pot-bound.

A second method is to sow *Euphrasia* seed in pots and, at the same time or later, sow seed of host-plants in the same pots. Alternatively, germinated seedlings or rooted portions of host-plants can be added to the pots. This method was used for *E. pseudokernerii* in 1951–52.

Germination in *Euphrasia*, however, is always rather uncertain (Yeo 1961). Wastage of pot capacity and host-plant supplies can be avoided and the number of plants per pot controlled, if the *Euphrasia* seedlings are transplanted after germination. This method can be used either for pot culture or for cultivation in open ground, and it is possible to use seedlings germinated in cultivation or collected wild in March, April or May. Transplanting hosts and *Euphrasia*s, at approximately the same time, into the pots in which they are to be grown has been my standard method of culture. For cultivation in open ground the *Euphrasia*s and their hosts are planted in bituminized paper pots which are then planted in the soil and gradually rot.

For almost all cultures the potting soil used was John Innes compost no. 1, or slight variants of it.

PRESENCE AND ABSENCE OF HOST-PLANTS

The growth of several species of *Euphrasia* with and without hosts has been compared. In 1952, *E. pseudokernerii* (serial no. E42), from S. Lincolnshire, was grown from seed with several different hosts, and with no host. Diagrams of some of the plants can be seen in Fig. 1, p. 8. Flowering occurred without a host, but the diagrams show that these plants were

far weaker than some, at least, of those with hosts. Similar results were obtained with seedlings of *E. pseudokernerii* (E66) collected from Box Hill, Surrey, in April 1952.

In 1955, *E. nemorosa* (E507), collected from Cambridgeshire, was grown from seed in pots with four separate host-plants, and without a host. The weights of the plants after drying (Table 5, p. 12) show distinctly superior growth with three of the four hosts, and that the largest individual with a host was over five times the weight of the largest with no host. Two plants from this experiment are illustrated in Fig. 3, p. 21. The one grown with no host shows a very gradual increase in the size of the leaves on the main stem, and has few branches, which are confined to the upper cauline nodes and were still short at the time

TABLE 1. Length of Stem and Branches of *Euphrasia*.(Eight *Euphrasias* per pan, 6–8 survived in each.)

	Mean (cm)	Range	Mean (cm)	Range
1957	4 <i>Medicago lupulina</i> , 8 in. pan		No host, 8 in. pan	
<i>rostkoviana</i> , E669, v.c.49 ..	10.4	5–13.5	10.3	1–13.5
1962	2 <i>Sagina procumbens</i> , 2 <i>Trifolium occidentale</i> , 8 in. pan		No host, 5 in. pan	
<i>occidentalis</i> , E922, v.c.75 ..	33.0	10– 71	5.9	4– 8
<i>nemorosa</i> , E919, v.c.48 ..	49.7	8– 87	15.0	9–30
<i>confusa</i> , E907, v.c.45 ..	40.5	22– 84	12.7	7–17
<i>confusa</i> , E914, v.c.45 ..	72.3	11–160	9.5	4–14
<i>brevipila</i> , E917, v.c.45 ..	52.4	21–149	8.3	2–14
<i>rostkoviana</i> , E916, v.c.45 ..	42.1	24– 60	6.3	4– 9
<i>anglica</i> , E913, v.c.45 ..	59.9	27– 94	14.5	6–23
1963	As 1962		No host, 8 in. pan	
<i>confusa</i> , E929, v.c.26 ..	52.4	16–103	8.9	2–21
<i>brevipila</i> E940, v.c.98 ..	50.0*	32– 77	16.0	10–26

* Four plants; the other four plants in the pot had a similar size range, but were pressed later.

the plant was pressed. In the plant with a host, large leaves were formed lower down the stem, but near the apex the leaves were smaller, probably in correlation with the great development of the branches.

Further results are presented in Table 1.* The beneficial effects of providing a host are evident in all samples except the first. Even here, some benefit can be inferred, if it is assumed that the *Euphrasia*, had it not been parasitically established, would have been adversely affected by the competition of the *Medicago*. In fact some of the plants of E669 with *Medicago* showed visible indications of rather superior growth, compared with that with no host, which are not shown by the measurements. In view of the postulated competitive effect of the host the comparison in 1962 between plants with a host in 8 in. pans and plants with no host in 5 in. pans is probably not unfair. In fact, growth of host-less plants in 5 in. pans was much the same as in 8 in. pans.

An apparent indication of establishment on the host is that the apex of the plant becomes a fresher green, probably because of a more rapid expansion of the youngest leaves, which soon become conspicuously larger than their predecessors. After this, new leaves are formed at a greater rate, and usually the branches begin to grow. There is a great contrast between such plants and those with an apparently unsuitable host, which may remain almost static and are likely to die.

* *Euphrasias* often produce some flexuous capillary branches at the base; in all cases where branches have been measured these have been ignored.

In general, pot-grown *Euphrasias* which appear to be established on the host resemble well-developed wild *Euphrasias*; those that do not appear to be established, or are not provided with a host-plant, are inferior and resemble the starved-looking *Euphrasias* that can also be found in nature. The time from germination to establishment is usually 4 to 10 weeks, but may be as much as 17.

PROXIMITY TO HOST-PLANTS

In 1955, *E. nemorosa* (E507), from Cambridgeshire, was grown in pots at varying distances from the host-plant. A correlation appeared between the time required for apparent establishment on the host and the distance between host and parasite.

Euphrasias planted 2.5 cm from the host appeared to be established about a week earlier than those 4.5 cm from it, and about a fortnight earlier than those 6.5 cm distant. Another effect of distance was that, of the *Euphrasias* planted 6.5 cm from the host, a considerably lower percentage became established than was the case with those planted closer to the host.

LEGUMINOUS HOSTS

Comparisons of various host-species are given later, but the effect of some Leguminosae was distinctive and will now be described separately. The effect showed itself in the great vigour of the *Euphrasia* plants and in their dark green, often glossy, leaves. It was first seen in *Euphrasias* grown in their own turf in 1952. With *E. anglica* (E67 and E76), from Surrey, the legume concerned was *Medicago lupulina*, with *E. occidentalis* (E73), from S. Hampshire, it was *Trifolium repens*, and with *E. pseudokernerii* (E75), from Cambridgeshire, it was *Anthyllis vulneraria*. Each of these *Euphrasias* was also growing in other turves (either in the same pot or in separate ones) containing few or no Leguminosae, and here they were much less vigorous and were paler green. *M. lupulina*, with a slight admixture of *Anthyllis vulneraria*, had the same good effect on many plants of *E. nemorosa* (E74), growing in a turf collected near Cambridge.

Table 10, p. 17, shows that four Leguminosae were used as hosts more than once in pot culture, and that three of them usually gave medium or good growth. With these three the *Euphrasia* plants almost always had particularly dark green foliage.

In their luxuriant growth and dark green leaves, *Euphrasias* growing with suitable Leguminous species showed symptoms of a good supply of nitrogen, which they must have been getting either through their haustoria or through the soil after its release by the legumes. The former hypothesis seems more probable, in view of the differences existing between individual *Euphrasias* in separate turves in the same pot.

The legume which Table 10 shows was a poor host was *Trifolium dubium*. Its unsuitability was not caused by an absence of bacterial root-nodules, however, for these were seen to be present when the seedlings were planted out with the *Euphrasias*.

MUTUAL PARASITISM

Koch (1891) and Wettstein (1897) reported that *Euphrasia* plants can parasitize one another, and their work has been summarized in another paper (Yeo 1961), where their observations on haustorial connections between individual *Euphrasia* plants were confirmed. The cultural effect of this—the markedly superior development of a few plants in a pot containing many seedlings—has also been observed by the present writer. A further cultural effect, probably due to the same cause, is that occasionally some, but not all, of the *Euphrasias* in a pot provided with a host fail to show signs of establishment, or fail to grow much after establishment. For example, a plant of *E. anglica* (E180), from S. Somerset, and a plant of a form of *E. micrantha* (E231), from E. Donegal, each growing in a small pot with *Sagina apetala*, remained very small, while the other three *Euphrasias* in each pot grew quite vigorously. Further, a plant of *E. nemorosa* (E897), from W. Sussex, apparently established on 8 June 1961, had only 16 cm of stem and branches when pressed on 9 September, while by this date its nearest neighbour (growing about 3 cm away and established only a week earlier) had produced 290 cm.

TIME OF FLOWERING

The various species of *Euphrasia* are characterized by their time of flowering. Examples of late-flowering species are *E. pseudokernerii* and, in at least part of its range, *E. nemorosa*. These usually start flowering in late July or early August, at about the 10th to 16th node. Most species, on the other hand, begin to flower about mid-June at the sixth to tenth node; these are mountain meadow types (*E. brevipila* and *E. rostkoviana*) and pasture species (*E. confusa*, *E. anglica*, etc.). The high mountain species, *E. frigida*, *E. rivularis* and *E. cambrica*, usually begin flowering in June or July at the second to sixth node.

It will be seen from Fig. 1, however, that certain plants of *E. pseudokernerii* (E42) cultivated in 1952, some with no host and some with *Pelargonium* $\times$ *hortorum*, began flowering at the third to fifth node. The first flower buds were seen on 28 March, and the first flowers opened shortly before 21 April. The plants completed a very brief life cycle and died in a natural way and not from disease. This precocious flowering was evidently due to the very high temperatures prevailing in March in the greenhouse, which often exceeded 25° C. This suggests that temperature is one of the main factors controlling flowering in *Euphrasia*, and that given sufficiently high temperatures *E. pseudokernerii* can be made to flower at about as low a node as the high mountain species. On 21 March, these plants that flowered and died early had three or four leaves with visible teeth, whereas the plants numbered three and seven in Fig. 1, had only nought to two. It seems, therefore, that, being at a sufficiently early stage of development in March, these two plants were unable to respond to high temperatures by premature flowering and death. In fact, although one of them was without a host plant, both were ultimately able to develop more fully than those that appeared more vigorous in March.

Other plants of *E. pseudokernerii* (E42), grown as part of the same experiment but with *Plantago lanceolata* for host, flowered rather less precociously—early in May, at the fifth to seventh node—and they survived until July or August. Two plants of the same population of *E. pseudokernerii*, cultivated in 1952 in their own turf, flowered from the sixth to eighth node, then produced branches at higher nodes, and then flowered again. This was evidently the result of temperature fluctuations, and it shows that the conversion of a shoot from the vegetative to the flowering state is reversible.

Precocious flowering of very young plants after hot weather has occurred repeatedly in my greenhouse cultures. It is generally difficult to get naturally early-flowering forms to become established before coming into flower and, once flowering has begun to drain the reserves of tiny plants, there is little chance of subsequent establishment inducing vigorous growth. Thus in 1961 20 plants of a form of *E. brevipila* (E870), from Sweden, were grown with various host-plants. Sixteen *Euphrasias* had flower buds visible by mid-May. All but three of these produced one or two flowers and were then pressed, as they did not appear to be capable of producing any more; they were all about 1 cm tall. One of the three exceptions was a little larger and produced five flowers. The other two appeared to become established on the host, and were moderately vigorous.

Precocious flowering of *Euphrasia* sometimes takes place in nature, presumably as the result of an early hot spell. *E. pseudokernerii* and *E. nemorosa* were found flowering in Bedfordshire on 15 June 1952 and in Cambridgeshire on 12 June 1957, high temperatures having been recorded in Cambridge in mid-May 1952 and at the end of May in both 1952 and 1957. All these early-flowering *Euphrasias* appeared to be established on host-plants, and had begun flowering at the fifth to seventh node.

EFFECTS OF SOIL

No investigation was made of the influence of soil on growth, but the following observations suggest that small differences in soil constitution may be important for seedling *Euphrasias*.

Seedlings of *Euphrasia anglica* (E240) were collected in Leicestershire on 28 February 1953. They were intended to be a reserve for cultivation experiments but were not needed

for this purpose. Three or 4 days after collection, about 120 seedlings were removed from their turf and planted in two pots (numbered 1 and 2) in approximately equal numbers. On 22 May pot 1 had 42 seedlings and pot 2 had 39. In pot 1 the two smallest plants were pale green throughout, while the rest were medium green, but paler at the top; all the plants in pot 2, however, were distinctly chlorotic, the upper leaves being quite yellowish, and all the leaves appeared slightly fleshy. On 12 June, two plants in pot 1 had their first flowers open, three more were ready to bloom shortly, and others had flower buds. In pot 2 all the plants were chlorotic and no flower buds were visible.

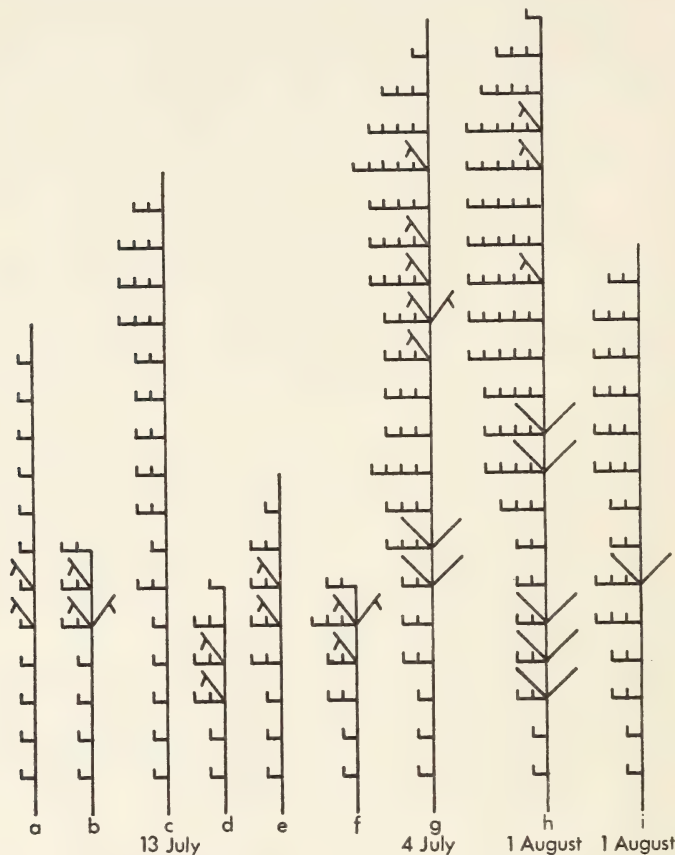


Fig. 1. Diagrams of *Euphrasia pseudokernerii* plants. (a)-(c) without a host; (d)-(g) with *Pelargonium × hortorum*; (h) with *Carex caryophyllaea*; (i) with *Bromus erectus*. Horizontal bars = nodes; cross-pieces on them show leaf-tooth number. Sloping bars = branches. Forks = flowers. Un-dated diagrams represent plants that had completed their development.

The poorer condition of the plants in pot 2, was probably due to differences of soil. The soil in pot 2 appeared lighter in colour and had less peat at the surface than that in pot 1; also, unlike the soil in pot 1, it had mosses and green algae developing on it by 22 May.

Euphrasia plants sometimes show chlorosis before establishment and, using John Innes compost, this is especially prevalent in *E. micrantha*, *E. anglica* and *E. rostkoviana*.

WATERING

During the spring and early summer, *Euphrasias* in pots in an unheated greenhouse are liable to die if there is a spell of cold, heavily overcast or damp weather. The entire plant wilts, and dies in a day or two; this can occur in unestablished or in vigorously growing

plants that have been established for a week or so. The best watering policy seems to be to keep the *Euphrasias* rather dry during April and the first part of May, as they endure this well, and then to water more freely to encourage growth. After watering, the plants and the soil surface should be encouraged to dry off quickly; and no water at all should be given in cold dull weather.

TABLE 2. Length measurements of *Euphrasia pseudokerneri* grown in 1952.

Pot No.	Host	Length in cm of stem plus branches of each plant
E42	1 None	5.0, 2.5, 1.5
	2 <i>Festuca ovina</i>	20, 16, 9, 6, 3, 0.5
	3 <i>Koeleria cristata</i>	1
	4 <i>Festuca ovina</i> and <i>Koeleria cristata</i> ..	46, 32, 11, 9, 5
	5 <i>Pelargonium</i> × <i>hortorum</i>	92, 2, 2, 1
	6 <i>Plantago lanceolata</i>	17, 13, 10, 4, 1
	7 <i>Prunella vulgaris</i>	1, 1, 1, 1, 1
	8 <i>Plantago lanceolata</i> and <i>Prunella vulgaris</i> ..	32, 28, 0.5
	9 <i>Thymus drucei</i>	0.5, 0.5, 0.5
	10 <i>Festuca ovina</i> and <i>Thymus drucei</i>	1
E70	1 Original turf	199, 60, 37, 25, 17, 7
	2 <i>Carex caryophyllea</i>	64
	3 <i>Bromus erectus</i>	18, 6
	4 <i>Sieglingia decumbens</i>	63, 30
	5 <i>Hieracium pilosella</i>	67

GROWTH OF *E. PSEUDOKERNERI*, *E. ANGLICA* AND *E. NEMOROSA* WITH VARIOUS HOST-PLANTS

The growth of *E. pseudokerneri* with various hosts was compared in 1952 by cultivation in pots. A group of pots 5½ in. in diameter was prepared in November 1951; the soil consisted of loam covered by a layer of sand. (It was hoped that it would be possible to trace haustorial connections easily in the sand layer, but there was little branching of roots in it as it turned out.) Seeds or plants of the host species were sown or planted in each pot, together with seed of the *Euphrasia* (E42), from S. Lincolnshire. Germination of the *Euphrasia* occurred in January, February and March. On 29 April 1952, seedlings of *E. pseudokerneri* (E70) were collected from the same locality and some of them were planted, at the same time as their host-plants, in pots 3½ in. in diameter. The rest of these seedlings were left in their turf, and this was also potted up; other species in the turf were *Carex caryophyllea*, *Thymus drucei* and three or four species of grass.

The development of the plants was regularly recorded, the dates of appearance of the leaves, branch initials and flower buds being noted, in addition to the leaf tooth number; notes were made later to show which branches developed and which flower buds opened. Some of these observations are reproduced in Fig. 1.

The E42 and E70 plants were eventually pressed and the total length of stem and branches measured (Table 2).

The plants were pressed on various dates but, with a few exceptions, all appeared to have completed or nearly completed their growth.

It is clear that some plants were good hosts; there is one inconsistent result in that the *Euphrasia* plant with *Festuca* and *Thymus* did not develop, although those in the two other pots containing *Festuca* developed quite well.

The dwarf plant with *Koeleria*, when dug up on 5 June, was found to have its roots surrounded by those of the grass, and a dwarf plant with *Thymus*, dug up dead on 10 May,

was found to have a few detached haustoria, suggesting that parasitic union had been effected but had not proved beneficial, presumably because the host failed to provide what the *Euphrasia* required. The occurrence of some feeble plants in pots with apparently good hosts has been discussed in general on p. 6. It is known, however, that in some of the E42 plants growth was prevented by precocious flowering.

TABLE 3. Number of *Euphrasia* plants of different degrees of vigour with various host species

<i>E. pseudokernerii</i> (E226), Surrey						
Host	Grade					
	1	2	3	4	5	6
	Poor		Moderate		Good	
<i>Anthyllis vulneraria</i>					1	4
<i>Medicago lupulina</i>				1	3	2
<i>Hieracium pilosella</i>			1	1	2	1
<i>Thymus drucei</i>	1	1		1	1	
<i>Dactylis glomerata</i>		1			1	
<i>Agrostis gigantea</i>		1	1	2		
<i>Festuca ovina</i>				1		
<i>Luzula campestris</i>				1		
<i>Achillea millefolium</i>				1		
<i>Sieglingia decumbens</i>		2	1	1		
<i>Carex flacca</i>	1		3			
<i>Brachypodium pinnatum</i>		3	1			
<i>Koeleria cristata</i>	1	2	1			
<i>Bromus erectus</i>		3				
<i>Plantago lanceolata</i>	1	1				
<i>Carex demissa</i>	1	1				
<i>Carex caryophyllea</i>	2	2				
<i>Carex pilulifera</i>	2					
<i>E. anglica</i> (E157), Surrey						
Host	Grade					
	1	2	3	4	5	6
	Poor		Moderate		Good	
<i>Luzula campestris</i>					1	
<i>Agrostis gigantea</i>				2	1	
<i>Anthyllis vulneraria</i>					1	
<i>Brachypodium pinnatum</i>				1		
<i>Medicago lupulina</i>			1			
<i>Carex caryophyllea</i>			3			
<i>Carex pilulifera</i>			1			
<i>Achillea millefolium</i>			1			
<i>Helianthemum chamaecistus</i>	1	2				
<i>Hieracium pilosella</i>		1				
<i>Bromus erectus</i>		1				
<i>Carex flacca</i>	2	1				
<i>Carex demissa</i>	2					
<i>Thymus drucei</i>	1					

The *Euphrasia* plants grown from seed took 72–95 days from germination to establishment. Those grown from wild-collected seedlings became established 40–60 days after potting-up with the host-plants.

In 1953, *E. pseudokerneri* (E226), this time collected in Surrey, was again grown with various hosts and compared with *E. anglica* (E157), also from Surrey. Four *Euphrasia* seedlings were planted in each pot, the pots being $3\frac{3}{4}$ –4 in. in diameter. For each species of *Euphrasia* there were two pots with each of 21 host species. There were two host-plants per pot, except in the case of *Achillea millefolium* where there was only one per pot. The hosts were of known origin and were in the form of young seedlings or portions of newly-divided plants. The pots were plunged in an ash-bed in a sheltered but sunny position at Leicester.

The *Euphrasias* and hosts were planted out from 28 to 31 March. By 20 April, many *Euphrasias* were dead and many damaged, apparently because of frost. Replacements were made, but not all the pots could be brought up to their full numbers.

Most of the *Euphrasias* were pressed on 20 September, but a few were pressed on 1 and 3 September. They were graded into six sizes; a 'type-plant' of *E. pseudokerneri* was chosen for each size, and the other plants of this species were then classified into the six grades by comparing them with the 'type-plants'. Silhouettes of two of the latter are shown in Fig. 2, p. 12. The plants of *E. anglica* were comparatively sparsely branched and these were graded according to their length of stem and branches, as indicated in Table 3, where the performance of both *Euphrasia* species is shown. The number of host species is less than 21 because, with some hosts, all the *Euphrasias* died. Owing to the small numbers of *Euphrasias* with each host species, it is inadvisable to conclude, from the results of this experiment, that any host is a poor one (though some are clearly good). Thus, the previous year *E. pseudokerneri* had grown well on *Plantago lanceolata* and on *Carex caryophyllea*, and on some occasions *E. anglica* has grown well on *Medicago lupulina*. It is shown in the experiment with *E. nemorosa* described next that some hosts, though they produce good growth in established plants, are also liable to give a high proportion of failures to become established. This factor could be responsible for the variations of behaviour with the hosts just mentioned. It cannot be claimed with confidence that *E. pseudokerneri* and *E. anglica* differ in their host reactions, but the table shows that, on the whole, *E. pseudokerneri* grew better with dicotyledonous plants than with monocotyledons, whereas this superiority of dicotyledons was not evident in the case of *E. anglica*.

In 1955, many plants of *E. nemorosa* (E507), from Cambridgeshire, were grown in $5\frac{1}{2}$ -in. diameter pots with four host species, and with no host (=NH). The four host species were:

Hieracium pilosella (=H),
Plantago lanceolata (=P),
Bromus erectus (=Bs),
Medicago lupulina (=M).

There were 1–6 *Euphrasias* per pot, and either one or three host-plants in the H, P, Bs and M pots. The *Euphrasias* and hosts were potted up as young seedlings. The *Euphrasias* were placed near the edges of the pots, and hosts were placed in the middle, except when only one *Euphrasia* and one host were present. During growth, the host-plants were cut back where they tended to shade *Euphrasias*.

The potting up was done on 8 and 9 April. Some replacements were already necessary on 10 April, and further deaths were observed throughout the period of cultivation. Observations were made on all plants about once a week from 8 May to 4 July. On 13 August a note was made of the survival or death of the plants, and the following day all were pressed.

The appearance of two of the *Euphrasias* can be seen in Fig. 3, p. 21. The overall mean weight of the plants with each host species is given in the fourth line of Table 4. H and P gave high mean weights, M a fairly high mean, and Bs a slightly smaller mean than



Fig. 2. Plants of *Euphrasia pseudokernerii*, $\times \frac{1}{2}$. Left, grown with *Hieracium pilosella* (size-grade 5). Right, grown with *Anthyllis vulneraria* (size grade 6).

TABLE 4. Mean weights (in g) of *Euphrasias* after pressing.
(The number of plants in each class is given in brackets.)

<i>Number of plants per pot</i>						
<i>Euphrasias</i>	<i>Hosts</i>	<i>H</i>	<i>P</i>	<i>Bs</i>	<i>M</i>	<i>NH</i>
1 or 2	1	·33 (8)	·48 (4)	·07 (3)	·23 (4)	·15 (12)
3 or 4	1 or 3	·41 (10)	·49 (8)	·08 (4)	·28 (14)	·14 (10)
5 or 6	1 or 3	·32 (5)	·17 (5)	·13 (6)	·25 (11)	·08 (6)
1 to 6	1 or 3	·36 (23)	·39 (17)	·10 (13)	·26 (29)	·13 (28)

TABLE 5. Variation of *Euphrasia* according to host species

	<i>H</i>	<i>P</i>	<i>Bs</i>	<i>M</i>	<i>NH</i>
Percentage established	73%	64%	64%	76%	—
Average wt. of plants (g)	·36	·39	·10	·26	·13
Standard deviation	·374	·363	·115	·151	·068
Wt. of largest individual (g)	1·6	1·3	·3	·7	·3
Mortality, 8 May–4 July	20%	16%	41%	3%	16%
Mortality, 8 May–13 August	23%	40%	55%	12%	16%

NH. The result with no host has been discussed on pp. 5 and 6. Many of the *Euphrasias* with *Bromus erectus* appeared to become established in the period 8 May to 21 June. Presumably they received little benefit from this host, and suffered competition from it.

Establishments occurred mainly during the first 4 weeks of the 8-week observation period. It was found that there was little variation in the time of establishment on the different hosts, but the total percentage of *Euphrasia* plants that became established varied according to host (Table 5).

Table 5 also shows that the mortality of the *Euphrasias* was low with the hosts *M* and *H*, and high with *P* and *Bs*; *M* and *H* also showed better establishment. This bears out an impression obtained during my work on *Euphrasia* that plants which are not established on the host are more liable to die than those which are. The very low mortality with no host (none between 4 July and 13 August) supports the theory that, if *Euphrasias* are in the same pot as a fully autotrophic plant from which they receive no benefits by parasitism, they will be at a severe disadvantage compared with *Euphrasias* in a pot by themselves.

For experimental work it is desirable to have a high percentage of plants becoming established, a high average weight, little variation in weight, and low mortality. *Euphrasias* with *Bs* and *NH* show little variation in weight, but both are unsatisfactory in their low average weight, as is *Bs* in its high mortality. *P* has the highest average weight, but its establishment percentage is relatively low and its mortality high. *H* and *M* present the best combinations of characters. Since plants weighing 0.2 g and upwards are quite well developed, *M*'s lower average weight than *H*'s is not a serious disadvantage, and it is more than counterbalanced by a smaller variation in weight and by lower mortality. The experiment, therefore, shows that *M* is the most useful host plant of those tested.

FURTHER HOST COMPARISONS INVOLVING *MEDICAGO LUPULINA*

I have generally used *Medicago lupulina* as the host on which to raise my *Euphrasias*. However, this has been less successful with species from the West, the North and the mountain areas of Britain than with the south-eastern species. In the case of *E. scottica* this could have been due to its being an inhabitant of wet places, and one year some plants of a sample of *E. scottica* (E782), from W. Ross, were grown in a pot embedded in wet peat, but this special treatment produced little or no improvement in their growth compared with the rest of the sample.

In 1960, when several northern and western species became available, samples were grown in a particularly cool and shady situation with *M. lupulina*, but again with poor results. At the same time some of these species, together with the southern *E. anglica* and the widespread *E. confusa*, were grown with various hosts in an unshaded greenhouse. For these, *Poa pratensis* and (as in the shady position) *M. lupulina* were very poor hosts, but quite good results were obtained with *Sagina procumbens* for *E. anglica* (E849), *E. brevipila* (E806), *E. confusa* (E803, E834), from Yorkshire, and *E. rostkoviana* (E855), while *Trifolium occidentale* D. E. Coombe gave good results with *E. brevipila* (E860) and *E. rostkoviana* (E857), both from Kirkcudbrightshire. In addition, some samples were planted with *M. lupulina* in the greenhouse, and gave slightly worse results than in the shade; these were *E. borealis* var. *zetlandica* Pugsl. (E851), *E. curta* (E853) and *E. rotundifolia* (E845).

These results suggested that temperature and humidity were not the main causes of difficulty in growing these plants, and that unsuitability of host-plant was probably the main cause.

Plants grown in 1961, largely from the same samples as were used in 1960, gave the results shown in Tables 6 and 7; these show, in most cases, a marked superiority of *Sagina*, *Trifolium*, or a mixture of the two, over *Medicago*. Two stocks of *M. lupulina* are referred to in Table 6, the new one being superior to the old for *E. confusa* $\times$ *E. occidentalis* and for *E. nemorosa*. The old stock of this host had been maintained and reproduced annually from seed since 1952, and the new one was obtained in 1961 by collecting seedlings from the herbaceous bed for Leguminosae in the University Botanic Garden, Cambridge. The new

TABLE 6. Total length (in cm) of stem and branches of *Euphrasia* grown with various host-plants, 1961. (No. before colon = no. of surviving *Euphrasias*; no. after colon = mean length; no. in brackets = length of largest plant. Every pot contained ten *Euphrasias* and four host-plants.)

	<i>E. brevipila</i> E806 E870		<i>E. confusa</i> × <i>occidentalis</i> E900	<i>E. anglica</i> E849	<i>E. nemorosa</i> E897	<i>E. micrantha</i> E891
<i>Vice-county</i>	65	(Sweden)	99	6	13	1
<i>Medicago lupulina</i> (old stock) 3 pots	3:8·7 (12)	5:1·6 (4)	5:6 (8)	4:13·3 (21)	4:49·3 (79)	2:10·5 (12)
<i>M. lupulina</i> (new stock) 3 pots	2:14 (15)	5:1·6 (4)	5:29 (75)	2:14 (16)	4:92·8 (138)	4:7·3 (22)
<i>Sagina procumbens</i> 3 pots	4:53·3 (85)	5:4·8 (14)	3:54·3 (88)	3:24·7 (43)	5:120 (249)	0:—
<i>Trifolium occidentale</i> 3 pots	4:19·8 (34)	5:2·8 (10)	5:13·4 (32)	5:27·3 (41)	5:52·8 (134)	3:36·3 (74)

stock was more vigorous, had larger leaflets and was less affected by heavy attacks of red spider mite.

It can be seen from Table 6 that *E. micrantha* failed to survive with *Sagina* as host, but in 1961 E837 grew very well on *Sagina procumbens* seedlings which germinated in its original seed pot. *E. micrantha* is particularly liable to show signs of ill-health before establishment, and this no doubt contributed to the poor results shown in these tables.

It thus seems to be the case that there are many species of *Euphrasia* (particularly the northern ones) for which *M. lupulina* is not a favourable host-plant. For some *Euphrasia* species, however, even if *Medicago* is usually unsuitable, there are certain populations which will grow well on it. For example, quite good plants of *E. brevipila* and *E. rostkoviana* have sometimes been grown on *Medicago*, and very vigorous plants of *E. brevipila* from Poland have also been grown on it.

TABLE 7. Total length (in cm) of stem and branches of *Euphrasias*.
(Explanation as for Table 6.)

	<i>E. borealis</i> var. <i>zetlandica</i> E851	<i>E.</i> <i>rotundifolia</i> E845	<i>E.</i> <i>scottica</i> E864	<i>E.</i> <i>curta</i> E853	<i>E.</i> <i>rostkoviana</i> E855
<i>Vice-county</i>	112	108	73	73	73
1960 Shady frame with <i>Medicago</i> <i>lupulina</i>	0:—	3:1.7 (2)	0:—	5:6 (10)	4:7.3 (8)
1961 Greenhouse with <i>Sagina pro-</i> <i>cumbens</i> mixed with <i>Trifolium occidentale</i>	7:7.6 (24)	3:5 (8)	2:31 (38)	6:14 (20)	1:90 (90)

CULTIVATION OF THREE *EUPHRASIA* SPECIES WITH FOUR HOST SPECIES

In this experiment *Euphrasia borealis* (E329), from NW Yorkshire, was grown indoors and outdoors, and *E. nemorosa* (E417), from Staffordshire, and *E. occidentalis* (E351), from W. Cornwall, were grown indoors only.

Medicago lupulina (=M), *Plantago lanceolata* (=P) and *Trifolium dubium* (=T) were used as host-plants for the *Euphrasias* indoors. Each *Euphrasia* species and each host species was represented by one pan, and each pan contained four seedlings of the host-plant near the centre, and eight seedlings of *Euphrasia* towards the edge; in addition, there was a second pan of *E. occidentalis* with *Medicago*, provided with six host seedlings. A total of six *Euphrasias* died and were replaced in the first 3 weeks.

E. borealis was grown outdoors with the same three hosts and with *Briza media* (=Ba), by the method described on p. 4. Each pot was planted with one *Euphrasia* and one host seedling on 11 May 1954. Replacements of dead *Euphrasias* were made from time to time until 30 May. On 2 June the pots were embedded in the soil of the experimental ground; there was a row of ten pots with each host, and the rows were placed 2 ft apart. On 11 July observations were made on the state of the plants outdoors, and on 3 September, all but four very small ones were pressed.

Stem and branch lengths of the indoor and outdoor *Euphrasias*, after pressing, are given in Table 8, which shows the average size of the plants and, for the indoor cultures, the aggregate growth in each pot. (*E. borealis* and *E. occidentalis* are naturally more sparingly branched than *E. nemorosa*.) The growing period of *E. borealis* indoors with M was 21 days shorter than with P, but five or six of the eight plants with M had more or less finished growing when the plants were pressed on 23 July. *E. occidentalis* grew very much better with M in pot 2 than in pot 1. Pot 2, however, had been set up much earlier, and the *Euphrasias* had become established on the host 8 weeks earlier than those in pot 1. The death of all the indoor plants of *E. borealis* with T is probably accounted for by the unsatisfactoriness of this host.

TABLE 8. Total length (in cm) of stem and branches of *Euphrasias*.
(No. before colon = no. of surviving *Euphrasias*; no. after colon = mean length.)

	Ba	M	P	T	Total length for each pot		
					M	P	T
<i>occidentalis</i> (pot 1)	—	7:11	4:7.5	2:3.5	74	30	7
<i>occidentalis</i> (pot 2)	—	5:28	—	—	140	—	—
<i>nemorosa</i>	—	7:65	5:178*	7:12	453	890	84
<i>borealis</i> (indoors)	—	8:15	5:28	0:—	119	139	—
<i>borealis</i> (outdoors)	0:—	4:10	5:42	3:2	—	—	—

* Length estimated from the measurements of selected branches.

This indoor cultivation can be summed up by saying that M and P were good hosts for *E. nemorosa* and *E. borealis*, M was fairly good for *E. occidentalis*, and T was very poor for all the *Euphrasias*. It will be noted that more *Euphrasias* of all species survived with M than with P. The difference between M and P in the results for vigour and survival of *E. nemorosa* is thus the same as that obtained with a different population of *E. nemorosa* in 1955.

Though P was a better host for *E. borealis* outdoors than in, M showed the reverse behaviour. Possibly, in open soil, the roots of M branch at too deep a level to benefit the *Euphrasias*. Four out of five outdoor plants of *E. borealis* with P were very vigorous with large

or very large leaves. A sixth plant was also vigorous, but, owing to some accident, only a fragment of it was alive at the time of pressing, so that it could not be measured.

The observations that were made on 11 July on the plants of *E. borealis* in this trial are given in Table 9; here, as in Table 8, *P* appears as the best host for *E. borealis* outdoors, *M* is again second best, and *T* and *Ba* are both very poor.

TABLE 9. Observations on *E. borealis* outdoors, 11 July, 1954.

	Host			
	<i>Trifolium dubium</i>	<i>Plantago lanceolata</i>	<i>Briza media</i>	<i>Medicago lupulina</i>
Number alive	8	10	5	9
Number apparently host-established	0	8 or 9	0	3 possibly
Number flowering	3	8	3	5

GARDEN CULTIVATION

In 1953, at Leicester, a considerable number of plants of *E. nemorosa* and *E. stricta* was grown with *Plantago lanceolata* raised from seed (Yeo 1962). The bituminized paper pots (see p. 4) were plunged in the experimental plot on 31 March to 2 April. Between 22 and 26 April many dead plantains and Euphrasias were replaced. For this purpose the pots were lifted out of the ground. Of the 448 plants present after replacements had been made, 337 were alive on 19 July. Pronounced signs of establishment on the host in a few plants, and slight symptoms in many others, were seen on 12 May, 7 to 8 weeks after potting up. By 19 July only two plants out of 337 were not established. Nearly all the plants that were healthy became extraordinarily large-leaved and vigorous. Generally they were much more luxuriant than the most vigorous plants to be found in nature. Most of them were similar in size to a plant of *E. nemorosa* grown in the same way in 1956 which weighed 21 g after drying, and their upper cauline leaves were commonly 16–19 mm long and 16–18 mm wide. They may be contrasted with another plant of *E. nemorosa*, grown in a greenhouse, which was about as large as the normal maximum for wild plants of this species of *Euphrasia*, and which weighed only 1.6 g (with a stem-plus-branch length of 214 cm).

The host-plants were also very vigorous and were several times cut back severely to stop them from covering the Euphrasias and to check their growth somewhat. The last time the severe cutting-back was done, some Euphrasias were getting bushy, and the plantains overshadowed by them did not recover their vigour. Subsequently, these Euphrasias appeared to suffer somewhat. It appears that, when the plantain is liable to be overshadowed, some of its leaves that project out beyond the shadow of the *Euphrasia* should be left untrimmed.

Many of the Euphrasias that died did so in July, after establishment on the host and after a period of wilting. It was thought that the wilting was caused by the fraying of the base of the stem, which resulted from the twisting of the stem as the head of the plant blew about in the wind. The movement of the plants in the wind doubtless brought on the wilting symptoms, but the stems may previously have been weakened by attacks of damping-off fungus at the seedling stage, as weaknesses at the bases of the stems were found in *E. nemorosa* cultivated in the greenhouse in 1955. The weak zone in these plants was discoloured and thinner than normal, and it sometimes broke when a plant was pulled up for pressing. In the absence of wind, the weakness had no effect on the vigour of the plants, some of the largest having the weakest stems. Damping-off had been particularly troublesome among the young seedlings of this population.

TABLE 10. Host-plants and *Euphrasia* species grown with them.
(Country of origin of *Euphrasia* indicated if not Great Britain or Ireland.)

	No. of samples in which the indicated degree of vigour was attained		
	Poor	Medium	Good
Clay-pot cultivation			
<i>Ranunculus repens</i>			
<i>E. anglica</i>		1	
<i>Coronopus squamatus</i>			
<i>E. stricta</i> Lehm... .. .		1 (Channel Is.)	
<i>E. brevipila</i>			1 (Poland)
<i>Helianthemum chamaecistus</i>			
<i>E. anglica</i>	1		
<i>Sagina apetala</i>			
<i>E. nemorosa</i>		1	
<i>E. confusa</i>		1	
<i>E. rostkoviana</i>		1	
<i>E. anglica</i>		1	
<i>Sagina procumbens</i>			
<i>E. micrantha</i>		1	1
<i>E. occidentalis</i>			1
<i>E. nemorosa</i>			1
<i>E. stricta</i> Lehm... .. .		1 (Channel Is.)	
<i>E. confusa</i>	1	1	2
<i>E. brevipila</i>		1 (Sweden)	1
<i>E. rostkoviana</i>			1
<i>E. anglica</i>			1
<i>Pelargonium</i> × <i>hortorum</i> Bailey			
<i>E. pseudokerneri</i>			1
<i>Medicago lupulina</i>			
<i>E. micrantha</i>		1	3 (1 North America)
<i>E. scottica</i>		1	
<i>E. scottica</i> × <i>E. confusa</i>	1	1	
<i>E. curta</i> var. <i>rupestris</i> Pugsl.		1	
<i>E. occidentalis</i>	1	2	15 (2 France)
<i>E. nemorosa</i>		6 (1 France)	12 (1 France)
<i>E. stricta</i> Lehm... .. .	1 (Germany)	1 (Poland)	5 (2 France, 2 Germany, 1 Channel Is.)
<i>E. pseudokerneri</i>			6
<i>E. confusa</i>	3	2	6
<i>E. borealis</i>		1	
<i>E. brevipila</i>	6 (2 Sweden)	6 (1 Poland)	4 (1 Sweden)
<i>E. rostkoviana</i>	1	2 (1 Italy)	2 (1 Poland)
<i>E. montana</i>	1		
<i>E. hirtella</i>		1 (France)	

TABLE 10—cont.

	No. of samples in which the indicated degree of vigour was attained		
	Poor	Medium	Good
Clay-pot cultivation			
<i>Medicago lupulina</i> —cont.			
<i>E. anglica</i>	1	6	5
<i>E. anglica</i> × <i>E. nemorosa</i>			1
<i>E. vigursii</i>		1	
<i>E. salisburgensis</i>		1	1
		(France)	(Austria)
<i>E. salisburgensis</i> var. <i>hibernica</i> Pugsl.			1
<i>Trifolium repens</i>		1	
<i>E. stricta</i> Lehm.		(Poland)	
<i>Trifolium occidentale</i> Coombe			
<i>E. micrantha</i>			1
<i>E. nemorosa</i>		1	
<i>E. confusa</i>			1
<i>E. borealis</i>		1	
<i>E. brevipila</i>		1	1
		(Sweden)	
<i>E. rostkoviana</i>			1
<i>E. anglica</i>			1
<i>Trifolium dubium</i>			
<i>E. occidentale</i>	1		
<i>E. nemorosa</i>	1		
<i>E. borealis</i>	1		
<i>Anthyllis vulneraria</i>			
<i>E. foulaensis</i>			1
<i>E. curta</i> var. <i>rupestris</i> Pugsl.		1	
<i>E. occidentale</i>		1	
<i>E. pseudokernerii</i>			1
<i>E. anglica</i>			1
<i>E. confusa</i>			1
<i>Epilobium parviflorum</i>			
<i>E. rostkoviana</i>		1	
<i>Calluna vulgaris</i>			
<i>E. micrantha</i>	1	1	
<i>Calluna vulgaris</i> and <i>Erica cinerea</i> mixed ..			
<i>E. micrantha</i>			1
<i>Thymus drucei</i>			
<i>E. occidentale</i>		1	
<i>E. pseudokernerii</i>	1		1
<i>E. anglica</i>	1		
<i>E. salisburgensis</i>			1
			(Austria)
<i>Prunella vulgaris</i>			
<i>E. pseudokernerii</i>	1		
<i>Plantago lanceolata</i>			
<i>E. occidentale</i>	1	1	1
<i>E. nemorosa</i>			2
<i>E. pseudokernerii</i>	1		1
<i>E. borealis</i>			1
<i>E. anglica</i>	1		
<i>Plantago coronopus</i>			
<i>E. occidentale</i>	1		

TABLE 10—cont.

Clay-pot cultivation	No. of samples in which the indicated degree of vigour was attained		
	Poor	Medium	Good
<i>Achillea millefolium</i>			
<i>E. pseudokerneri</i>		2	
<i>E. anglica</i>		1	
<i>Leontodon autumnalis</i>			
<i>E. foulaensis</i>	1		
<i>E. occidentalis</i>	2		
<i>E. anglica</i>	8		
<i>E. vigursii</i>	1		
<i>Hieracium pilosella</i>			
<i>E. nemorosa</i>			1
<i>E. pseudokerneri</i>			2
<i>Luzula campestris</i>			
<i>E. micrantha</i>	1		
<i>E. occidentalis</i>	1		
<i>E. pseudokerneri</i>		1	
<i>E. rostkoviana</i>	2	2	1
<i>E. anglica</i>			1
<i>E. rivularis</i>		1	
<i>Carex demissa</i>			
<i>E. pseudokerneri</i>	1		
<i>E. anglica</i>	1		
<i>Carex flacca</i>			
<i>E. pseudokerneri</i>		1	
<i>E. anglica</i>	1		
<i>Carex pilulifera</i>			
<i>E. micrantha</i>	1		
<i>Carex caryophyllea</i>			
<i>E. pseudokerneri</i>			1
<i>E. confusa</i>	6	1	
<i>E. anglica</i>		1	
<i>Sieglingia decumbens</i>			
<i>E. occidentalis</i>		1	
<i>E. nemorosa</i>		1	
<i>E. pseudokerneri</i>		1	1
<i>Festuca ovina</i>			
<i>E. pseudokerneri</i>		1	1
<i>Poa pratensis</i>			
<i>E. confusa</i>	2		
<i>E. rostkoviana</i>	1		
<i>Poa trivialis</i>			
<i>E. micrantha</i>		1	
<i>E. pseudokerneri</i>		1	
<i>Dactylis glomerata</i>			
<i>E. pseudokerneri</i>			1
<i>Bromus erectus</i>			
<i>E. occidentalis</i>		1	
<i>E. nemorosa</i>		1	
<i>E. pseudokerneri</i>	1	1	
<i>E. anglica</i>		1	
<i>Brachypodium pinnatum</i>			
<i>E. pseudokerneri</i>		1	
<i>E. anglica</i>		1	

TABLE 10—cont.

	No. of samples in which the indicated degree of vigour was attained		
	Poor	Medium	Good
Clay-pot cultivation			
<i>Koeleria cristata</i>			
<i>E. micrantha</i>	2		
<i>E. confusa</i> × <i>E. micrantha</i>	4		
<i>E. curta</i> var. <i>rupestris</i> Pugsf. ..	1		
<i>E. nemorosa</i>	2		
<i>E. pseudokerneri</i>	1	1	
<i>E. confusa</i>	1		
<i>Agrostis tenuis</i>			
<i>E. occidentalis</i>		1	
<i>E. nemorosa</i>		1	
<i>Agrostis gigantea</i>			
<i>E. pseudokerneri</i>		1	
<i>E. anglica</i>			1
Cultivation in open ground			
	Poor	Good	Very Good
<i>Medicago lupulina</i>			
<i>E. borealis</i>	1		
<i>Trifolium dubium</i>			
<i>E. borealis</i>	1		
<i>Plantago lanceolata</i>			
<i>E. occidentalis</i>		1 (France)	
<i>E. nemorosa</i>			9
<i>E. pseudokerneri</i>		1	
<i>E. confusa</i>			2
<i>E. stricta</i> Lehm.			1
<i>E. borealis</i>		1	
<i>Luzula campestris</i>			
<i>E. anglica</i>			2
<i>Briza media</i>			
<i>E. borealis</i>	1		
<i>Koeleria cristata</i>			
<i>E. micrantha</i> form	1		
<i>E. vigursii</i>		1	

Other Euphrasias were also tried with other hosts in 1953. Two Euphrasias were planted in each bituminized pot, and the hosts were pieces of divided plants with some roots present; one piece per pot was used.

The most successful populations were two of *E. anglica* (E168 and E219), from Leicestershire, each represented by ten pots with *Luzula campestris*. On 31 May (about 8 to 9 weeks after potting up) many of these Euphrasias showed signs of establishment on the host, and on 21 June nearly all were established. The plants grew vigorously, having fairly large leaves and numerous branches. They did not attain anything like the size of the largest plants of *E. nemorosa* grown outdoors with *Plantago lanceolata*, however, probably because of their lower node of flowering.

On *Koeleria cristata*, a form of *E. micrantha* (E231), from E. Donegal, made little progress. On 26 June, two plants out of 16 showed signs of being established on the host,

though five others (apparently not established) were flowering. On 31 August, three out of the 12 survivors may have been established, but none was vigorous. In *E. vigursii* (E197), from S. Devon, the first signs of establishment on the same host were seen (in one plant) on 18 May, but it was not until 30 July that nearly all were established. They were, therefore, about 5 weeks behind *E. anglica* in becoming established. They eventually became about as vigorous as the plants of their parent wild population, and they varied quite considerably in vigour.

The same method of cultivation was used at Cambridge in 1954. In one experiment, populations of *E. nemorosa* and *E. confusa* were grown; mortality was very heavy, but the survivors grew very vigorously on *Plantago lanceolata* grown from seed.

In 1956, the method was again used to see whether better survival could be obtained at Cambridge. *E. nemorosa* (E608), from Cambridgeshire, was grown in four rows of ten pots each. The 40 pots were each planted with one *Euphrasia* and one *Plantago lanceolata* seedling on 4 April. The rows of pots were then planted in the garden, each on a different date. However, the mortality of the *Euphrasia*s awaiting planting in the garden was nearly as severe as that of those already planted out, so that late planting-out gave little advantage. In fact, there were again very few survivors, but most of them grew extremely vigorously.

LIST OF HOST-PLANTS

The host-plants employed in all my experiments are listed in Table 10, together with a rough indication of how well various *Euphrasia* samples grew on them. This indication is based on the most vigorous *Euphrasia* plant raised in each case.



Fig. 3. Plants of *Euphrasia nemorosa* after pressing on 14 August 1955, $\times \frac{1}{2}$. Left, one of two plants grown in a pot with no host; weight 0.2 g. Right, one of three plants grown in a pot with one plant of *Medicago lupulina*; weight 0.7 g.

Particularly poor hosts seem to be *Leontodon autumnalis* and *Koeleria cristata*; Gramineae in general seem to be mediocre hosts, while some of the best hosts are to be found among the Leguminosae. Indications that *Medicago lupulina* may be a better host for some species of *Euphrasia* than for others have already been mentioned; *Luzula campestris* may be a similar case, for it appears to be better on the whole for the species of the diploid Series Hirtellae (*E. anglica*, *E. rostkoviana* and *E. rivularis*) than for the tetraploid species of two other Series.

TABLE 11. Growth of *Euphrasias* without host-plants.

Species	Date when pressed	Pot diam.	No. of <i>Euphrasias</i>	Height in mm	No. not flowering	No. fruiting
		inches				
<i>micrantha</i> , E185A, S. Somerset ..	2/9/53	5½	fairly numerous	20-40	few	rather few
<i>occidentalis</i> , E192, E. Cornwall ..	2/9/53	5½	fairly numerous	6-15	few	many
2 pots	2/9/53	5½	very numerous	2-15	many	many
<i>occidentalis</i> , E351, W. Cornwall	9/7/54	3	5	45-80	0	5
2 pots	9/7/54	3	18	15-55	4	10
<i>nemorosa</i> , E196, S. Devon	2/9/53	5½	extremely numerous	10-50	many	moderate no.
<i>nemorosa</i> , E421, Surrey	9/7/54	3	4	10-40	3	0
2 pots	9/7/54	3	9	8-20	5	3
<i>nemorosa</i> , E417, Staffordshire ..	27/8/54	3	15	17-35	11	0
<i>confusa</i> , E172, S. Somerset	2/9/53	5½	fairly numerous	7-35	few	moderate no.
<i>confusa</i> , E208, Derbyshire	2/9/53	5½	numerous	6-36	few	many
<i>brevipila</i> , E325, W. Sutherland ..	9/7/54	3	6	7-30	1	5
<i>brevipila</i> var. <i>reayensis</i> Pugsl., E308, W. Sutherland	24/7/54	3	6	37-70	1	1
<i>rostkoviana</i> , E239, S. Kerry	26/8/53	5½	15	12-65	2	13
<i>anglica</i> , E180, S. Somerset	2/9/53	5½	fairly numerous	10-40	several	many

BEHAVIOUR OF EUPHRASIA WHEN GROWN WITHOUT A HOST

A silhouette of a *Euphrasia* plant fruiting in the absence of a host-plant can be seen in Fig. 3. Table 11 shows how the surplus seedlings of *Euphrasia* grew in their seed-pots without hosts in 1953 and 1954. The seedlings were too crowded to be fairly compared with plants grown in the presence of a host. However, the table shows that fruiting took place in nearly all samples. The capsules contained perfectly normal-looking seeds. The conditions of growth of three samples, E351 (*E. occidentalis*), E417 and E421 (both *E. nemorosa*), were closely similar, but the first grew much better than the other two, being evidently less affected by the lack of a host. *E. nemorosa* and *E. confusa* were the only species which produced branches and these are normally the most branched species.

DISCUSSION

Euphrasias in cultivation are decidedly more subject to disease than autotrophic plants from similar habitats. This applies both before and after establishment, but it varies greatly from one population to another and also from species to species. Careful treatment can minimize losses to some extent and, though some losses must be expected, there is no serious obstacle to the cultivation of the majority of *Euphrasia* species for experimental purposes, even when this requires the pricking-out of young seedlings.

A wide range of possible host species for *Euphrasia* in cultivation was reported by Heinricher and this has been amply confirmed by my cultures. This lack of host-specificity has also been demonstrated in the field by Wettstein (1897) and Crosby-Browne (1950). These facts make it appear unlikely that the existence of numerous critical species in *Euphrasia* is related to host-specificity. It may be noted that *Euphrasia micrantha* can grow on a number of hosts and not only on *Calluna vulgaris* and *Erica cinerea*, though it is rarely found in nature except in close proximity to one or both of these species.

Certain species appear to be unsuitable as hosts for all species of *Euphrasia* tried, while others vary in suitability according to the species of *Euphrasia*.

There are a number of possible factors involved in the unsuitability of host-plants, though it has not been possible to investigate these in most of the cultures described.

Euphrasias may be prevented from parasitizing plants growing with them by the inability of the haustoria to penetrate their roots, owing to their physical structure or to physiological obstacles. There might also be physiological obstacles to the formation of the haustoria themselves, or to the absorption of nutriment once the haustoria had penetrated. These obstacles to absorption could be complete or only partial. Extraction of nourishment must also be affected by the quantities of food materials available in the host. Most of these factors could be influenced by the age, stage of growth and vigour of the potential host. If penetrability of roots varies inversely with their age, some parts of the root system of an individual plant will be more impervious than others; one can imagine the susceptible zone of a root system growing rapidly away from a *Euphrasia* plant, so that the parasitic attack becomes increasingly unsuccessful. On the other hand, a host-plant which continually produces new roots from the crown will continue to be susceptible to attack by a *Euphrasia* growing near it.

The possibility also exists of intraspecific variation in susceptibility on the part of hosts and in parasitic capacity on the part of the Euphrasias; such variation might affect whole populations or only individuals.

There seems to be little connection between the suitability of a host and its systematic position. It would seem that the good growth of *Euphrasia* on most Leguminosae is connected with the nitrogen-fixing activities of the root-nodules of these plants, notwithstanding the clearly established unsuitability of nodulated *Trifolium dubium*.

Euphrasias grown in cultivation normally retain their important taxonomic characters, and it is therefore clear that modifications caused by hosts are not the cause of the systematic complexity of the group. In fact, the hosts appear to cause only variation in vigour. Late establishment may have a marked effect on the habit of a *Euphrasia*, but this can occur with any host on which establishment is possible.

The marked effect of a soil difference on the growth of *Euphrasia* without a host probably explains the generally greater success (compared with that of earlier workers) that I have had in growing *Euphrasia* in this way. It may also explain some of the variation in the results of Heinricher and Wettstein which led to a public dispute between them (Heinricher 1898c, Wettstein 1898).

The parasitism of *Euphrasia* may contribute to its marked gregariousness in nature. One sometimes finds dense isolated colonies, apparently consisting of hundreds of plants packed into a few square feet, with very few outliers. Weight of numbers may help them to compete with other vegetation, and where the density falls below a critical value the Euphrasias may, under some conditions, be entirely eliminated. The decline of an artificial colony in my garden following a disturbance which buried deeply many of the seeds, suggested that seedling density was important; this may act through autoparasitism allowing a sufficient number of seedlings to survive a difficult period early in their lives in a sufficiently vigorous condition.

ACKNOWLEDGMENTS

The work described in this paper was commenced under a research scholarship of the University of Leicester and with the help of Professor T. G. Tutin. Professor Tutin,

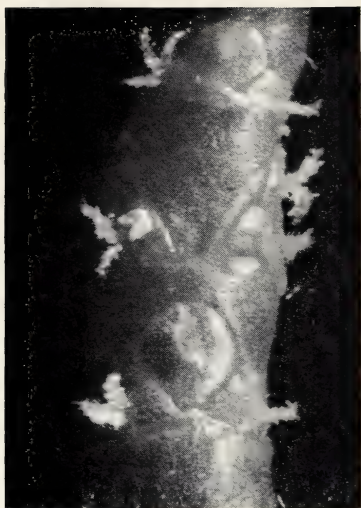
Mr. E. K. Horwood and numerous other persons and institutions have kindly supplied seed and information on localities from which I was able to collect *Euphrasia* seed.

Postscript.—In 1963 a plant of *Stellaria media* coming up in a pot of *E. nemorosa* seedlings led to very quick establishment and remarkably vigorous growth. This host, and other quick-growing weeds (see p. 3), may be useful in the cultivation of the more precocious-ly flowering Euphrasias. As, however, the host in this instance quickly declined in vigour, they should perhaps be combined with other, slower-growing species.

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PLATE 1



(a)



(b)



(c)



(d)

Inflorescences of annual tetraploid *Salicornia* spp., $\times 7$ approx. (a) Variation in stigma morphology. (b) In the two lower lateral florets the stigmas are protruding before the anthers; in the central florets immediately above, the anthers are dehiscing in contact with their stigmas. (c) Simultaneous development of anthers and stigmas in the lower central floret and in the dissected floret. (d) A further inflorescence showing simultaneous development of anthers and stigmas.

NOTES ON THE STIGMA MORPHOLOGY AND FLOWERING BEHAVIOUR IN BRITISH SALICORNIAE

By I. K. FERGUSON
Trinity College, Dublin

ABSTRACT

Moss transferred *S. perennis* Mill. to the genus *Arthrocnemum*. This paper sets out to show that two of the characters, the shape of the stigma and the sequence of maturation of the reproductive organs, that Moss used to separate the genera *Salicornia* and *Arthrocnemum* are very variable in plants from the British Isles. If this is accepted it would seem that the criteria for the definition of the genus *Arthrocnemum* will need reconsideration once more.

INTRODUCTION

In a posthumously published paper primarily concerned with South African Chenopodiaceae Moss (1948) transferred *S. perennis* Mill. to the genus *Arthrocnemum*, and I understand that the combination *A. perenne* is being taken up in *Flora Europaea*. This paper draws attention once more to the confused and unsatisfactory position with regard to the delimitation of these two genera.

Arthrocnemum was first proposed by Moquin (1840), who included *S. perennis* Mill. in his original delimitation of the genus. Moquin uses the absence of albumen in the seed and of wings on the perianth, together with the mode of insertion of the florets, as characters to separate the genus from *Salicornia*. It seems doubtful however, whether these characters possess the validity which he attributed to them as they have been adopted by few subsequent botanists. The absence of albumen in the seeds does not seem to be constant throughout the traditional limits of the genus (Moss 1954). De Fraine in an extensive investigation of the anatomy of the genus *Salicornia* makes no reference to any difference in the insertion of the florets between *S. perennis* Mill. and the annual species in the British Isles. In my own observations I have found that small differences do exist between *S. perennis* Mill. and the annual species of *Salicornia* in the British Isles in the shape of the florets and in the degree to which the central floret separates the laterals and also in the arrangement of the wings of the perianth. However, the former characters are very variable among the annual Salicorniae that I have seen and it is doubtful whether they are sufficiently constant to serve as a basis for generic separation.

In a later paper Moss (1954) redefined the genera according to the following criteria.

Arthrocnemum: perennial; protogynous; stigma bifid; some of the branches not terminating in an inflorescence.

Salicornia: annual; protandrous; stigma tufted; branches all terminating in an inflorescence.

Salicornia perennis Mill. certainly differs from the annual species of the British Isles in the first and last of these four characters. This paper sets out to show, however, that in the shape of the stigma and in order of maturation of reproductive organs of the flower, no clear separation is possible. If this is accepted it would seem that the criteria for the definition of the genus *Arthrocnemum* will need reconsideration once more. I hope, at a later stage, to undertake a limited investigation of these criteria throughout the range of the two genera.

STIGMA MORPHOLOGY

The stigma in *S. perennis* Mill. may be bifid or trifid; the branches are usually about 1 mm in length and often persistent after fertilization (Fig. 1). In annual species of *Salicornia* the stigmas are variable even within the same plant, being 'tufted' (that is very shortly branched with branches often unequal in length), bifid, or trifid, and often persistent

(Fig. 1 and Plate 1a). The stigmas of annual material collected in the field are usually shorter than those of *S. perennis*, with branches usually about 0.5–0.7 mm in length. Tetraploid plants cultivated from seed from six populations resembling *S. lutescens* Ball & Tutin, however, produced stigmas with very long branches of more than 1 mm in length and indistinguishable from those of *S. perennis* (Fig. 1). In diploid plants referable to *S. europaea* agg. and *S. pusilla* Woods the branches of the stigmas are usually shorter and more slender than those of *S. perennis* but are very variable, and in cultivation they may be indistinguishable from those of *S. perennis*.

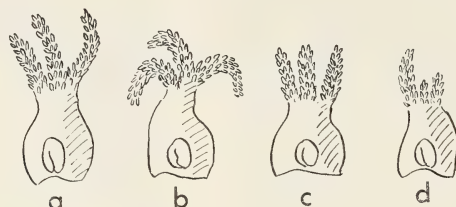


Fig. 1. Stigmas of *Salicornia*, $\times 10$ approx. (a) *S. perennis*. (b) from an annual tetraploid plant in cultivation. (c) and (d) from annual tetraploid plants in the field.

These observations are in harmony with the illustrations in Smith's *English Botany*, where *S. perennis* (t. 1691) and an annual species closely resembling *S. lutescens* Ball & Tutin (t. 415) are both depicted with trifid stigmas, though the branches of the former are longer. A third illustration (t. 2475) shows another annual species with a tufted stigma. Tutin (1952) describes the stigmas in *S. perennis* as bifid and those in the annual species as tufted. Later (Tutin 1962) he retains the description of the stigma in *S. perennis* as bifid but omits any description of those in the annual species.

FLOWERING

I have found from observations in the field that *S. perennis* Mill. is protogynous; this is in agreement with Moss (1954) and Dalby (1962).

Among the annual species I have observed that in tetraploid plants resembling *S. lutescens* Ball & Tutin and *S. dolichostachya* Moss, both in the field and in cultivation, either the stigmas protrude just before the undehiscent anthers are exerted (Plate 1b, seen in the two lateral florets of the lower segment) or the anthers and stigmas emerge simultaneously (Plate 1c and d). It thus appears that some annual *Salicorniae* are weakly protogynous or homogamous. This view to some extent supports Dalby (1962) who says 'usually it seems that *Salicornia* is weakly protogynous and sometimes it may be markedly so (as for example *S. perennis*)'. Plate 1b further supports Dalby's view 'that it is very likely that many of the annual forms are self-pollinated in nature, as ripe dehiscing anthers may be seen in contact with presumably receptive stigmas, and their pollen spilling on to the stigmatic papillae (see Fig. 1)'. However, his figure does not show this very clearly.

In some diploid plants I have confirmed the observations of Ball & Tutin (1959) that the flowers may be cleistogamous. In others the anthers are exerted after dehiscence; it is difficult, however, to observe the sequence of development in either of these conditions. Further observation is required.

I have observed that plants in cultivation and in the field may sometimes have unisexual flowers, either of the organs failing to develop. I have also observed that the stigmas frequently elongate and persist after fertilization. Elongation must occur after fertilization has taken place as the stigmatic papillae have always been found to have collapsed when it commences. These phenomena may have contributed to misinterpretation in the past of the sequence of development of the anthers and stigmas.

ACKNOWLEDGMENTS

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INFRASPECIFIC VARIATION IN *LATHYRUS NISSOLIA* L.

By J. F. M. CANNON

Department of Botany, British Museum (Natural History)

ABSTRACT

The varieties described for *Lathyrus nissolia* by Continental authors are reviewed and their findings are clarified with the aid of cultural experiments and statistical techniques. Two well-marked varieties are recognized and their distributions are plotted on a map. Only one variety appears to occur naturally in the British Isles. Some preliminary observations are made on the breeding biology of the species and problems demanding further field study are indicated.

As *Lathyrus nissolia* is a very distinct species which is clearly separated from the rest of the genus by its grass-like phyllodes (hereafter referred to as leaves), its circumscription has been understood from early times and its taxonomy is free from troubles at the specific level. When, however, its infraspecific variation is examined a great confusion of taxa is found. This is due in part to the rather subtle nature of the characters involved and partly to the consideration by some of the early authors of too little material, both in the herbarium and in the field. My own interest in the subject was aroused by the fact that although the major Continental Floras all recognized varieties of this species, very little notice had been taken in British botany of their conclusions. Lousley writing in the Botanical Exchange Club Report for 1934 was almost alone in drawing attention to the Continental work and his note does not seem to have received the attention it deserved. The reason for this lack of interest by British botanists is now clear, since as a result of this study it will be seen that only one infraspecific taxon is represented in this country and the absence of interest was therefore probably occasioned by frustration rather than neglect.

HISTORICAL

A. Kerner was the first to draw attention to the variation within the species when he described *Lathyrus gramineus* in 1863. This he believed to be a related species which differed from *L. nissolia* by 'petiolis angustioribus concavis et leguminibus germinibusque glaberrimis'. Thus, by implication, Kerner suggested that *L. nissolia* (*sensu stricto*) has broader leaves and a hairy pod. As will be shown later, this was an error which was perpetuated by later authors till the present time. *L. gramineus* A. Kerner is a later homonym of *L. gramineus* Gray, which is itself a nomenclatural synonym of *L. nissolia* L. Uechtritz, writing a letter to the editor of the *Oesterr. Bot. Zeitschr.* in 1864, pointed out that *Orobis* (*Lathyrus*) *nissolia* was quite a variable plant, especially with regard to leaf width. He suggested that Kerner's *L. gramineus* was a variant of this species and went on to point out that the glabrous-podded forms are of frequent occurrence throughout the range of the species, to an extent that some authors of Floras have described it as having glabrous pods. He then made a short reference to a form which he referred to as *O. nissolia genuinus* which had a short fine pubescence. In making these observations, Uechtritz showed that he had an appreciation of the variability of this species unequalled by any of the older authors. Subsequent authors have considered that this letter includes a valid publication of the name *O. nissolia genuinus* and have presumed the trinomial to be of varietal rank. It seems clear to me, however, that he only used *genuinus* meaning 'in the strict sense' and did not visualize it as a formal nomenclatural unit. Freyn (1878) in a paper on the flora of Southern Istria provided a varietal epithet for the forms represented by Kerner's *L. gramineus*. He noted that his var. *glabrescens* had a narrow leaf and a glabrous or almost glabrous pod. In doing this he undermined the excellent observations about variation in leaf width made earlier

by Uechtritz and paved the way for later authors to further confuse the situation. In 1885 Uechtritz also provided a varietal epithet (var. *liocarpus*) for the glabrous-podded forms, citing *L. gramineus* A. Kerner as a synonym.

In his Flora of Lower Austria (1893) G. Beck recognized two varieties: α *pubescens* G. Beck which he described as being hairy-podded and β *gramineus* G. Beck which has a glabrous or somewhat rough pod. He cited var. *glabrescens* Freyn as a synonym of the latter. In the addendum to the Flora, Beck provided an additional name (var. *puberulus*) for var. *pubescens*. Since he gave no reason for this action, we must regard this as the publication of a later superfluous nomenclatural synonym.

Rouy, in *Flore de France* (1899) provided two further varietal epithets with the following descriptions:

lanceolatus Pétioles lancéolés-linéaires (4–10 mm de large); plante plutôt robuste.

linearis (*L. gramineus* Kern.) Pétioles étroitement linéaires (2–3 mm de large); plante plutôt grêle.

These descriptions are important as they draw attention for the first time to a possible slight difference in leaf shape. Unfortunately Rouy was influenced by Kerner's early remarks on the narrowness of the leaves of the glabrous-podded forms and introduced the size restrictions shown above. In his general description Rouy refers to the pods being 'pubescents ou presque velus'. It is strange that he made no reference to the pods of the varieties. Ascherson & Graebner also writing in 1899 proposed a forma *gramineus* Aschers. & Graebn. and referred to its glabrous pods without mentioning the leaves. Hegi (1924) recognized two varieties, using the epithet *genuinus* Uechtr. ('pod hairy, leaves moderately broad') and *glabrescens* Freyn ('pod glabrous or somewhat rough, leaves smaller about 3 mm broad').

Finally Fiori in his Flora of Italy of 1925 proposed a var. *typicus*, with linear-lanceolate leaves 4–10 mm broad and with hairy pods, and a var. *gramineus* with linear leaves 2–3 mm broad and with glabrous pods. He cited var. *glabrescens* Freyn and var. *linearis* Rouy as synonyms of the latter and derived its epithet from Gray and Kerner. As we have already seen, *L. gramineus* Gray is a direct nomenclatural synonym of *L. nissolia* L.

My own studies in this field originated in an attempt to apply this maze of observations to the British material. Much time was spent looking for hairs on the pods of the broader-leaved forms, but it eventually became apparent that this kind of plant was not represented in the British flora (except by one specimen at the British Museum (Isle of Wight 1916) which, must, I think, be considered to be of adventive origin or a curatorial error). In considering the interpretation of the glabrous-podded variety, I was for a long time misled by the insistence of some Continental authors that narrow leaves went with glabrous pods. The situation seemed especially difficult as the British material included some conspicuous plants with exceptionally broad leaves of up to 1 cm in width. Early attempts to apply the var. *glabrescens* concept to British plants suggested that there might be two glabrous-podded varieties, but eventually it became clear that a continuous range of variation existed both in this country and on the Continent.

Some consideration was then given to finding additional reliable features to support the pod-pubescent character. At this stage Uechtritz's excellent remarks of 1864 were unknown to me, but inspection of the material at the British Museum and Kew suggested that a slight but constant difference in leaf shape was associated with the pod character. The plants with hairy pods had narrow-lanceolate leaves, while those with glabrous pods had linear-lanceolate leaves. As already noticed this was suggested by Rouy but he confused the issue by also suggesting an absolute difference in leaf width. In order to express this difference statistically a ratio was devised whereby the leaf length was divided into six equal parts and the width at one sixth from the apex (W_1) was divided by the width at one third from the apex (W_2). This is referred to hereafter as the *leaf ratio*. Fig. 1 shows a simple plastic scale which was made to facilitate the division of the leaves into six equal parts. By aligning the mid-rib of the leaf parallel to one of the horizontal lines of the scale, so that

its tip and base touched outermost sloping lines, the one-sixth and one-third points could quickly be found with an accuracy adequate for the present purpose.

As a pilot experiment fifty leaves each were measured from glabrous and hairy-podded specimens in the British Museum herbarium and average ratios worked out for them. The hairy-podded plants had a ratio of about 0.5, while the ratio of the glabrous-podded forms was about 0.7. At this point it became essential to clarify the nomenclatural position in

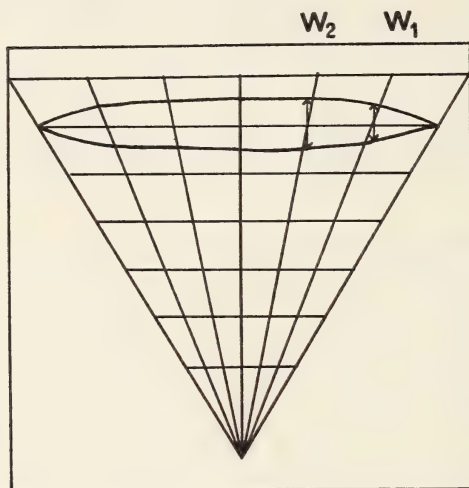


Fig. 1. Diagram showing the use of a simple transparent plastic scale for finding the positions for the measurement of the leaf-widths used in the *leaf ratio* determinations.

respect of these two varieties. Continental authors have always referred to the hairy-podded variety as being typical *L. nissolia* but when the Linnaean type was examined (Herb. Linn. no. 905/2) it was found to fit very exactly into the glabrous-podded group; the correct name for these plants is therefore var. *nissolia*. *L. nissolia* var. *pubescens* G. Beck (1893) is the correct name for the hairy-podded variety.

A synonymy of varietal names is given below:

LATHYRUS NISSOLIA L. VAR. NISSOLIA

Lathyrus gramineus A. Kerner, Oesterr. Bot. Zeitschr. **13**, 188 (1863) non Gray (1821).

L. nissolia var. *glabrescens* Freyn, Verh. K. K. Zool-bot. Ges. Wien **27**, 325 (1878).

L. nissolia var. *liocarpus* Uechtritz, Jahres-Bericht. Schlesischen **62**, 310 (1885).

L. nissolia var. *gramineus* G. Beck, Fl. Nied-Oesterr., 882 (1892).

L. nissolia var. *linearis* Rouy in Rouy & Fouc., Fl. France **5**, 253 (1899).

L. nissolia forma *gramineus* Aschers. & Graebn., Fl. Nordost. Flachl., 99 (1899).

Fig. 2. Graph showing the relation of mean leaf ratio and mean pod vein number for eleven populations. The lines represent twice the standard error of the means. ▲ = Linnean type specimen.

Fig. 3. Graph showing the relation of mean leaf ratio and mean pod diameter for eleven populations. The lines represent twice the standard error of the means. ▲ = Linnean type specimen.

Fig. 4. Graph showing the relation between mean pod vein number and mean pod diameter for eleven populations. The lines represent twice the standard error of the means. ▲ = Linnean type specimen.

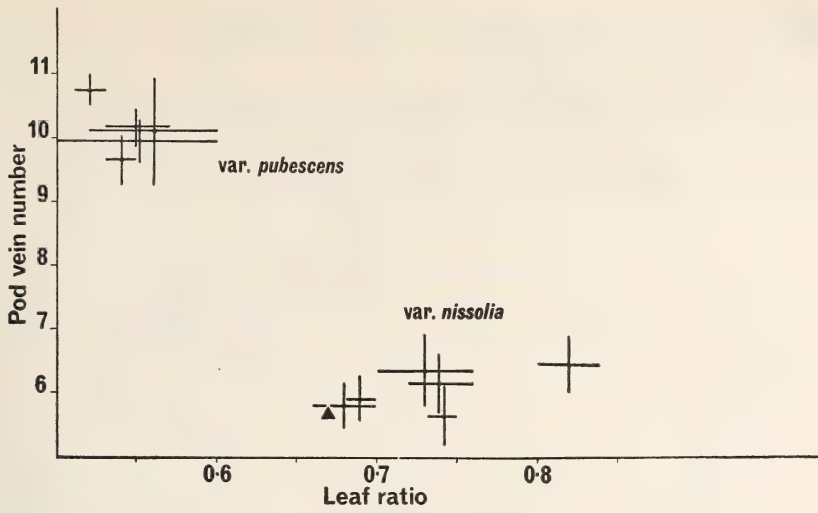


Fig. 2

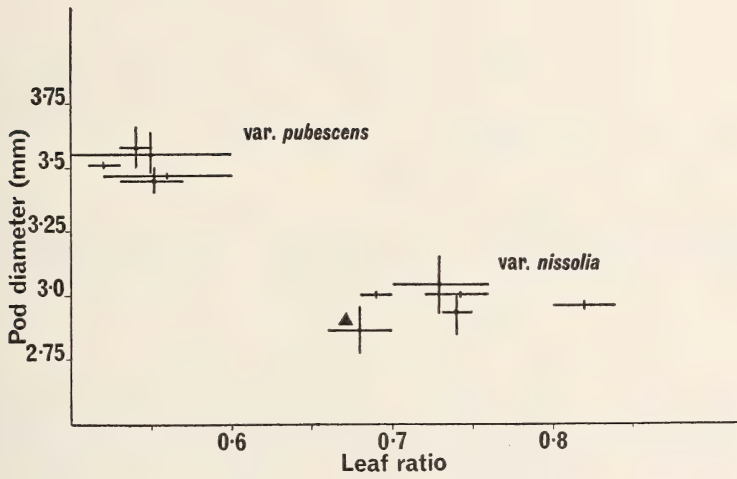


Fig. 3

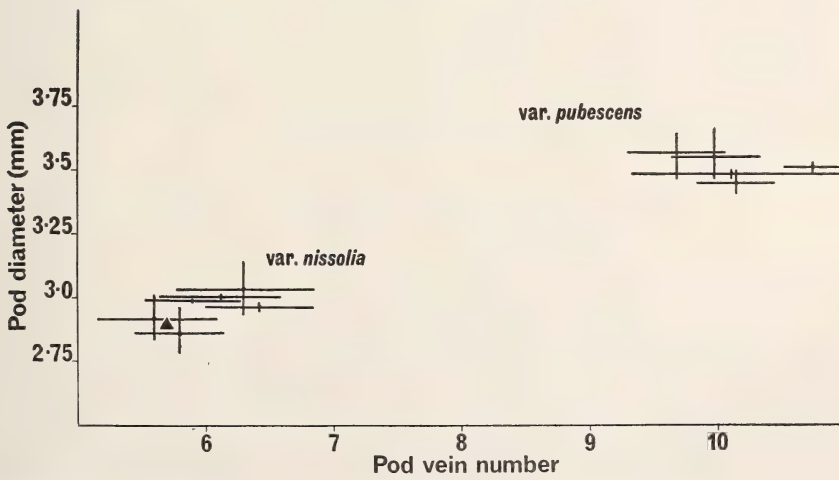


Fig. 4

L. nissolia subsp. *amanus* Rechinger. Ark. för Bot. 5, 268 (1960).

(See discussion later in this paper.)

LATHYRUS NISSOLIA VAR. *PUBESCENS* G. Beck, op. cit., 882 (1892).

Lathyrus nissolia var. *puberulus* G. Beck, op. cit., 1329 (1893). Illegitimate substitute name.

L. nissolia var. *lanceolatus* Rouy in Rouy & Fouc., Fl. France 5, 253 (1899).

L. nissolia var. *typicus* Fiori, Nuova Fl. Anal. Ital. 1, 909 (1925).

EXPERIMENTAL TAXONOMY

Having reached these conclusions by more or less traditional methods, it seemed clear that cultural methods with statistical investigation would provide the best means of further clarifying the separation of these varieties. Through the courtesy of the directors of several botanic gardens and by direct collection in the field, seeds of ten strains of *L. nissolia* were obtained for culture the following season. The seeds were sown directly in the ground in patches so that clumps would be formed by the growing plants. Previous experience had shown that germination is very slow and irregular unless the testa is filed before the seeds are sown. The following characters were observed in the living plants. The foliage of var. *nissolia* is rather yellowish-green compared to that of var. *pubescens* which is relatively glaucous bluish-green. I have not been able to detect this colour difference in herbarium material. The colour difference is most noticeable when the plants are massed in clumps, under these conditions the plants can be separated by this character at a distance of several yards. In my experience plants of var. *nissolia* are in full flower 4 months plus after planting, while plants of var. *pubescens* sown on the same day come into flower 3 months plus after planting. The generally quicker growth rate of var. *pubescens* is noticeable at all stages when the plants are grown side by side.

Var. *nissolia* is very variable in height, from 10 cm dwarfs to 100 cm giants. Its stem is often nearly simple, sometimes with a second main branch from near the base. Var. *pubescens* on the other hand is rather uniform in stature, varying between about 25–35 cm. It frequently has a rather bushy growth habit with up to six or seven stems of equal magnitude rising from the base. In addition to the leaf ratio character already described, two other characters were tested statistically on the cultured populations. These were (1) The number of major veins on a pod valve at a position half way along its length (*Pod vein number*) and (2) the diameter of the pod measured at the same position. For each culture 50 leaves and 50 pods were collected, only one of each being taken from each plant. Only lower leaves from fully developed plants were used and likewise only fully grown but unripened pods were selected. The results of the analysis are shown graphically in Figs. 2, 3 and 4. In each case the mean value for the 50 samples is plotted together with lines representing twice the standard error of the mean which is used as an indication of the variability within each population. Some measurements were also made of the Linnean type specimen and figures representing this plant are included on the graphs. In each case its clear association with the glabrous-podded variety can be seen.

LATHYRUS NISSOLIA SUBSP. AMANUS RECHINGER

In 1952 Dr. K. Rechinger kindly drew my attention to his then unpublished subsp. *amanus* from the Amanus range in northern Syria. This is founded on Haradjian nos. 222, 266 and 275 in the Delessert Herbarium at Geneva. Rechinger's description reads 'Differt a planta typica pedunculo folium fulcrantum aequante vel eo longiore'. I later had the opportunity of examining the type material and was unable to find any additional features by which it could be separated from var. *nissolia*. While I have not seen another specimen with such relatively long peduncles, I have seen plants ranging widely between the var. *amanus* condition and the more normal state. For these reasons I prefer to regard the Amanus material as a highly localized population of the type variety. Judging from the

material that has reached the major European herbaria from Asia Minor, *Lathyrus nissolia* is a rare and scattered plant in this region. I would therefore suppose that this long-peduncled population has developed in the seclusion of the Amanus mountains and the character has become established in the population through the habitual self-pollination which I believe is normal in this species.

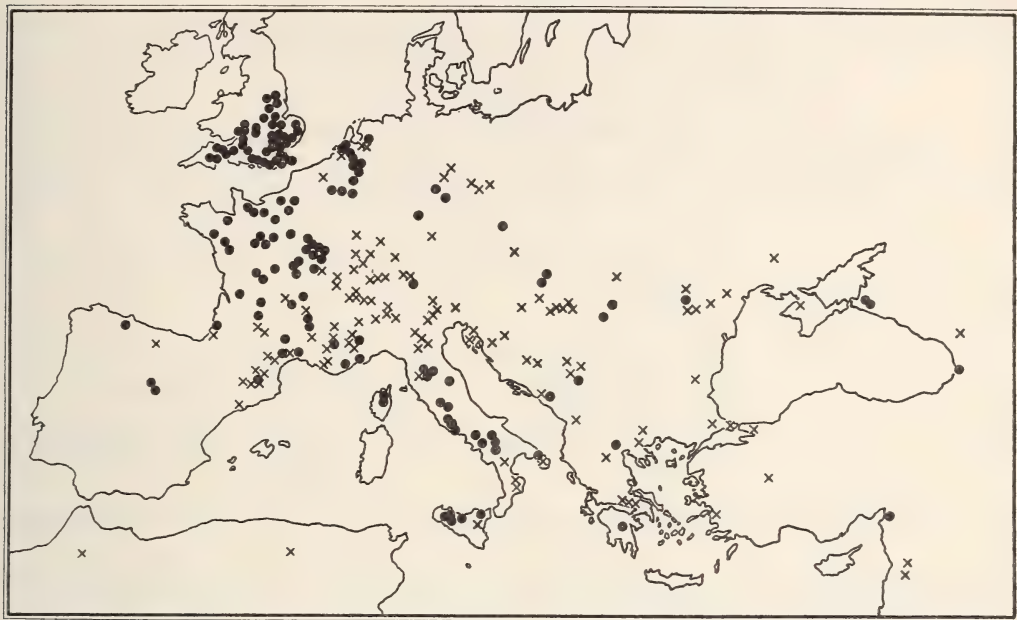


Fig. 5. Map showing the distribution of the varieties of *Lathyrus nissolia*. ● = var. *nissolia*, x = var. *pubescens*.

DISTRIBUTION

The accompanying map (Fig. 5) shows the distribution of the two varieties throughout the known range of the species. The British range is adapted from the map in the *Atlas of the British Flora* while the remainder has been plotted from the records provided by specimens which I have examined myself. It will be noted that while the distribution is sympatric over the greater part of the range, the British Isles only has var. *nissolia* with the exception of one record of var. *pubescens* from the Isle of Wight. A specimen in the British Museum Herbarium forms the basis for this record. The label provides no additional information other than the date 1916. In view of the lack of any other records and absence of var. *pubescens* from the north-west part of France, I am disposed to regard the Isle of Wight record as either an adventive stray or else the result of some curatorial error involving a mixing of labels. Apart from a broadly Continental trend in the distribution of var. *pubescens*, compared with the exploitation of more oceanic conditions by var. *nissolia*, no obvious distributional patterns can be seen from the map.

CHROMOSOME NUMBER

The chromosome number of this species has been reported as being $2n = 14$ on several occasions including Simonet (1932) and Senn (1938). The vast majority of *Lathyrus* species have been found to be diploids with the base number 7; only four species have been recorded as polyploids. One of the most interesting of these was reported by Marks in 1950. He found that a tetraploid form of *Lathyrus pratensis* was common in this country. A detailed cytological investigation of *L. nissolia* would very probably prove rewarding.

GENERAL SUMMARY AND CONCLUSIONS

One of the most important observations resulting from this study is that individual plants can always be placed with comparatively little difficulty into one or other of the two varieties. Plants with markedly intermediate characters do not seem to occur and I have not detected any hybrids among the very large number of sheets that I have examined. Attempts to produce artificial hybrids under cultural conditions were not successful. My observations suggest that this species is habitually self-pollinated—despite the apparent adaptation of its flowers towards entomophily. Buds enclosed in bags to prevent the access

TABLE 1

Character	var. <i>nissolia</i>	var. <i>pubescens</i>
1. Pods	Glabrous or somewhat scabrous	With short bristly hairs
2. Leaf shape	Linear lanceolate (leaf ratio about 0·7)	Narrowly lanceolate (leaf ratio about 0·5)
3. Mean pod diameter	About 3·0 mm	About 3·5 mm
4. Mean pod vein number	About 6	About 10
5. Colour of living plant	Relatively yellowish-green	Relatively blue-green
6. Growth rate	In full flower four months plus after planting	In full flower three months plus after planting
7. Habit	Very variable in height, stem often simple	Relatively uniform in height and frequently with a rather bushy habit with several stems of equal size

of insects always set seed perfectly normally, while emasculated flowers were never found to set any seed, although unprotected by bags. I have never observed the flowers being visited by any insects, in the wild or in cultivation. These observations are confirmed by Kirchner who says '... the flowers frequently do not open at all but nevertheless set healthy fruits, being cleistogamously fertilized'. Knuth does not record any insect visitors to these flowers in his *Handbook of Flower Pollination*. This habitual self-pollination presumably provides an explanation of why hybrids apparently do not occur and also why the varieties remain distinct despite the very large overlap in their ranges. The question remains as to what status in the taxonomic hierarchy should be accorded to these taxa. Since interbreeding does not seem to occur and since the individuals can always be assigned to a variety without undue difficulty, it would seem that they might well be regarded as distinct species or at least sub-species. But since the evidence from genetics and cytology remains to be clarified, I prefer for the present to retain the existing varietal status, for which validly published names are available, rather than to further burden the literature with additional names at a new status which may prove undesirable after further studies have been executed. I am content for the present to draw attention to the interesting infraspecific variation of this plant, with the hope that other workers will make observations on its biology in the field, especially in those areas where both varieties are known to occur. It would be interesting to know if the difference in flowering times encountered under cultural conditions holds good when the varieties are growing in the same area in the wild and if natural hybrids ever occur in regions where both varieties are present. The characters which separate the two varieties are summarized in Table I.

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CHROMOSOME NUMBERS OF *EPILOBIUM* IN BRITAIN

By PETER H. RAVEN and D. M. MOORE

*Division of Systematic Biology, Stanford University, Stanford, Calif., U.S.A.
and Botany Department, The University, Leicester*

ABSTRACT

The 14 species of *Epilobium* occurring in Britain are shown to have $2n = 36$. Chromosome numbers of *E. lanceolatum* and *E. tetragonum* subsp. *lamyi* are given for the first time and a further 11 species have not hitherto been counted from British material. The artificial F_1 hybrid *E. montanum* $\times$ *adenocaulon* is of reduced fertility, but shows no meiotic irregularities. The rôle of self-pollination in reducing interspecific hybridization is stressed.

Chromosome numbers have been reported for the majority of European species of *Epilobium* and they were summarized by Löve & Löve (1961, p. 256–7), but there seems to have been only one published record dealing with British plants. Rutland (1941, p. 210) gave the somatic chromosome number of *Epilobium palustre* as $2n = 36$ without specifying the locality from which the material originated. A few of the counts reported in the present paper were mentioned by Clapham (1962).

All counts reported here were made during studies of meiosis in pollen mother cells, the anthers being fixed in 1:3 acetic alcohol and squashed in acetocarmine. With the exception of *E. alsinifolium*, all the chromosome numbers were determined by the senior author during the tenure of a United States National Science Foundation post-doctoral fellowship spent in London during 1960–61. The authors are grateful to Professor D. H. Valentine, Dr. C. R. Metcalfe and Dr. K. Jones for the facilities afforded Raven while he was making his cytological studies and to Mr. A. Eddy for collecting plants of *E. alsinifolium*. Vouchers for the chromosome counts are deposited in the herbarium, Department of Botany, British Museum (Natural History) and in the Dudley Herbarium, Stanford University. Details of the collections from which plants were counted are given in Table 1.

TABLE 1. Chromosome vouchers of British species of *Epilobium*.

<i>E. adenocaulon</i> Hausskn. MIDDLESEX, Chiswick, <i>Raven 18060</i> (garden progeny). SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16086</i> .
<i>E. alsinifolium</i> Vill. WESTMORLAND, Moorhouse Nature Reserve, altitude c. 1,800 ft, <i>Moore 464</i> (garden progeny).
<i>E. anagallidifolium</i> Lam. WESTMORLAND, at head of Knock Ore Gill, by road to Radar Station, altitude c. 2,500 ft, <i>Raven 16277</i> (garden progeny).
<i>E. angustifolium</i> L. MIDDLESEX, Twickenham, <i>Raven 16490</i> .
<i>E. hirsutum</i> L. DERBYSHIRE, along hedgerow 2 miles north of Derby, <i>Raven 16194</i> .
<i>E. lanceolatum</i> Seb. & Mauri. SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16087</i> .
<i>E. montanum</i> L. OXFORDSHIRE, Bagley Wood, <i>Raven, 15915</i> .
<i>E. nerterioides</i> A. Cunn. KENT, Bayham Abbey, <i>Raven 16168</i> (progeny grown at Chelsea Physic Garden).
<i>E. obscurum</i> Schreb. WESTMORLAND, Glencoyne Wood, Ullswater, <i>Raven 16226</i> .
<i>E. palustre</i> L. WESTMORLAND, Glencoyne Wood, Ullswater, <i>Raven 16225</i> .
<i>E. parviflorum</i> Schreb. SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16488</i> .
<i>E. roseum</i> Schreb. SURREY, weed by the herbarium, Royal Botanic Gardens, Kew, <i>Raven 16193</i> .
<i>E. tetragonum</i> L. subsp. <i>lamyi</i> (F. W. Schultz) H. Lév. SURREY, Ewell, <i>Pennington</i> in 1961.
<i>E. tetragonum</i> subsp. <i>tetragonum</i> . KENT, sand pit behind Covers Farm, Westerham, <i>Raven 16485</i> .

All collections of *Epilobium* cited in Table 1, formed 18 bivalents at meiotic metaphase I; no meiotic irregularities were observed. All numbers except that for *E. palustre* are being reported from Britain for the first time; *E. lanceolatum* and *E. tetragonum* subsp. *lamyi* do not appear to have been counted before. The list includes all British species of *Epilobium*, including the two introduced ones, *E. adenocaulon* and *E. nerterioides*. The segregate genus *Chamaenerion* is not recognized here for reasons discussed in detail elsewhere (Raven 1962a, 1962b).



Fig. 1. Chromosome pairing at first meiotic metaphase in the artificial F_1 hybrid between *E. montanum* (Turkey) and *E. adenocaulon* (Middlesex) showing 18 bivalents.

DISCUSSION

These additional chromosome numbers re-emphasize that barriers to hybridization in *Epilobium* sect. *Epilobium* (*Lysimachion*) are not a result of aneuploid differences in chromosome number. Judging from reports in Britain and on the Continent, hybrids are probably possible between all combinations of species except those involving *E. angustifolium* and *E. nerterioides*. Many if not most of these hybrids are at least partly fertile.

Meiosis in interspecific hybrids in *Epilobium* has been studied by Hair (1942) and by Lewis & Moore (1962). These authors studied natural hybrids and in no case were meiotic irregularities observed. In an effort to extend their observations, we artificially duplicated one of the hybrids frequently encountered in Britain, that between *E. montanum* and the introduced North American *E. adenocaulon*. Our strain of *E. adenocaulon* was from Chiswick (see Table 1), whereas our seeds of *E. montanum* were from Turkey (Prov. Bolu, Ala Dağ, alt. 700 m, Khan, *Prance & Ratcliffe* 515). Both of the parents consistently formed 18 bivalents at meiotic metaphase I. The hybrid plants (*Raven* 18557) were more vigorous than the parents, with darker, larger flowers, irregularly lobed stigmas, and the short capsules caused by a low seed set (c. 10 per cent. and below). Judged by staining in acetocarmine, their pollen was approximately 15 per cent. fertile (based on 200 pollen grains from each of four F_1 plants). Just as in the cases of natural hybrids analyzed previously, meiosis in this hybrid was quite regular (Fig. 1).

The reduced fertility certainly may help to maintain species distinctions in such a case, but we are still in large measure faced with the problem, posed by Valentine (1951), as to how the species maintain themselves in the absence of strong genetical, geographical and ecological barriers to interbreeding. The relatively small percentage of hybrids found in mixed populations of two or more species of *Epilobium* in Britain suggests that a part of the answer may be in the high degree of self-pollination characteristic of most species of the genus. Of the 14 British species of *Epilobium*, only two are outcrossed to any appreciable degree—*E. hirsutum* and the very distinct *E. angustifolium*, which is presumably incapable of forming hybrids with the other species. In all other species found in Britain, the anthers surround the stigma and shed pollen directly on it, and the high degree of autogamy resulting from this doubtless tends to decrease sharply the proportion of hybrids that might otherwise be expected. This explanation was adduced by Lewis & Moore (1962) for the rarity of hybridization between the North American species *E. adenocaulon* and *E. brevistylum* Barbey in the Rocky Mountains. These authors also postulated that the hybrids they were studying were genotypically not so well adapted as the parental species to the communities in which the parents grew, and consequently they were less likely to become established

in the undisturbed habitats available. In Colorado, where Lewis & Moore studied hybridization in the genus, the summers are long and dry so that the habitats occupied by *Epilobium* are of rather limited extent, normally consisting of wet meadows and streamsides where the plants are members of relatively stable communities. In Britain, on the other hand, the climate is generally much moister throughout the year and many species of *Epilobium* are decidedly weedy, frequently growing in ecologically open communities in which there is a rapid turn-over of individuals. Even under these conditions the proportion of hybrids still remains extremely low. This tends to suggest that habitual autogamy and, possibly, lowered cross-compatibility (Valentine 1951, p. 86) may be far more important in maintaining the species as discrete units, at least for the 'weedy' species, although lowered hybrid fitness probably operates when interspecific crosses do occur.

The evidence presented here further emphasizes that the gross chromosomal rearrangements that have been so important in the evolution of the tribe Onagreae have apparently had no part in the differentiation of species in other tribes of the family (Lewis & Moore 1962, Raven 1963 and unpubl.).

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STUDIES ON BRITISH PANSIES

I. CHROMOSOME NUMBERS AND POLLEN ASSEMBLAGES

By A. PETTET

*Department of Botany, University of Southampton**

ABSTRACT

The chromosome counts and pollen assemblages of a range of British pansies are given. With the exception of what is believed to be an aberrant count for *Viola nana* Corb. (*V. kitaibeliana* in Dandy, 1958), the chromosome counts confirm those cited by past workers. The polymorphic pollen assemblages which can be characterized by the most abundant grain type and the associated subsidiary types show that the taxa can be divided into two main groups.

In the case of the two variable and often confused species, *V. tricolor* and *V. arvensis*, differences in their pollen assemblages confirm their separation on the basis of chromosome counts and such is the agreement between the two criteria that the former should be a reliable criterion for the separation of the two taxa.

1. INTRODUCTION

The *Melanium* subgenus of *Viola*, comprising those plants better known as pansies, forms a very variable group not readily divisible into coherent taxa. Past treatments of the complex of variation surrounding *V. tricolor* sensu lato have ranged from the acceptance of a few rather variable species to the erection of many, narrowly-defined microspecies. The cytogenetical studies on European pansies by Clausen (1921, 1922, 1924, 1926, 1927, 1931) and the cytological investigations of British plants by Fothergill (1944) have, however, done much to clarify and stabilize the species concept in the subgenus. The Jordanian microspecies recognized by Drabble (1909, 1926, 1927 *a-c*, 1928) were shown to be indistinguishable on the basis of chromosome number and chromosome morphology, although Drabble's major groupings of these—*Luteae*, *Curtisiae*, *Tricolores*, *Arvenses* and *Nanae*—could be characterized by such features. On this basis the *Tricolores* are not separable from the *Curtisiae*, or the *Luteae* from the *Nanae*. The latter pair are, nonetheless, readily divisible on morphological features.

As Clausen (1927, 1931) pointed out whilst discussing the concept of species within the subgenus *Melanium*, it is quite impossible to give a definition covering all cases. Morphological differences coupled with complete or partial sterility fail to delimit all taxa satisfactorily because there are some morphologically uniform taxa which contain several intersterile cytotypes. On the other hand, differences in chromosome number used as the only means of delimiting species also fail because of the limited association between morphological appearance and chromosome number. In the particular case of the *tricolor-arvensis* group of annuals, Clausen (1922) recommended the retention of two species, *V. tricolor* L. and *V. arvensis* Murr., as the basic units, mainly on the grounds that two different chromosome numbers were associated with two reasonably well-defined morphological types which had differing edaphic ranges. It is sometimes felt, however, that this division into two species is not always one easy to maintain, for their limits are blurred by a rather complex variation which itself may be further complicated by the reputedly frequent occurrence of hybridization and introgression of the two species.

During an investigation into the possibility of frequent interspecific hybridization between *V. tricolor* and *V. arvensis* a considerable number of observations were made on the cytology and pollen morphology of a representative range of British pansies. Since these observations emphasized the distinctness of the two taxa within the British Isles

* Now at Department of Botany, University of Khartoum.

and are pertinent to the problem of hybridization to be discussed in detail elsewhere, they form the basis of the present paper.

There is, perhaps, little need to stress the value of cytology in understanding the complex variation in the pansies, but the potential value of pollen morphology appears relatively unknown.

Wittrock (1897) was the first to describe the quantitative differences in the polymorphic pollen assemblages of *V. tricolor* and *V. arvensis* and to use them as an additional character in discriminating between the two taxa. These differences were subsequently mentioned by Clausen (1922) although he made little use of the character in his final analysis of the taxa. Since then the taxonomic value of the character has been overlooked with the one recent exception when Mullenders & Mullenders (1957) used it as a criterion for deciding whether *V. maritima* Schweigg. (= *V. curtisii* Forst., *V. sabulosa* Bor.) should be considered as a species distinct from *V. tricolor* subsp. *tricolor*.

Before detailing the observations on the cytology and pollen morphology of this group of plants—where there has been considerable difference of opinion over specific limits in the past—it would be wise to define the limits of taxa used in this account. With the exception of certain modifications in application the specific names used here largely follow the usage of Warburg (1952) as the observations were originally made within this framework. The main exception concerns the *tricolor*–*arvensis* complex where much of the work was concentrated and where the three groups of plants were distinguished as follows:

V. tricolor: Flowers blue, purple or predominantly so; upper petals longer than sepals (usually more than $\times 1\frac{1}{2}$); stylar flap large and relatively conspicuous.

V. arvensis: Flowers all cream or occasionally with upper petals tipped with blue-purple; upper petals shorter than, or sometimes as long as, the upper sepals; stylar flap so reduced as to be, or appear to be, absent.

Intermediates between V. tricolor and V. arvensis (subsequently abbreviated to 'AT-intermediates'): Flowers cream, or predominantly so; upper petals longer than upper sepals (usually $\times 1\frac{1}{4}$ – $1\frac{1}{2}$); stylar flap present but approximately intermediate in size between that of *V. arvensis* and *V. tricolor*.

The AT-intermediates formed a rather arbitrary group which was meant to cover all those plants not readily ascribable to *V. tricolor* and *V. arvensis*, and which might be considered to be putative hybrids. Observations on these and experimentally-produced hybrids between *V. tricolor* and *V. arvensis* will be the subject of a following paper.

It will be seen that *V. tricolor*, as here defined, is more or less equivalent to *V. tricolor* subsp. *tricolor* of Warburg (1952); in consequence, *V. tricolor* subsp. *curtisii* of the latter is here referred to as *V. curtisii*.

2. CHROMOSOME COUNTS

Previous chromosome counts for taxa represented in the British Isles made on British and other European pansies by Clausen (1921, 1926, 1927, 1931) and Fothergill (1944) may be summarized as :

<i>V. lutea</i>	$2n = 48$
<i>V. curtisii</i>	$2n = 26$
<i>V. tricolor</i>	$2n = 26$
<i>V. arvensis</i>	$2n = 34$
<i>V. nana</i>	$2n = 48$

It would thus appear that chromosome number offers an important criterion for the separation of *V. arvensis* from *V. tricolor*, and *V. arvensis* from the *V. kitaibeliana* complex (includes *V. nana*), two pairs of taxa difficult to delimit satisfactorily on purely morphological criteria. Counts reported by Fothergill (1944) for *V. variata* var. *sulphurea* ($2n = 26$, $2n = 28$) and *V. contempta* ($2n = 40$) refer to AT-intermediates as defined above and will be discussed in another paper.

TABLE 1. List of chromosome counts.

	Reference Number of Population	Locality	Chromosome number	
			PMC (n)	RT (2n)
<i>lutea</i>	L18	Moorhouse, Westmorland	24	—
	L27	Malham Tarn, Yorkshire	24	—
	L28	Combs Dale, Derbyshire	24	—
	L50	Widdybank Fell, Teesdale, Co. Durham	24	—
	L52	Schiehallion, Perthshire	24	—
	L58	Wardlow Hay Cop, Derbyshire	24	—
<i>curtisii</i>	TC44	Aberffraw, Anglesey.	13	—
	TC67	Kenfig Burrows, Glamorgan	13	—
	TC68	Broughton Burrows, Gower, Glamorgan	13	—
	TC69	Llangennith Burrows, Gower, Glamorgan	13	—
	TC81	Castlegregory, Co. Kerry, Ireland	13	—
	TC83	Corbally, Co. Waterford, Ireland	13	—
<i>tricolor</i>	T10	nr. Aberystwyth, Cardiganshire	13	26
	T14	nr. Durham, Co. Durham	13	26
	T20	Orpington, Kent	13	—
	T23	nr. Aberfeldy, Perthshire	13	—
	T25	Lawers Burn, Perthshire	13	—
	T34	Feltham, Middx.	13	—
	T79	High Force, Teesdale, Co. Durham	13	—
	T80	Yetholm, Roxbs.	13	—
<i>arvensis</i>	A1	Southampton Common, Hampshire	17	—
	A2	Highfield, Southampton, Hampshire	17	—
	A5	Swaythling, Southampton, Hampshire	17	—
	A6	Sholden Downs, nr. Deal, Kent	17	—
	A7(A)	Kingsdown, nr. Deal, Kent	17	34
	A10	nr. Aberystwyth, Cardiganshire	17	34
	A11	nr. Aberystwyth, Cardiganshire	17	—
	A12	nr. Durham, Co. Durham	17	—
	A21	Frome, Somerset	17	—
	A22	Porton, nr. Salisbury, Wiltshire	17	34
	A26	nr. Southampton, Hampshire	17	34
	A29	Long Down, New Forest, Hampshire	17	—
	A32	Kempshott, nr. Basingstoke, Hampshire	17	34
	A35	Stoborough, nr. Wareham, Dorset	17	—
	A36	nr. Hursley, Hampshire	17	—
	A37	nr. Hursley, Hampshire	17	—
	A38	nr. Rockland Broad, Norfolk	17	—
	A47	nr. Perranporth, Cornwall	17	—
	A48	St. Martin's, Isles of Scilly	17	—
	A49	St. Mary's, Isles of Scilly	17	—
	A55	Chilworth, nr. Southampton, Hampshire	17	—
	A59	Twyford, nr. Winchester, Hampshire	17	—
	A61	Arne, Dorset	17	—
	A66	St. Mary's, Isles of Scilly	17	—
	A70	nr. Eastleigh, Hampshire	17	—
	A71	nr. Romsey, Hampshire	17	—
	A72	nr. King's Somborne, Hampshire	17	—
	A75	nr. Corhampton, Hampshire	17	—
<i>nana</i>	N45	St. Brelade's Bay, Jersey	24	—
	N46	St. Ouen's Bay, Jersey	24	—
	N64	Tresco, Isles of Scilly	24	—
	N65	Bryher, Isles of Scilly	24	—

(a) *Methods*

For reasons of practical convenience most chromosome determinations were made from squash preparations of PMC meiosis although confirmatory observations were sometimes made on similar preparations of root-tip mitosis.

In the latter case root-tips were pretreated for approximately four hours with a saturated solution of 8-hydroxyquinoline before fixation in 1:3 acetic alcohol and stained with acetic-orcein as in the technique of Tjio & Levan (1950).

When PMC meiosis was used satisfactory stages in division were found when the flower buds were *c.* 2 mm long and almost invariably occurred during the late morning. Flower buds were fixed in Carnoy's solution for approximately $\frac{1}{2}$ hour and then were transferred to 1:3 acetic-alcohol, containing a little ferric acetate or chloride, and were usually stored at -15°C in this solution until needed. The PMCs were subsequently stained with acetocarmine solution. Observations were usually made on temporary slides ringed with a rubber solution to avoid the loss of contrast in staining sometimes experienced when the slides were being made permanent by the dry-ice method (Conger & Fairchild 1953).

In most cases counts were made from several cells on each slide and, wherever possible, repeated on 1-5 plants in each population examined. Whenever a population was morphologically variable, counts were also made from as many of the main types as possible.

(b) *Observations*

Details of the counts obtained are given in Table 1 and illustrated in Figs. 1 and 2. With but a single exception they agree with those already listed. The exception concerns a single plant of *V. nana* from six originally collected from Tresco, Isles of Scilly, and transplanted to the gardens at Southampton University. This plant had $2n = 50$, instead of $2n = 48$ as in the other five examples from the same population. The count was repeated on three different buds from the same plant and in all of these meiosis appeared perfectly

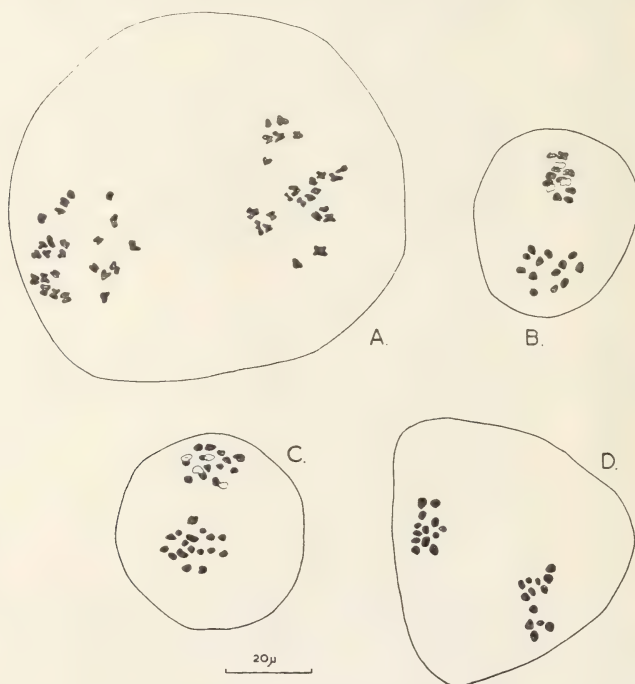


Fig. 1. Meiosis in PMCs. (a) *V. lutea* (L50): Prometaphase of second division, $n = 24$; (b) *V. tricolor* (T14): Second metaphase, $n = 13$; (c) *V. arvensis* (A75): Late stages of first anaphase, $n = 17$; (d) *V. curtisii* (TC44): Late stages of first anaphase, $n = 13$.

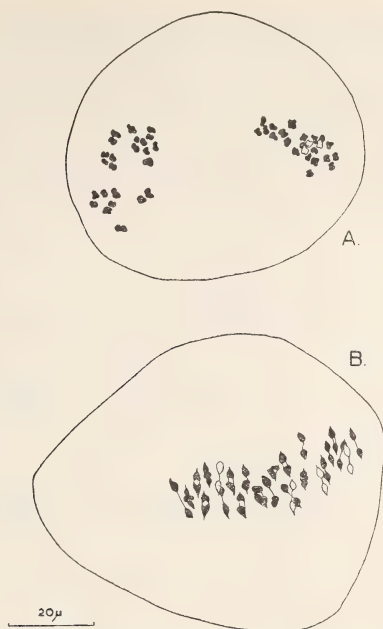


Fig. 2. Meiosis in PMCs of *V. nana* (N64). (a) Second metaphase, $n = 24$; (b) First metaphase with 25 bivalents, $n = 25$.

regular with the formation of 25 bivalents and without the expected occurrence of unpaired chromosomes or chromatid bridges. Since this particular plant was morphologically indistinguishable from others having chromosome numbers typical of *V. nana* and the count could not be repeated in other plants raised from seed collected from the original population, it was probably of little significance, being merely an aberrant chromosomal form which may have arisen as a result of primary nondisjunction of chromosomes or misdivision of a centromere in the previous generation.

Incidental observations on chromosome behaviour at meiosis have indicated some differences between the taxa studied. In many plants of *V. arvensis* 0.5–1.0% of the PMCs had two (or four) univalents which had failed to pair and were either lagging on the metaphase plate or lying disorientated in the cytoplasm (Fig. 3). Chromatid bridges were recorded only twice in this species. In plants of *V. nana* the only irregularities observed were one or two chromatid bridges at first anaphase in many PMCs of a single plant of N65; otherwise meiosis was perfectly regular. In this connection it is interesting to note that Clausen (1931), describing material of this taxon from Jersey, also observed 'slight irregularities' although he stresses that the plants had a 'fairly constant chromosome number'. He gave, however, no indication of the nature of these irregularities or how constant the chromosome number was.

In *V. tricolor* the frequency of chromosomal irregularity varied considerably from population to population. Although most plants examined had regular meiosis, others showed well-defined irregularities. Dicentric bridges and acentric fragments, suggesting the presence of large inversions, were observed in nearly all plants examined from T10 (Fig. 3). In both T25 and T79 some plants had chromatid bridges visible at first anaphase in most PMCs but poor staining made it difficult to be sure of their cause. As in *V. arvensis*, disorientated univalents were rare, being found with a similar frequency.

The situation in both *V. lutea* and *V. curtisii* was roughly parallel to that in *V. tricolor*. Plants from the majority of populations had regular meiosis whilst others in certain populations, notably L50 and L58 (*V. lutea*) and TC44 (*V. curtisii*) had high frequencies of chromatid bridges.

These differences in frequency of chromosomal irregularities might be associated with the breeding system of the taxa involved. Thus, meiosis in the predominantly inbreeding plants of *V. arvensis* and *V. nana* was most nearly always regular, whilst in the outbreeding plants of *V. tricolor*, *V. lutea* and *V. curtisii* chromosomal irregularities were more frequently observed. Presumably the nearly complete genetic homozygosity of the inbreeders would be responsible for their meiotic regularity, whereas the greater chromosomal heterozygosity in the outbreeders was responsible for their chromosomal irregularities.



Fig. 3. Some irregularities in PMC meiosis. (a) *V. arvensis* (A36): Second prophase with univalent and fragment (X) in cytoplasm; the upper complement contains 16 chromosomes, the lower 17 chromosomes. $2n = 34$. (b) *V. arvensis* (A36): Prometaphase of second division with chromatid bridge persisting from first division; disorientated univalent (Y) from first division to one side; each complement has 17 chromosomes but the number has been maintained by the precocious division of the other univalent (X and X^1). $2n = 34$. (c) *V. tricolor* (T10): Late stages of first anaphase with two chromatid bridges and two acentric fragments (X and X^1). $2n = 26$. (d) *V. curtisii* (TC44): First anaphase with two chromatid bridges. $2n = 26$. (e) *V. arvensis* (A37): Second anaphase with a chromatid bridge between two chromosomes of upper complement; a univalent from the first division lying disorientated in cytoplasm; upper group of cells with 16 pairs of chromosomes, lower with 17 pairs of chromosomes.

3. POLLEN POLYMORPHISM

Specific references to the pollen morphology of *V. tricolor* and its immediate allies contain a number of confusing statements. Faegri & Iversen (1950) place *V. tricolor* into their group, the *Stephano-colporatae*, i.e. pollen characterized by four furrows with median pores. Wittrock (1897), comparing pollen of different species of pansies, stated that *V.*

tricolor had mainly 4-colpate grains with some 3- and 5-colpate grains, whereas *V. arvensis* had mainly 5-colpate grains with a few 4-colpate ones. On the other hand, data for these same two taxa given later by Erdtman (1952) would suggest they are not so readily distinguishable since both are recorded as having assemblages of 4-colpate grains, but with the occasional 5-colpate grains in *V. arvensis*. Counts given by Mullenders & Mullenders (1957) show *V. tricolor* subsp. *tricolor* with mostly 5-colpate and a few 4- and 6-colpate grains, and *V. maritima* Schweigg. (= *V. curtisii* Forst., *V. sabulosa* Bor.) with mostly 4-colpate, some 5-colpate and a few 3-colpate grains.

(a) Methods

Wherever possible, slides were made of a small sample of plants from each population with pollen from one flower of each representative plant being mounted on a slide. For good staining and ease of mounting a slight modification of the methylene-green/glycerine-jelly method of preparing pollen grains (Wodehouse 1935) was used.

Pollen grains were first stained on the slide with a weak solution of eosin in absolute alcohol and this was allowed to evaporate almost to dryness before the grains were mixed in a warm solution of methylene green in glycerine jelly and then covered with a coverslip. As the grains expanded fully before the jelly set, their furrow configuration was immediately obvious.

Pollen from both fresh and dried flowers was treated in this manner although pollen from the former was the most convenient to handle since the anthers had merely to be tapped on the slide to release the pollen. Anthers from herbarium specimens of less than a year's standing could be similarly treated after their dissection from the flower since the pollen still expanded quite readily in the glycerine jelly. Pollen from older or badly prepared herbarium specimens did not expand so readily, so the technique was slightly altered. The flowers were dissected to expose the anthers and then left overnight in an humid atmosphere to allow the grains to swell before the staining and mounting. Such material gave slightly inferior preparations but there was usually little difficulty in identifying the different pollen types.

The pollen assemblage of each plant was assessed by counting the different grain types on the slide. Both fully developed and aborted grains were counted over the entire field under the coverslip to avoid possible bias due to the differential movement between the larger, fully-developed grains and the smaller, aborted ones through the warm glycerine jelly on mounting. This usually entailed the counting of 300–1,200 grains.

(b) Observations

The counts for all plants of the populations studied are summarized in Table 2 and Fig. 4, which give the frequencies of the different pollen grains as mean percentages for the population. More detailed data for the individual slides are available in Pettet (1960).

These counts showed that the taxa represented by these populations could be divided into two groups according to the most abundant grain type and the less frequent types associated with it:

- (i) *V. lutea*, *V. curtisii* and *V. tricolor*: mostly 4-colpate grains, with some 5- and a few 3-colpate grains.

Although 6-colpate grains normally did not occur in this group, a few examples were found in several plants from L50 (*V. lutea*) and TC68 (*V. curtisii*). In all cases their frequencies were very low, being of the order of 1 per 200–300 grains, and their appearances were of abnormal or unreduced pollen. They were larger than normal grains and had thickened exines and often poorly developed colpae. Two exceptional assemblages were also found. One plant in L50 had 71% of its assemblage composed of 5-colpate grains (cf. second group below), whilst another plant of L58 (*V. lutea*) had a greater proportion of 3-colpate grains than of 4-colpate ones.

TABLE 2. Pollen Assemblages of various populations

	Reference number of population	Number of Individuals	Mean percentage frequency of pollen grain types				Pollen abortion		Micrograins	
			3-colpate	4-colpate	5-colpate	6-colpate	Mean percentage	Range in percentages	Mean percentage	Range in percentages
<i>lutea</i>	L50	22	2.55	89.85	7.55	0.04	7.7	1.9-27.7	0.6	0.0-1.9
	L58	10	7.64	90.53	1.84	—	26.6	7.8-49.9	1.9	0.0-12.6
<i>curtisii</i>	TC44	22	0.43	82.77	16.74	0.06	34.8	4.9-65.5	0.5	0.0-1.7
	TC67	15	3.68	89.49	6.83	—	17.4	5.9-41.4	0.3	0.0-0.9
	TC68	10	0.07	82.58	17.32	0.03	9.1	3.8-14.9	0.4	0.0-0.9
	TC81	2	0.06	97.40	2.54	—	3.1	2.3-3.9	0.7	0.7-0.7
<i>tricolor</i>	T10	18	0.43	90.92	8.65	—	17.7	3.1-47.4	0.4	0.0-1.8
	T14	2	—	81.35	18.65	—	2.8	2.2-3.4	No information	
	T25	23	0.48	91.37	8.15	—	3.3	0.9-20.1	0.2	0.0-0.9
	T80	10	0.13	95.92	3.96	—	18.8	3.8-47.7	0.6	0.0-2.1
<i>arvensis</i>	A2	20	—	11.53	86.41	2.06	8.2	0.0-39.3	0.7	0.0-7.4
	A7(A)	18	—	7.70	91.85	0.35	4.4	0.0-26.5	0.1	0.0-0.3
	A10	10	—	9.87	89.70	0.43	2.3	0.5-5.8	No information	
	A10(A)	4	—	0.07	68.89	31.04	2.2	0.9-3.3	No information	
	A26	7	—	6.02	91.88	2.10	3.8	0.5-16.1	No information	
	A29	10	—	5.93	89.21	4.86	2.1	0.0-5.6	0.3	0.0-1.9
	A33	4	—	3.13	95.81	1.06	1.0	0.4-2.1	0.1	0.0-0.4
	A36	10	—	5.39	94.04	0.57	4.9	0.0-11.8	No information	
	A37	9	—	9.66	89.82	0.52	1.4	0.0-3.4	No information	
	A42	2	—	26.86	72.19	0.95	2.8	2.6-3.0	0.3	0.0-0.5
	A66	9	—	0.77	91.37	7.80	1.9	0.7-4.1	0.2	0.0-0.8
<i>nana</i>	N45	9	—	8.63	87.45	3.92	48.5	32.8-63.1	0.1	0.0-0.8
	N64	12	—	25.21	74.50	0.29	2.3	0.0-5.7	0.1	0.0-0.6
	N65	12	—	13.61	86.04	0.35	3.5	0.0-13.4	0.1	0.0-0.7

- (ii) *V. arvensis* and *V. nana*: mostly 5-colpate grains, with some 4- and 6-colpate grains. Tri-colpate grains were never recorded in this group but the frequency of the 6-colpate grains suggests that the latter correspond to them here. The 4-colpate grains were normally more frequent than the 6-colpate grains except in A10(A) (*V. arvensis*) where the latter were found in consistently higher percentages. A single plant with an exceptional assemblage resembling that of group (i) was recorded in N64 (*V. nana*).

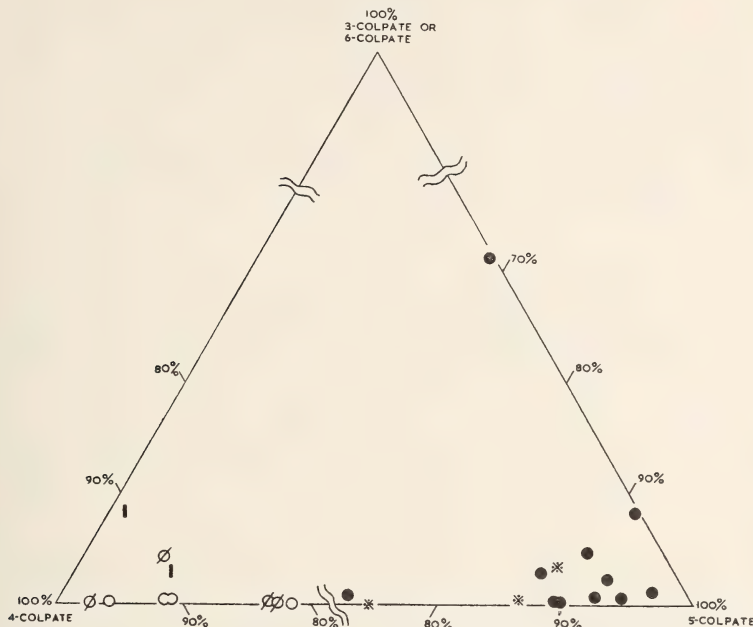


Fig. 4. Scatter diagram of mean percentage frequencies of grain types for populations listed in Table 2
 I = *V. lutea*; Ø = *V. curtisii*; O = *V. tricolor*; ● = *V. arvensis*; * = *V. nana*.

The scatter-diagram of mean frequencies of pollen types for each population (Fig. 4) shows the distinctness of these two groups. Within the left-hand group the assemblages of *V. curtisii* and *V. tricolor* are very similar and not readily distinguishable; *V. lutea* may differ from both by having a slightly higher frequency of 3-colpate grains with a corresponding reduction of 5-colpate grains but the data are too few to be certain. Within the right-hand group *V. arvensis* and *V. nana* are basically similar although *V. nana* may have a tendency towards a lower frequency of 5-colpate grains than *V. arvensis*, but the latter is rather widely-ranging in this respect.

Although within any one population the assemblages were relatively uniform in composition, differences from plant to plant did occur, but, with the exception of those already mentioned, these were not sufficient to cut across the limits of the groups defined above. It may be supposed that this variation was controlled partly by genetic differences and partly by environmental differences between individual plants. That this was not the whole explanation was shown by some chance counts on a series of duplicate slides. These are given in Table 3 and represent counts of slides made from different flowers of the same plant collected at the same time. The differences between duplicates in the ratio of 'most frequent grain type' to 'rest of assemblage' were mostly significant when tested statistically. This means that the differences were unlikely to have been the outcome of random sampling and suggests, perhaps, the conditions experienced by flowers on different branches of the same plant were sometimes sufficient to cause the small anomalies. It is, of course, unlikely that

TABLE 3. Variation in pollen assemblages of duplicate slides

Plant Number	Date	Slide	Total grains scored	Percentage frequency of pollen grain types				Significance level
				3-colpate	4-colpate	5-colpate	6-colpate	
T10/T4	Sept. 1956	a b	763 742	0.13 0.14	89.38 92.72	10.49 7.14	— —	} Significantly different P < 0.05 > 0.01
T14/2	Oct. 1956	a b	193 374	— —	70.98 70.32	29.02 29.68	— —	} Not significantly different
A12/2	Sept. 1956	a b	929 372	— —	10.44 13.44	89.45 86.56	0.11 —	} Not significantly different
A12/12	Sept. 1956	a b	451 329	— —	16.19 12.77	83.81 86.93	— 0.30	} Not significantly different
A13/4	Sept. 1956	a b	875 389	— —	15.43 31.36	84.59 68.64	— —	} Significantly different P < 0.001
A13/8	Sept. 1956	a b	425 621	— —	10.82 5.47	88.47 93.08	0.71 1.45	} Significantly different P < 0.01 > 0.001
A29	Oct. 1956	a b	624 293	— —	0.96 —	95.51 99.66	3.53 0.34	} Significantly different P < 0.01 > 0.001
A33	Sept. 1957	a b	589 410	— —	15.28 7.23	84.72 92.77	— —	} Significantly different P < 0.001

differences between flowers such as these would ever cause the assemblage of *V. arvensis* to resemble that of *V. tricolor*, or vice versa.

Data on the incidence of aborted grains and micrograins are also summarized in Table 2. Aborted grains were easily distinguishable from normal ones. They were smaller, contained little or no cytoplasm and in consequence lacked the granular appearance of the normal grains; the furrow configuration was present but usually inconspicuous because of their shrunken state; with methylene blue and eosin they usually stained a blue-green in contrast to the purple colour of the normal grains. Micrograins were somewhat similar to the aborted grains but different in that they were much smaller, lacked furrows, had very thin walls and consequently stained very lightly.

Whereas the aborted grains were merely pollen grains which had failed to develop completely and mature, the micrograins frequently owed their origin to the aggregation of cytoplasm around lagging and disorientated chromosomes or chromosome fragments. Since, then, micrograins are not strictly pollen grains they were not included in the total grain count for the calculation of percentage pollen abortion. Their incidence was expressed, however, as a percentage of the total grain count to indicate very roughly the incidence of chromosomal abnormalities during pollen formation.

A perusal of the data given in Table 2 will show that there was a tendency for the mean frequency of pollen abortion to be higher in the predominantly outbreeding taxa, *V. lutea*, *V. curtisii* and *V. tricolor*, than in the predominantly inbreeding taxa, *V. arvensis* and *V. nana*. This is probably a reflection of the greater heterozygosity for chromosomal interchanges in the former. (The anomalous high values of N45 were probably caused by the very heavy aphid infestation of the plants prior to pollen collection.) In contrast, the mean incidence of micrograins is more or less uniformly low throughout the range of populations where information is available.

4. DISCUSSION

A comparison of the chromosome counts with the type of pollen assemblage for the different taxa shows a certain agreement between the two sets of data.

It should be noted that the two very variable and often confused species, *V. tricolor* and *V. arvensis*, are readily separable on the basis of both these characters. In fact, the close association between the two characters means that a determination of the pollen assemblage would be sufficient to place any doubtful specimen into one of the two species. Details of this character are now to be found in the second edition of Clapham, Tutin & Warburg's *Flora* (Warburg 1962). This should be of particular use with herbarium specimens where identification is often difficult because of poor preservation or undue fading of the flowers, and where counting of chromosomes cannot be contemplated.

In the case of the closely related taxa, *V. tricolor* and *V. curtisii*, neither the chromosome numbers nor the pollen assemblages offer grounds for their separation into two distinct species. This is contrary to the statement of Mullenders & Mullenders (1957) who maintained they were separate species largely on the basis of pollen assemblages. In the light of this present work it seems that, although the Mullenders emphasized their plants to be *V. tricolor* subsp. *tricolor*, they were in fact dealing with *V. arvensis* or something closely related to it. This is supported by the ecological details given by them which indicate that most of the plants were growing in calcareous soils. In Britain and Scandinavia at least, *V. tricolor* subsp. *tricolor* is confined to soils ranging from acid to neutral, whereas *V. arvensis* is characteristically found on calcareous soils (cf. Ferdinandsen 1918, Clausen 1922). Study of the AT-intermediates to be discussed in detail in another paper also indicates how this confusion probably arose.

The figures given in Erdtman (1952) showing that *V. arvensis* has 4-colpate with a few 5-colpate grains must also be based on a similar confusion over specific limits since this type of assemblage is found in *V. tricolor* and not *V. arvensis*. There is little reason for believing that Scandinavian plants of the latter species are any different from British examples in this respect, especially since Wittrock's original diagnoses of pansies using this character

refer in particular to Scandinavian plants, and they are in complete accordance with the present findings.

Finally, in addition to recommending the use of pollen assemblages for decisions on critical plants of *V. tricolor* and *V. arvensis*, the uncertain value of a high level of pollen abortion as a criterion for putative hybridity should also be emphasized. Clausen (1931) has already shown most interspecific hybrids to be relatively fertile, and very few to be completely sterile, whilst the data given above show that a certain amount of pollen abortion could be expected in at least some examples of the outbreeders, *V. tricolor*, *V. curtisii* and *V. lutea*, without the complications of interspecific hybridization.

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STUDIES ON BRITISH PANSIES

II. THE STATUS OF SOME INTERMEDIATES BETWEEN *VIOLA TRICOLOR* L. AND *V. ARVENSIS* MURR.

By A. PETTET

*Department of Botany, University of Southampton**

ABSTRACT

Plants morphologically intermediate between *Viola tricolor* L. and *V. arvensis* Murr. have, in the past, been interpreted either as hybrids between the two species or as 'stabilized' hybrid segregates. Several recent gatherings of such intermediates (AT-intermediates) and putative hybrids have been studied and compared with experimentally produced F_1 and F_2 hybrids.

Observations on the morphology and cytology of the experimentally produced hybrids largely confirm previous accounts. Pollen assemblages, not previously examined in any detail, were shown to be variable in both generations, ranging in character from that of *V. tricolor* to that of *V. arvensis*. Percentage pollen abortion was generally below 40% with a mean value of 22.8% for the F_1 and 24.4% for F_2 . The incidence of micro-grains was usually greater than 2% with the mean value dropping from 7.4% in the F_1 to 3.9% in the F_2 .

One gathering of intermediates from a mixed population of *V. tricolor* and *V. arvensis* was shown to be indistinguishable from experimentally produced hybrids. AT-intermediates from populations composed otherwise of *V. arvensis* or entirely of the intermediate form were shown to be indistinguishable from *V. arvensis* on the basis of chromosome number and pollen morphology.

Observations on successive generations of AT-intermediates grown in an experimental garden showed the original gatherings were composed of two general elements, (i) plants losing their intermediate features and becoming indistinguishable from the small-flowered *V. arvensis*, and, (ii) plants retaining their characteristics which were presumably genetically controlled.

The first group simulate AT-intermediates through phenotypic plasticity. It is suggested that the second group represent either the original outbreeding forms of *V. arvensis* or intermediate stages in the development of the inbreeding régime typical of *V. arvensis*, rather than 'stabilized' hybrid segregates. In consequence of this it seems advisable to widen the circumscription of *V. arvensis* to include these extreme morphological forms.

1. INTRODUCTION

During a study of the cytology and pollen morphology of some British pansies (Pettet 1964) it was found convenient to divide the *Viola tricolor*-*V. arvensis* complex of annual pansies into three main groups, viz. (i) *V. tricolor*, (ii) *V. arvensis*, and (iii) intermediates between these, designated 'AT-intermediates'. The last-mentioned had cream, or predominantly cream flowers, the upper petals longer than the upper sepals (petals usually $1\frac{1}{4}$ - $1\frac{1}{2}$ $\times$ the length of the sepals) and stilar flap intermediate in development between those of *V. tricolor* and *V. arvensis*. In brief, the AT-intermediates had flowers resembling those of *V. tricolor*, except that they were cream-coloured, had a smaller stilar flap and a somewhat reduced ratio of upper petal to upper sepal. As was previously stated, the AT-intermediates so defined should not be considered a distinct entity—only one of convenience encompassing those plants not readily ascribed to either *V. tricolor* or *V. arvensis*. Some individuals can be equated with the cream-flowered species or varieties of Drabble's *Tricolores* (Drabble 1909, 1927a), e.g. *V. contempta* Jord., *V. variata* Jord. var. *sulphurea* Drabble, but others are not so readily identified with these microspecies. Wittrock (1897), Kristofferson (1923) and Clausen (1922, 1926) have reported similar plants from a number of different places on the Continent and a study of specimens in the herbaria of Kew and

* Now at Department of Botany, University of Khartoum.

the British Museum (Nat. Hist.) has shown that AT-intermediates occur not infrequently in Britain.

Clausen (1922, 1926) examined a number of intermediates occurring in mixed populations of *V. tricolor* and *V. arvensis* and showed them to be hybrids on cytological evidence and on comparison with experimentally produced hybrids. Others occurring without either parent were found to be cytologically regular and these Clausen suggested were 'stabilized' hybrid segregates of long standing. By way of confirmation for this conclusion Clausen showed how, after a few generations, some segregates of intermediate morphology derived from the interspecific cross *V. tricolor* $\times$ *V. arvensis* were morphologically and cytologically relatively constant and possessed chromosome numbers either similar to the *V. tricolor* parent or higher than the *V. arvensis* parent (Clausen, 1924). The report of aberrant chromosome numbers for two cream-flowered *Tricolores* pansies by Fothergill (1944), viz. *V. variata* var. *sulphurea* with $2n = 26$ and $2n = 28$, *V. contempta* with $2n = 40$, might suggest that stabilized hybrid segregates as visualized by Clausen do actually occur in Britain. It should be noted, however, that morphologically similar plants with large cream flowers have been derived from an intraspecific cross between two lines of *V. arvensis* (Clausen 1931) and these had a lower chromosome number ($2n = 32$) than the parent lines with $2n = 34$ as a result of the loss of a pair of chromosomes during meiosis of the initial hybrid.

Evidence for Clausen's conclusion that AT-intermediates represent segregates from past hybridizations is thus strong and this view is reflected in certain of the more recent treatments of the complex, e.g. some of the cream-flowered members of Drabble's group, the *Tricolores*, are quoted as synonyms for the interspecific cross *V. tricolor* $\times$ *V. arvensis* in the *List of British Vascular Plants* (Dandy 1958).

During work on British pansies a number of gatherings of putative hybrids and AT-intermediates was made and a critical comparison of these with a number of experimentally produced hybrids between *V. tricolor* and *V. arvensis* carried out. In view of the light that this comparison has thrown on the nature of the variation in the *V. tricolor*-*V. arvensis* complex and the reported importance of interspecific hybridization to this problem, the results of this aspect of the work form the body of this paper. Clausen has already described experimentally produced hybrids but, to facilitate appropriate comparisons, a summary of the main features of the experimental hybrids used in this study has also been included. Those points not pursued in any detail by Clausen have been elaborated but for all features of the experimentally produced hybrids fuller details may be found in Pettet (1960).

2. EXPERIMENTALLY PRODUCED HYBRIDS

Cross-pollination of flowers of *V. arvensis* and *V. tricolor* was easily effected with a sterilized needle about 4-5 days after emasculation of the flowers, and plenty of viable seed normally obtained. In hot and dry weather the emasculated flowers were slipped into a piece of cellophane drinking-straw, sealed at one end to avoid losses from the drying-out of the flowers. When the fertilized capsules started swelling the straws were replaced by small muslin bags to collect the seed and prevent the violent discharge of the capsule.

The F_2 generation of the cross was obtained simply by selfing the F_1 hybrids.

(a) Morphological features

Of those features used to separate *V. tricolor* from *V. arvensis*, floral characters appeared to be most useful in distinguishing F_1 and F_2 hybrids from the parental species and these are summarized in Table 1. Leaf and stipule characters were generally of little value because of their variation in both parent species, especially in *V. arvensis*. Occasionally stipule characters were of value in distinguishing F_1 hybrids from the two parental species. Where the *tricolor* parent had a narrow, non-leafy stipule mid-lobe and the *arvensis* parent had a wide, leafy stipule mid-lobe, it was possible to recognize the intermediate type of stipule

mid-lobe in the hybrid. Usually, however, the stipule characters were rarely as clear cut as this and thus of limited value.

The floral characters of the F_1 have been found useful in distinguishing the hybrid from the parental species in the field. The slow change in flower colour some time after the flowers have opened—1–2 days or more if the weather is hot—is particularly striking once recognized. There is, of course, a similar colour change in the flowers of *V. tricolor* but it is much faster and the changes occur as the flower unrolls.

TABLE 1. Floral characters of the F_1 and F_2 generations of the cross *V. tricolor* $\times$ *V. arvensis*.

Character	F_1 generation	F_2 generation
Vertical length of flower	13–20 mm, mostly c. 15 mm	(5–) 7–8–9 (–13) mm
Flower colour:		
(i) Young flowers	All petals cream	All petals white, or whitish suffused with very pale blue, or occasionally pale cream
(ii) Old flowers	Upper petals blue but lacking deep blue or blue-purple typical of <i>V. tricolor</i> ; lateral petals cream, suffused with pale blue, or occasionally all cream; lower petals all cream, or cream edged with pale blue	Usually all petals bluish, sometimes deep blue; or upper petals pale blue, lateral petals whitish or very pale cream, lower petals very pale cream
Length of upper petal:		
Length of upper sepal	(1–) $1\frac{1}{4}$ – $1\frac{1}{2}$ (–1): $1\frac{3}{4}$	($\frac{1}{2}$ –) $\frac{3}{4}$ – $1\frac{1}{2}$: 1
Length of spur:		
Length of sepaline appendages	(1–) $1\frac{1}{4}$ – $1\frac{1}{2}$: 1	$1\frac{1}{4}$ – $1\frac{3}{4}$ (– $2\frac{1}{2}$): 1
Development of stylar flap	Intermediate between those of parent species	Variable, mostly intermediate but some almost as large as that of <i>V. tricolor</i> and other reduced

Because of the variability to be seen in the F_2 generation it might not be possible to identify every example as belonging to this generation on purely morphological features unless the parents were accompanied by both filial generations. The general impression was that of small, pale, *tricolor*-like flowers on rather poorly developed plants. Amongst the families grown, however, one feature was noticed which may occur generally throughout the generation and thus be an aid in distinguishing the F_2 in the field. In contrast with the F_1 and parental plants where the upper petals were ovate-oblong and were held more or less vertically and overlapped to varying degrees, the flowers of the F_2 had the upper petals narrowly oblong and widely aligned at angles up to approximately 45° from the vertical. This produced a different aspect to the flower and one which should be fairly easy to observe in the field.

(b) Pollen assemblages

The method of preparation and examination of pollen has previously been described in detail (Pettet 1964).

In contrast with the parental species the pollen assemblages of both filial generations of hybrids showed a great variability in the development of the grains. Although the number of colpae was normally obvious, it was possible to find a gradation from the relatively 'perfect' grains to the fully aborted ones, with grains in the intermediate stages showing various degrees of deeper staining and lesser expansion. This gradation in development was also reflected in the marked variability of grain size. In addition, it was occasionally possible to find grains clearly abnormal in their development, e.g. grains fused together by a common part of the exine or grains with large numbers of poorly developed colpae.

TABLE 2. Pollen assemblages and incidences of pollen abortion and micro-grains of F₁ Hybrids

Parents of Cross ♀ ♂	Plant no.	Slide no.	Number of grains scored	Percentage frequency of pollen-grain types				Number of grains counted	Percentage of aborted pollen	Percentage of micro-grains
				3-colpate	4-colpate	5-colpate	6-colpate			
T10 × A10	1	i	196	—	18.88	80.10	1.02	577	64.65	12.99
		ii	321	—	7.16	81.93	10.90	553	37.98	7.96
		iii	264	—	6.06	84.09	9.85	418	33.01	2.87
		iv	290	—	15.17	81.72	3.10	418	27.99	3.11
		v	295	—	4.41	91.53	4.07	440	31.36	3.86
T10 × A10	2	i	304	—	67.43	32.57	—	338	10.06	2.66
		ii	844	—	58.06	41.94	—	943	10.07	2.23
		iii	842	—	69.72	30.28	—	940	9.47	3.09
		iv	432	—	49.31	50.69	—	504	13.09	1.59
		v	691	—	76.84	23.16	—	771	7.52	2.08
		vi	479	—	66.81	33.19	—	591	16.24	2.03
		vii	602	—	55.98	44.02	—	692	11.85	2.46
		i	191	—	41.36	58.64	—	393	50.64	4.83
		4	430	—	50.70	49.07	0.23	568	23.06	4.05
		5	352	—	17.61	80.49	1.42	485	26.80	4.12
T10 × A12	1	i	912	—	87.06	12.94	—	1,132	17.67	8.92
		ii	647	—	88.25	11.75	—	761	14.45	8.41
		i	553	0.36	89.15	10.49	—	593	30.01	14.33
		2	433	1.62	96.99	1.39	—	487	10.06	13.76
		i	632	—	59.18	40.66	0.16	699	8.58	9.73
		i	653	—	74.96	25.04	—	660	13.03	6.36
A33 × T10	1									
A33 × T10	2									
A36 × T10	1									
A42 × T10	1									

(i) *F*₁ generation

The pollen assemblages and incidences of pollen abortion and micro-grains of the various *F*₁ hybrids are given in Table 2. These show an unexpected and wide variability in contrast to the relative uniformity of the gross morphological features of the *F*₁ hybrids. Some plants have assemblages indistinguishable from those of *V. tricolor* (cf. Pettet 1964), e.g. crosses involving A12, A33 and A42; others have assemblages resembling those of *V. arvensis*, e.g. crosses involving A10 (Nos. 1 and 5); and yet a few have 4-colpate and 5-colpate grains in approximately similar proportions as Clausen (1922) supposed hybrids to have, e.g. crosses involving A36 and A10 (Nos. 2, 3 and 4).

TABLE 3. Direction of cross and type of pollen assemblage.

Pollen-contributing parent	Predominantly 'tricolor' assemblage	Intermediate assemblage	Predominantly 'arvensis' assemblage
<i>tricolor</i>	3	1	—
<i>arvensis</i>	1	3	2

It can be seen from Table 3 that the direction of the cross seems to control the pollen assemblages of the progeny. Where the pollen-contributing parent was *V. tricolor* the assemblages of the *F*₁ tend to resemble a *tricolor* assemblage; similarly, when *V. arvensis* was the pollen-contributing parent, there was a tendency, although less marked, for the *F*₁ assemblage to resemble an *arvensis* assemblage. Unfortunately the number of plants involved was too small to allow a more definite conclusion.

The percentage abortion was generally low. Except for two high values, viz. 64.65% and 50.64%, all the values were below 40% with the majority below 30%. These values are similar to those already recorded for certain populations of *V. tricolor*. The incidence of micro-grains, on the other hand, was higher than found for either parent species, where it was usually less than 1%.

(ii) *F*₂ generation

The pollen assemblages and incidences of pollen abortion and micro-grains of the two experimentally produced families of the *F*₂ generation are given in Table 4. In many respects these assemblages were similar to those of the *F*₁ hybrids, ranging in character from those resembling *V. tricolor* to those resembling *V. arvensis*, but they differed from the *F*₁ in the tendency for the majority of the assemblages to cluster about the intermediate state. From Tables 4 and 5 it may be seen that the percentage abortion in the *F*₂ was similar to that in *F*₁, but that the incidence of micro-grains in the *F*₂ was decidedly lower.

As a character for distinguishing hybrids from their parent species pollen assemblages need to be used with caution; not all assemblages will be intermediate in character and some will resemble *V. tricolor* or *V. arvensis* to a greater or lesser extent. However, a combination of a moderate degree of pollen abortion (frequency greater than 10%) and an unusually high incidence of micro-grains (frequency greater than 1% of the total grain assemblage) would seem sufficient to identify at least the majority of *F*₁ and *F*₂ hybrids whose assemblages of functional pollen resembled one or other of the parent species. Irregular size and development of the grains, with the presence of the occasional abnormal grain, would provide further confirmation of hybridity, although the former features may not be easy to determine in pollen from old herbarium material where expansion and staining of the grains is not always uniform.

TABLE 4. Pollen assemblages and incidences of pollen abortion and micro-grains of F₂ hybrids

Parent hybrid	Plant no.	Slide no.	Number of grains scored	Percentage frequency of pollen-grain types				Number of grains counted	Percentage of aborted grains	Percentage of micro-grains
				3-colpate	4-colpate	5-colpate	6-colpate			
T10 × A10/1	1	i	150	—	59.33	40.00	0.67	334	43.11	7.49
		ii	114	—	70.18	29.82	—	223	26.91	3.14
		iii	133	—	50.38	49.62	—	338	39.94	4.73
		iv	235	—	60.00	39.57	0.43	412	31.55	3.16
	2	i	92	—	34.78	65.22	—	336	54.46	0.60
		ii	78	—	57.69	42.31	—	351	56.69	2.56
	3	i	271	—	82.29	17.71	—	271	8.63	4.06
		ii	266	—	77.44	22.56	—	266	8.39	3.76
	4	i	85	—	10.59	89.41	—	301	68.44	6.98
	5	i	216	0.93	50.00	48.61	0.46	282	12.06	3.90
	6	i	258	—	43.02	56.59	0.39	407	26.04	8.60
T10 × A10/2	7	i	249	—	57.43	42.57	—	290	16.38	1.38
	8	i	239	—	61.92	38.07	—	323	20.74	0.93
	9	i	457	—	39.17	60.61	0.22	714	18.77	0.98
	10	i	241	—	17.84	81.33	0.83	444	14.98	4.25
	11	i	376	—	41.75	57.98	0.27	669	15.25	2.54
	1	i	529	—	33.46	66.54	—	640	14.84	3.59
	2	i	491	—	49.69	50.31	—	558	10.57	1.08
	3	i	661	—	45.54	54.46	—	747	10.84	0.80
	4	i	93	—	4.30	73.12	22.58	332	42.77	14.76
	5	i	454	—	39.21	60.57	0.22	600	19.50	2.50

(c) Cytology

The fixation of young flower buds and the staining of the pollen mother cells (PMC) have been described in a previous paper (Pettet 1964).

Chromosomes in the PMCs of the hybrids were sometimes difficult to stain satisfactorily so that not all the available material could be studied in detail. Sufficient buds stained well enough, however, to give a representative sample of the available experimental hybrids.

TABLE 5. Changes in the mean incidence of pollen abortion and micro-grains in F_1 and F_2 .

	Mean Values	
	F_1 (N = 10)	F_2 (N = 16)
Percentage pollen abortion	22.84	24.42
Percentage micro-grains	7.43	3.90

(i) Meiosis in the F_1 generation

Although chromosome pairing at first metaphase of meiosis was variable no multivalents were observed in the F_1 hybrids. Most frequently 13 or 14 bivalents were formed with 4 or 2 univalents left unpaired respectively; less frequently 12 bivalents associated with six univalents were observed when pairing was less complete, or 15 bivalents and no univalents when pairing was complete.

Subsequent behaviour of the bivalents during anaphase and telophase was usually normal with regular segregation to the poles. At times, however, one to several bivalents could be seen lagging in the equatorial region (Fig. 1) and, since disorientated bivalents were often found in the peripheral cytoplasm during the later phase of meiosis, it would

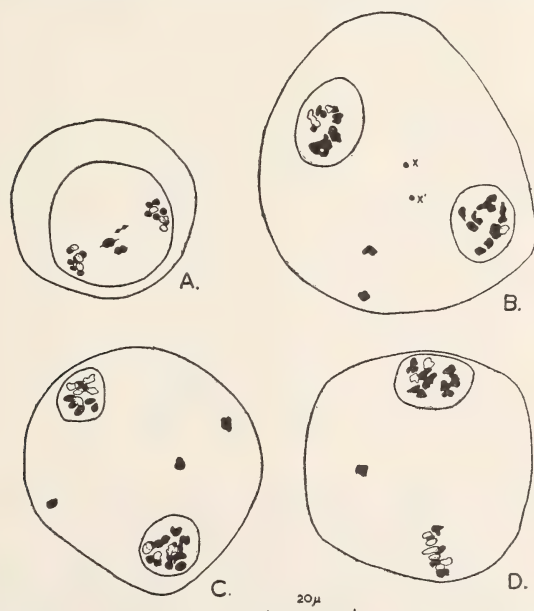


Fig. 1. PMC meiosis in F_1 generation of *V. tricolor* $\times$ *arvensis*. (a) A30 $\times$ T10. Late stage of first anaphase with two lagging bivalents and a dividing univalent. (b) A33 $\times$ T10. Interkinesis with two bivalents and a divided univalent (X and X') which lagged during first division of meiosis. (c) A33 $\times$ T10. Interkinesis with three bivalents lying free in the cytoplasm. (d) A33 $\times$ T10. Nonsynchronization of divisions within the same PMC. Interkinesis and early second metaphase with a bivalent lying free in the cytoplasm from the first division of meiosis.

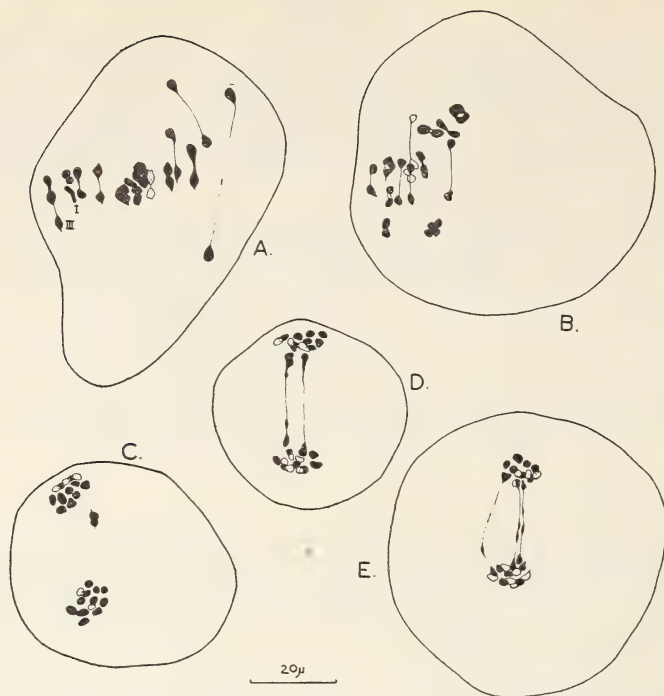


Fig. 2. PMC meiosis in F_2 generation of *V. tricolor* $\times$ *arvensis*. (a) $2n = 28$. First metaphase. Twelve bivalents, one trivalent and one univalent. (b) $2n = 28$. First metaphase. Complete pairing with the formation of 14 bivalents. (c) $2n = 28$. Late stages of first anaphase. One lagging bivalent. (d) $2n = 27$. Late stage of first anaphase. Two chromatid bridges with 13 chromosomes at upper pole and 14 at lower pole. (e) $2n = 28$. Late stage of first anaphase. Three chromatid bridges.

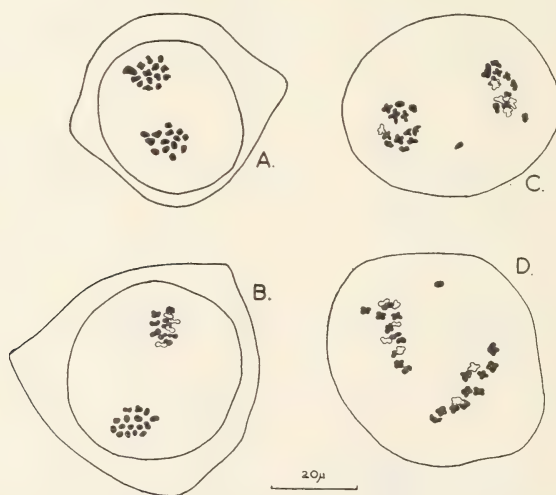


Fig. 3. PMC meiosis in F_2 generation of *V. tricolor* $\times$ *arvensis*. (a) $2n = 28$. Second metaphase. Equal segregation of chromosomes in first division with 14 chromosomes going to each pole. (b) $2n = 29$. Second metaphase. Unequal segregation of chromosomes during first division with 13 in the upper complement and 16 in the lower complement. (c) $2n = 28$. Second prometaphase. Univalent from first division lying disorientated in cytoplasm. Fourteen chromosomes in right-hand complement, 13 in left-hand complement. (d) $2n = 28$. Beginning of second metaphase. Unequal segregation of chromosomes during first division with 15 in left-hand complement and 12 in right-hand complement. Disorientated univalent from first division lying in cytoplasm.

appear that these lagging bivalents often failed to separate completely and were lost to the following phases of meiosis.

The behaviour of the unpaired univalents varied. Most frequently they remained disorientated in the cytoplasm and were to be observed as somewhat ill-defined chromosomes lying apart from the general cluster of chromosomes. Occasionally unpaired univalents became orientated on the metaphase plate and moved to one or other of the poles, subsequently to participate in the second division of meiosis. Very rarely univalents reorientated on the metaphase plate and divided precociously to give two very small chromosomes which, in the few cells in which they were observed, may have moved to the poles to become included in the subsequent divisions of meiosis. The situation shown in Fig. 1 suggests, however, that the division of the univalents sometimes occurred too late for the products to reach the poles before telophase and interkinesis.

Exclusion of disorientated and lagging univalents and bivalents from the main chromosome mass during meiosis would, of course, lead to a reduction in the chromosome numbers of the developing tetrads. Provided this produced no markedly deleterious effect on their development this would lead to the formation of pollen grains with chromosome numbers lower than the haploid number of the parent, and eventually with numbers resembling that of *V. tricolor*. Very occasionally irregular segregation of chromosomes during anaphase produced complements containing numbers higher than the haploid number of the parental hybrid and, no doubt, these would give rise to pollen grains with increased chromosome numbers. The infrequency of such events, however, makes it unlikely that they materially affected the general trend towards a decrease in number and possibly a stabilization at $n = 13$ as observed by Clausen (1922, 1926).

(ii) Meiosis in the F_2 generation

The loss of chromosomes during meiosis in the F_1 hybrids was reflected in the chromosome numbers observed in the F_2 generation. Most plants had $2n = 28$, but plants with $2n = 27$ and $2n = 29$ were occasionally found (Figs. 2 and 3).

In contrast with the F_1 hybrid, chromosome pairing during meiosis (plants with $2n = 28$) was most frequently regular and complete. Multivalents were not observed except for a single example of a trivalent observed in one PMC of a plant with $2n = 28$ (Fig. 2). This regularity of chromosome pairing suggests that chromosome loss and segregation in both PMCs and megaspore mother cells (MMCs) of the F_1 had not been completely haphazard and that homologous chromosomes were rarely included in the same complement.

At times, however, chromosome pairing and segregation were not completely regular. As in the F_1 , two or more chromosomes sometimes failed to pair, or bivalents remained disorientated during first metaphase and later passed into the peripheral cytoplasm. These malfunctioning chromosomes, and possibly the extra univalents observed in the odd numbered plants, might well have represented the extra *arvensis* chromosomes which paired autosyndetically and segregated regularly in the F_1 .

Even though chromosome segregation proceeded with greater regularity in the F_2 , counts made at second metaphase showed that unequal chromosome segregation still occurred from time to time.

One noticeable difference between meiosis in the F_1 and F_2 deserves mention. During first and second anaphases in the F_1 chromatid bridges were rare, whereas in the F_2 they were more frequent and sometimes even numerous. The reasons for this difference are not immediately obvious although several possibilities exist. Perhaps the most likely explanation is that both F_1 and F_2 were heterozygous for a similar number of chromosomal interchanges but more frequent chiasmata formation in the F_2 made them more readily detectable in that generation.

3. PUTATIVE HYBRIDS AND AT-INTERMEDIATES

Details of the location and numbers of putative hybrids and AT-intermediates which were available for study are given in Table 6. Most were found singly or in relatively small

numbers in populations otherwise composed solely of plants typical of *V. arvensis*, although two collections came from populations composed entirely of AT-intermediates and one from a mixed population of *V. tricolor* and *V. arvensis*. Mixed populations have been recorded from time to time in the past but only the one example (Table 6) was found in the 3 years' fieldwork (1956–59) of the present study. The presence of these AT-intermediates in such a population suggested hybridization had taken place under field conditions.

TABLE 6. Putative hybrids and AT-intermediates available for study.

<i>Plant No.</i>	<i>Locality</i>	<i>Habitat</i>	<i>Frequency</i>
T10/A10	Nr. Aberystwyth, Cards.	Derelict field	Slightly under 1% of population composed of both <i>V. tricolor</i> and <i>V. arvensis</i>
A2/24	Southampton, Hants	Disturbed gravel	Single plant with 23 others which were typical of <i>V. arvensis</i>
A5/6	Southampton, Hants	Corporation Rubbish Tip	Single plant with 8 others which were typical of <i>V. arvensis</i>
A12/1	Durham, Co. Durham	Allotments	Single plant with 19 others which were typical of <i>V. arvensis</i>
A30	Ruislip, Middlesex	Barley field	Whole population of this form
A36/11, 12	Nr. Hursley, S. Hants	Barley field on chalk	Two plants in a very large population of plants typical of <i>V. arvensis</i>
A37/10	Hursley, S. Hants	Barley field on chalk	Single plants in very large population of plants typical of <i>V. arvensis</i>
A38i	Rockland, Norfolk	Barley field	Single plant in very large population of plants typical of <i>V. arvensis</i>
A41	Black Isle, Cromarty, Scotland	Root-crop field	Whole population of this form

(a) *Putative hybrids in mixed population of V. tricolor and V. arvensis*

A number of the putative hybrids were removed from the population to the garden at Southampton but only three plants survived the transfer. These were morphologically indistinguishable from F_1 hybrids subsequently produced from the two supposed parent species of the same population. All three plants were found to have a chromosome number of $2n = 30$ and a meiotic behaviour closely resembling the F_1 hybrids already described. The pollen assemblages of two plants were intermediate in character between those of *V. tricolor* and *V. arvensis*, while the third plant had an assemblage which more closely resembled that of *V. tricolor*. There is little doubt, then, that these three plants were F_1 hybrids. Since all putative hybrids in this population were relatively uniform there is no evidence to suggest they represented anything other than F_1 hybrids. This was confirmed by a critical examination of the herbarium specimens taken when the population was first studied which failed to reveal any F_2 or backcross hybrids.

(b) *AT-intermediates from unmixed populations*

The more important gross morphological features of the AT-intermediates from unmixed populations are given in Table 7. Although not completely identical with F_1 or F_2 hybrids (Table 1), they resembled them closely enough to raise doubts about their identity. To investigate the possibility that they were hybrids or hybrid-derivatives these plants were removed from the field for further observations and experimental work.

(i) *Observations on phenotypic plasticity and genetic heterozygosity*

A number of observations on phenotypic plasticity and genetic heterozygosity were made whilst growing these plants for experimental purposes and these are summarized in

TABLE 7. Morphological characteristics of AT-intermediates

Plant no.	Stipule shape	Shape of stipule mid-lobe	Flower colour	Vertical length (mm)	Upper petal/ Upper sepal	Spur/sepaline appendage	Stylar flap
A2/24	Pinnate	Lanceolate, leafy and crenately notched	All petals cream	14	1.25-1.5:1	1-25:1	Present but reduced
A5/6	Pinnate	Ovate-lanceolate, leafy and crenately notched	All petals cream	15	1.5:1	1-1.25:1	Present but reduced
A12/1	Palmate-pinnate	Ovate-lanceolate, leafy and crenately notched	All petals cream	17-18	1.75-2:1	1.25-1.5:1	Present, intermediate in size between that of <i>V. tricolor</i> and <i>V. arvensis</i>
AT30	Pinnate	Lanceolate, leafy and crenately notched	Upper petals pale blue; lateral and lower petals cream tinged blue	16-18	1.5-1.75:1	1:1	Intermediate
A36/11, 12	Pinnate	Ovate-lanceolate, leafy and crenately notched	All petals cream	15	1.25-1.5:1	1:1	Present but reduced
A37/10	Pinnate	Ovate-lanceolate, leafy and crenately notched	All petals cream	15	1.25-1.5:1	1.25:1	Present but reduced
A38i	Pinnate	Ovate-lanceolate, leafy and crenately notched	Upper petals deep purple; lateral and lower petals cream	18	1.5-1.75:1	1.5-2:1	Present but very poorly developed
AT41	Palmate-pinnate	Lanceolate, hardly leafy, entire	All petals cream	17-18	1.5-1.75:1	1.25-1.5:1	Present, intermediate in size between that of <i>V. tricolor</i> and <i>V. arvensis</i>

TABLE 8. Summary of observations on phenotypic plasticity and genetic heterozygosity of AT-intermediates (less than 40 plants/generation are indicated in brackets)

<i>Plant no.</i>	<i>Morphological changes after removal to experimental garden</i>	<i>Morphological features of F₁ generation</i>	<i>Morphological features of F₂ generation</i>	<i>Morphological features of F₃ generation</i>
A2/24	Plant did not survive long enough for any changes to be observed	Flowers smaller; resembling those of other members of original population; uniform with no apparent segregation (10 plants)	Flowers as in F ₁ ; $\pm$ typical of original population; uniform	Flowers as in F ₁ and F ₂ ; uniform
A5/6	Flowers initially large but becoming reduced in size by late autumn until resembling those of original population	Flowers small; resembling those of other members of original population; uniform with no apparent segregation	Flowers as in F ₁ ; uniform	—
A12/1	Retained features throughout succeeding winter	Retained features of parent plant except flowers were slightly larger (1 plant)	Retained features of parent plant; uniform (36 plants)	Flowers as in F ₁ and F ₂ ; uniform
AT30	Retained features throughout succeeding winter	Retained features of parent population; uniform	Retained features of parent population; uniform	—
A36/11, 12	Plants did not survive long enough for any changes to be observed	Flowers smaller; indistinguishable from those of other members of original population; uniform with no apparent segregation	Flowers as in F ₁ ; uniform	—
A37/10	Plant did not survive long enough for any changes to be observed	Retained features of parent plant; uniform	Flowers as in F ₁ ; uniform	—
A38i	Plant did not survive long enough for any changes to be observed	Segregation for flower colour and size (see Table 9) (14 plants)	—	—
AT41	Retained features throughout succeeding winter	Retained features of parent population; uniform	Flowers as in F ₁ ; uniform	—

Table 8. From this it is clear that the AT-intermediates do not form a single, coherent entity. They were, in fact, composed of two general elements:

- A. Plants which lost the characteristics of AT-intermediates, becoming indistinguishable from the small-flowered *V. arvensis* with which they were originally growing. The original characters of these plants obviously formed extreme phenotypic expressions of those typical of *V. arvensis*. (A2/24, A5/6, A36/11 and A36/12).
- B. Plants which retained their characteristics $\pm$ unchanged through several generations. These presumably had a genetic basis. Compared with group A, plants of this group had flowers tending to have a somewhat larger upper petal/upper sepal ratio and a better developed stylar flap (cf. Table 7). (A12/1, A30, A37/10 and A41).

Of those AT-intermediates examined only one, A38i, appears to have been heterozygous for flower size and colour, the features of the F_1 being summarized in Table 9.

TABLE 9. Segregation of floral characters in fourteen plants of F_1 of A38i

Number of plants	Colour of upper petals	Upper petal/ Upper sepal	Spur/Sepal appendage	Honey-guide streaks
4	Cream	1.5:1	1.5-2:1	unbranched
2	Cream	1.5:1	1.5-2:1	branched
3	Cream	1-1.25:1	1.5-2:1	unbranched
1	Cream	1.5:1	1.25:1	unbranched
1	Cream	1.5:1	1.25:1	branched
1	Cream	1:1	1.5-2:1	unbranched
1	Cream with large, deep-purple blotch covering c. $\frac{1}{3}$ petal	1.5:1	1.5:1	branched
1	Cream with large, deep purple blotch covering c. $\frac{1}{4}$ petal	1.25:1	1.5:1	unbranched

(ii) Pollen assemblages

With the exceptions of A5/6 and A38i, the pollen assemblages of all plants taken from the field have been examined. In the case of A38i eight plants of the F_1 generation were examined instead.

It will be seen from the counts given in Table 10 that the AT-intermediates had assemblages closely resembling those of *V. arvensis* (cf. Pettet 1964). Penta-colpate grains were most abundant, comprising more than 80% of the total assemblage although in the F_1 of A38i the proportion was slightly lower, Tetra-colpate and 6-colpate grains occurred as subsidiary types, the former being the more frequent. The incidence of pollen abortion was also roughly at the same level as in *V. arvensis* rather than in the experimental hybrids, and the same applies to the incidence of micro-grains where these were counted.

Although no detailed counts for the succeeding generations of these plants were made, a few sample counts showed, with one exception, no striking changes in the relative proportions of grain types. In the case of A12/1 counts showed certain anomalous features and they are listed separately in Table 11.

The counts from the parent plant, A12/1, showed initially an assemblage similar to that of *V. tricolor*, but later one midway between those of *V. tricolor* and *V. arvensis*. Counts from flowers of the single F_1 plant generally confirmed the first count, indicating assemblages similar to those of *V. tricolor*, except for the first slide which had an assemblage midway between those of the two species. This was rather puzzling, and in order to eliminate any variation in the assemblages caused by seasonal differences, the entire sample from the F_2 was collected at the same time.

TABLE 10. Pollen assemblages and incidences of pollen abortion and micro-grains of AT-intermediates (excluding A12/1 and its progeny)

Population no.	Plant no.	Number of grains scored	Percentage frequency of pollen-grain types				Number of grains counted	Percentage of aborted grains	Percentage of micro-grains
			3-colpate	4-colpate	5-colpate	6-colpate			
A2	24	257	—	1.17	98.83	—	263	0.38	0.00
A30	1	94	—	11.70	88.30	—	143	6.10	Not scored
A36	2	407	—	5.41	94.59	—	521	3.26	Not scored
	11	342	—	5.85	93.57	0.58	396	1.26	Not scored
A37	12	362	—	3.31	96.69	—	381	0.52	Not scored
	10	192	—	14.06	85.94	—	221	6.33	Not scored
A41	1	117	—	8.55	91.45	—	277	0.36	Not scored
	2	96	—	11.46	88.54	—	194	0.52	Not scored
	3	285	—	13.68	86.32	—	419	0.00	Not scored
	4	169	—	10.06	89.94	—	376	0.00	Not scored
A38:	1	667	—	28.04	71.66	—	670	0.30	0.29
	2	485	—	26.39	73.40	0.30	492	1.22	0.20
(F ₁ generation)	3	220	—	14.09	85.45	0.46	221	0.45	0.45
	4	576	—	2.43	94.44	3.13	597	0.50	0.84
	5	388	—	22.68	77.32	—	391	0.51	0.00
	6	629	—	10.49	89.35	0.16	632	0.16	0.00
	7	237	—	27.00	72.57	0.42	242	1.24	0.00
	8	484	—	29.13	70.25	0.62	512	5.47	3.13

TABLE 11. Pollen assemblages and incidences of pollen abortion of micro-grains of A12/1 and its progeny

Generation	Plant no.	Slide no.	Number of grains scored	Percentages frequency of pollen-grain type				Number of grains counted	Percentage of aborted grains	Percentage of micro-grains
				3-colpate	4-colpate	5-colpate	6-colpate			
A12/1	1	i	712	—	80.06	19.94	—	744	3.76	0.40
		ii	751	—	49.40	50.60	—	817	7.47	0.00
	1	i	1,025	—	57.95	42.05	—	1,045	1.34	0.00
F ₁		ii	1,395	—	74.45	25.45	—	1,418	0.99	0.14
		iii	1,213	—	72.88	27.12	—	1,221	0.66	0.16
		iv	1,051	—	80.49	19.51	—	1,066	1.41	0.19
F ₂	1	i	665	—	43.76	56.24	—	759	12.12	0.00
	2	i	660	—	29.39	70.61	—	697	3.16	0.14
	3	i	530	—	23.02	76.98	—	579	6.39	0.52
	4	i	198	—	29.80	70.20	—	262	22.90	0.76
	5	i	351	—	22.79	77.21	—	376	6.38	0.27
	6	i	631	—	27.42	72.43	0.16	647	1.55	0.00
	7	i	556	—	26.44	73.56	—	566	1.24	0.00
	8	i	677	—	40.62	59.38	—	688	1.02	0.00
	9	i	574	—	30.31	69.69	—	589	1.36	0.34
	10	i	356	—	51.69	48.31	—	364	1.92	0.00

Counts from most plants of this generation showed assemblages similar to those of *V. arvensis* but plants 1, 8 and 10 had assemblages midway between the two main types. In view of the comparative uniformity in gross morphological features of the various generations of this line and the absence of any similar variation in counts from other plants, except perhaps in those of hybrids, this variation was unexpected. Unlike the hybrids, however, the variation here was not associated with cytological disturbances for, as shown below, chromosome behaviour at meiosis was regular.

It is thus difficult to explain these changes, especially as the genetical basis of pollen polymorphism is not fully understood. The variation in the assemblages recorded for the parent plant from the original population, and the comparative uniformity in the reversed assemblages of the F_2 , suggest the differences here are not primarily controlled by genic segregation. Most of the variation must instead be explicable on the grounds of the plasticity of pollen morphology of this particular line of plants—a unique situation not observed elsewhere.

TABLE 12. Chromosome numbers of AT-intermediates

Population number	Plant no.	Chromosome number	
		n (PMC)	2n (RT)
A2	24	17	34
A5	6	17	—
A12	1	17	—
AT30	1-4	17	—
A36	11	17	34
	12	17	—
A37	10	17	—
A38i	1	17	—
AT41	1-5	17	—

(iii) Cytology

All plants collected from the field were examined cytologically and their chromosome numbers are recorded in Table 12. In every case the number is identical with that of *V. arvensis* and, like the latter, meiosis in all plants was regular with the formation of seventeen bivalents. Only very occasionally were PMCs found with a pair of unorientated univalents in the cytoplasm, or more infrequently still, with chromatid bridges present at first anaphase. However, these were no more frequent than to be observed in most plants of *V. arvensis*.

4. DISCUSSION

From the observations elaborated above it is obvious that not all the AT-intermediates are of recent hybrid origin even though they resemble experimentally produced hybrids between *V. tricolor* and *V. arvensis* in gross morphology. In fact only those plants taken from a mixed population of the two putative parent species were found to be F_1 hybrids. The rest, from populations where at least *V. tricolor* was absent, were of two general sorts, viz. firstly, plants of *V. arvensis* simulating intermediates, and secondly, genetically determined (presumably) AT-intermediates. These two groups are both of interest in the unravelling of the taxonomic problems of the annual pansies, but for different reasons.

The first shows that phenotypic plasticity occurs in populations of *V. arvensis* and may occasionally be sufficient to blur the limits of the species and cause confusion in the naming of plants. Any doubts about such plants, however, should be easily resolved by an examination of the pollen morphology. The second group, on the other hand, raises problems over interpretation and perhaps, incidentally, over the recent evolution of the annual pansies.

On the basis of pollen morphology and cytology—perhaps more reliable indicators

of affinity in this instance than gross floral morphology—the genetically determined AT-intermediates appear most closely allied to *V. arvensis*. This suggests that two possible interpretations of their origin need be considered. Either they arise from past hybridization or there has been confusion over the real limits of *V. arvensis* and they represent extreme variants of this species. Past hybridization may have involved intraspecific or interspecific crosses. The possibility of intraspecific crosses in *V. arvensis* (cf. Clausen 1926), coupled with chromosome instability and loss, being responsible can be eliminated since this would lead to a reduction below $2n = 34$. On the other hand these plants may be 'stabilized' hybrid segregates following interspecific hybridization and subsequent introgression as envisaged by Clausen, but this raises a number of difficulties.

There is no doubt that hybridization between *V. tricolor* and *V. arvensis* does occur for, apart from the F_1 hybrids mentioned here, there are several reports of naturally occurring hybrids by other workers, e.g. Wittrock (1897), Clausen (1922, 1926). The question to be really considered is whether the occurrence of hybridization materially alters the variation patterns of the two species involved. Normally *V. tricolor* and *V. arvensis* do not grow together. Ferdinandsen (1918) and Clausen (1922) have both shown the two species to have their optimal developments on different soil types. *V. tricolor* occurs most frequently on acidic soils, *V. arvensis* on basic soils, with only a slight overlap on neutral to weakly acid soils. This edaphic differentiation was thought by Clausen to be sufficient to prevent hybridization occurring frequently enough to break down entirely the specific limits of the two species.

When the two species hybridize, however, the F_1 is fertile and may produce much seed. Thus it would seem that only a few mixed populations where hybridization occurs would be sufficient to produce a whole range of segregates of intermediate morphology, providing these were not at a marked competitive disadvantage in the population. In the only mixed population seen during the present study F_1 hybrids alone were found. This may have been quite fortuitous as the two species may not have been growing together until the previous year, providing too little time to produce the second generation. However, observations on F_2 and subsequent hybrids grown in the experimental garden showed them to be rather weak and suggest that under field conditions they may be at a distinct disadvantage—an assessment which is borne out by Clausen's observations on similar hybrids.

Even if hybrids can compete successfully in the field introgression will not necessarily occur. The F_1 and F_2 hybrids have been found to be capable of at least some self-pollination and under field conditions it seems likely that they would be largely self-pollinating. Should backcrossing occur it is more likely to be to the *tricolor* parent, which is a fairly well adapted outbreeder, than to the *arvensis* parent which, with its reduced flowers, is virtually always self-pollinating.

As Clausen has already shown, and as has been observed in this study, the chromosome number in successive hybrid generations most frequently reduces from $2n = 30$ of the F_1 towards $2n = 26$ as a result of loss of the extra *arvensis* chromosomes. Yet no AT-intermediates were discovered with these lower numbers. Increase in chromosome number beyond $2n = 34$ through irregular segregation of chromosomes has also been reported by Clausen, and the chromosome number ($2n = 40$) quoted by Fothergill (1944) for *V. contempta* Jord., a yellow-flowered *Tricolores* pansy, could possibly be due to this. However, the increase of chromosome number reported by Clausen was of rare occurrence and was associated with chromosome instability. Consequently it is unlikely to have lasting effects on the variation pattern of these pansies.

The production of plants with a stable chromosome number of $2n = 34$ from hybrid segregates requires repeated backcrossing to the *arvensis* parent but this is unlikely to produce AT-intermediates as described above. It is known (Clausen 1926) that a number of inhibitor genes producing reduction of floral parts are present on the extra chromosomes of *V. arvensis*. It is therefore likely that backcrossing to the typical, small-flowered *V. arvensis* would thus produce a small-flowered *arvensis*-type plant rather than the present AT-intermediates.

The interpretation of the AT-intermediates as extreme variants of a rather variable *V. arvensis*, whose exact limits have been confused in the past, raises fewer difficulties. The basis of the differences between *V. tricolor* L. and *V. arvensis* Murr. rests with Murray's reference (Murray 1770) to Haller's distinction (Haller 1745) between the two taxa:

tricolor: 'flore calyce duplo longiore'

arvensis: 'flore calyce paulo majori'

Somewhat incorrectly this distinction has come to be accepted as *V. tricolor* with 'upper petals longer than upper sepals' and *V. arvensis* 'with upper petals shorter, or as long as, upper sepals' (e.g. Clausen 1922, Drabble 1909, 1926, 1927a, 1927b, Warburg 1952). This general difference between the two taxa is associated with their reproductive behaviour. *V. tricolor* is well adapted to cross-pollination and has large, showy flowers with a well-developed stylar flap, whilst *V. arvensis*, as normally understood, is well-adapted to self-pollination and has reduced petals and a very much reduced stylar flap. The distinguishing features of *V. arvensis* are characteristic of successful exploiters of the ephemeral habitat offered by arable farmland, i.e. short life-cycle, increased flower production and reduced flowers promoting self-pollination (cf. Stebbins 1957). It is reasonable to assume, therefore, that *V. arvensis* (as normally understood) has developed from an outbreeding pansy mainly by selection of mutant genes present on the extra *arvensis* chromosomes which inhibit flower development to varying degrees. In view of the marked genetic similarity of the two species, as reflected in the pairing behaviour of the chromosomes in the F_1 hybrid, the original outbreeding *V. arvensis* also would resemble closely the present-day *V. tricolor*.

Therefore one can consider that the morphologically constant, and presumably genetically determined, AT-intermediates, A12/1, A30, A41 and A37, represent either forms closely allied to the original outbreeding *V. arvensis* from which the small-flowered inbreeding *V. arvensis* was developed, or represent the remnants of an intermediate stage between the two. The present variation between populations of the small-flowered *V. arvensis* can therefore be traced back to those differences originally present in the heterozygous, outbreeding progenitors and which have since become segregated out and distributed into the now almost completely inbreeding lines. Such lines are usually morphologically uniform and the presence of the morphologically constant AT-intermediates in these populations must result from the mixing of two separate populations.

On the basis of the available evidence it seems an economy of hypotheses to consider the cytologically regular and non-segregating AT-intermediates as being extreme variants of *V. arvensis* rather than 'stabilized' hybrid segregates. Taxonomically these plants are best considered as representatives of a variable *V. arvensis* Murr. since the observed variation suggests it would be possible to find a complete range in morphology from *V. arvensis*, *sensu stricto*, to the most extreme AT-intermediates defined above.

V. arvensis would then be taken to include: annual pansies with cream, or predominantly cream, never blue or purple, flowers; upper petals usually shorter than, or as long as, the upper sepal, although occasionally longer, up to about $\times 1\frac{3}{4}$; stylar flap usually reduced and appearing absent but sometimes developed enough to be seen with a hand-lens; pollen assemblage composed predominantly of 5-colpate grains with a few 4-colpate grains and occasionally some 6-colpate grains; chromosome number $2n = 34$.

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MIMULUS HYBRIDS IN BRITAIN

By R. H. ROBERTS

ABSTRACT

The hybrid *M. guttatus* × *luteus* has been synthesized and shown to be identical with naturally-occurring plants, which have been found to be widespread in Britain.

Plants of the putative hybrid *M. guttatus* × *cupreus* have also been found to occur in several northern localities.

INTRODUCTION

According to Loudon (1872) species of the genus *Mimulus* were first brought into the British Isles just over 200 years ago. They were introduced from the American continent and became popular as border and pot plants. A few of them became naturalized: *M. guttatus* DC., said to have been introduced in 1812, was already established as an escape by 1830 (Warburg 1962); it is now widely distributed on the banks of streams and rivers, and is recorded from all but a dozen of the vice-counties in Britain. *M. luteus* L. and *M. moschatus* Dougl. ex Lindl. have also become naturalized, but far less commonly; and more recently a fourth species, *M. cupreus* L., has been reported as a widespread escape in the English Lake District (McClintock 1957).

M. guttatus is a ± pubescent perennial, often glandular-pubescent, particularly on the upper part of the flowering stem, the pedicel and the calyx. It has a bilabiate yellow corolla, marked with small, red spots in the throat, and with the lower lip longer than the upper. It is a native of western North America, where it is very variable, being made up of many polymorphic populations growing in wet places (Vickery 1959).

M. luteus on the other hand is completely glabrous except inside the calyx and corolla, the latter usually marked with large, reddish-brown spots on the lobes, in addition to small ones in the throat. The lips of the corolla, moreover, are nearly equal. It is a smaller, more prostrate plant than *M. guttatus* and is a native of Chile.

M. cupreus is described as being very similar to *M. luteus*, differing from it only in its compacter habit, smaller leaves and copper-coloured flowers, which may or may not have small, dark spots in the throat. Like *M. luteus*, under which it was formerly placed as a variety (Bailey 1927), this also is a native of Chile.

M. moschatus is a densely and viscidly-hairy plant with a much smaller, pale yellow, normally unspotted corolla, and smaller leaves of a paler green. It originates from western North America.

THE NATURALIZED PUTATIVE HYBRID

Despite the descriptions given in the floras many plants of *Mimulus* have proved difficult to identify and have often been misrecorded. For example, at several places in Caernarvonshire plants were found which could not satisfactorily be placed under either *M. guttatus* or *M. luteus*; they showed considerable variation in pubescence and corolla marking, many of them being tall, robust plants, with large, heavily-blotched corollas.

In 1960 the intermediate character of a plant growing at Harlech, Merioneth, aroused the suspicion that it might be of hybrid origin—a view which was further strengthened when its pollen was found to be highly sterile. Consequently, similar plants from as many other localities as possible were examined. In many of these places the plants were so uniform as to suggest that they were, in fact, clones, and that propagation by seed did not occur there. Altogether, plants with highly sterile pollen from seven localities were taken into cultivation and, during the summer of 1961, pollen of four flowers from each of them was examined and an estimate made of the percentage of full pollen grains. This was done by mounting

the pollen from undehisced anthers in a few drops of aceto-carmin, when the full grains took up the stain and could readily be counted. The results (Table 1) show that the proportion of full grains varied from plant to plant and even from flower to flower on the same plant.

TABLE 1. Percentage of full grains in the pollen of the naturalized hybrid *M. guttatus* $\times$ *luteus*. Samples are from undehisced anthers of four flowers from each plant

Locality	Flower no.			
	1	2	3	4
Harlech	19	13	8	6
Bethesda	6	4	8	6
Llanllechid	0	3	8	14
Groeslon	1	0.5	1	10
Machynlleth	4	1	4	8
Nant y Garth	6	3	3	2
Penmachno	4	1	2	6

The plants from different localities were found to be very heterogeneous: they differed considerably in corolla size and marking, the latter varying from some which differed little from *M. guttatus*, to others in which the lobes were beautifully marked all over with a deep red or reddish-brown pattern of blotches and spots. But all of these plants possessed short, frequently very sparse pubescence, mainly on the upper parts of the flowering stems (particularly on the leaf bases and the nodes), on the pedicels and the calyces.

Herbarium specimens of *Mimulus* from various localities in Britain were also examined and a very large number of these proved to be similar to the putative hybrid and to have highly sterile pollen. It therefore appeared that these plants were surprisingly widespread and a short series of experiments was carried out in an attempt to get further light on them.

EXPERIMENTAL POLLINATIONS

In order to attempt the artificial synthesis of the hybrid a search was made locally for *M. guttatus* and *M. luteus*. *M. guttatus* was found at a few places in Caernarvonshire; a plant from one of these, and another from Dolgellau, Merioneth, were grown for experimental crossing. The search for *M. luteus* was less successful. Although this species had been recorded from two Welsh vice-counties (Hyde & Wade 1957), when the specimens supporting these records were examined, both were found to be of the putative hybrid. Eventually, a plant of *M. luteus* was obtained from a garden in Evesham, Worcs., and, later, seeds were collected from a herbarium specimen of *M. luteus* gathered in Caithness by D. P. Young in 1959. When these seeds were sown on damp blotting-paper they germinated in about 4 or 5 days and the seedlings were transplanted into pots of sterilized soil and grown on.

With these materials and the seven plants of the putative hybrid the following pollinations were carried out. Except in the case of the trial selfings, the flowers were first emasculated to prevent self-pollination and each flower covered with a cellophane bag, which was kept in place until the style had withered.

(a) Four flowers on each of the putative hybrid plants were selfed, but a few were pollinated with pollen from another of the hybrid plants.

(b) Several flowers on each hybrid plant were pollinated with *M. guttatus* and several with *M. luteus*.

(c) A number of flowers of *M. guttatus* were pollinated with *M. luteus* and a number of the reciprocal pollination also made.

After each pollination had been carried out the flower was labelled and the cellophane bag replaced.

RESULTS

The success of each pollination was estimated by gathering each mature ovary, whether it had developed into a capsule or not, and storing in a separate container to dry, after which it was examined for any seed set.

TABLE 2. Percentage of full grains in the pollen of the synthesized hybrid *M. guttatus* $\times$ *luteus*. Samples from four flowers per plant, referred to as H1, H2, etc.; R1 is the plant of the reciprocal cross

Plant	Flower no.			
	1	2	3	4
H1	5	3	4	4
H2	26	1	22	7
H3	0.5	1	0.2	0
H4	3	2	5	4
H5	6	6	6	3
H6	12	13	16	31
H7	20	18	5	2
H8	2	1	1	1
H9	5	4	4.5	4
H10	0.5	1	1	0
H11	5	3.5	1	6
H12	0	2	2	2
H13	5.5	2	5	6
H14	5	3	3.5	3.5
H15	1	0.4	0	4
R1	9	5	2	3

The results may be summarized as follows.

(a) In all the ovaries from the putative hybrids, whether selfed, or pollinated with each other, with *M. guttatus* or *M. luteus*, not one seed was set.

(b) The capsules of *M. luteus* which had been pollinated with *M. guttatus* were moderately well developed and, before being opened, gave the impression that fertilization had taken place. When they were examined, however, with one sole exception, they were found to contain empty testae. The exception was one capsule of the *M. luteus* plant from Evesham, which was found to contain two well-developed seeds out of 466, the others being empty testae like those in all the other capsules. One of these two seeds germinated and grew into a vigorous plant (R1 in Table 2).

(c) Capsules from *M. guttatus* pollinated with *M. luteus* had a good set of seed, over 800 were counted in one capsule, but the seeds were variable in size compared with those of the parent species. Percentage germination in these was fairly good (c. 30%). Fifty-five of the resulting seedlings were transplanted into sterilized soil and grown to maturity.

The synthesized hybrid plants

Fifteen plants of the artificially synthesized hybrid were chosen at random and during 1962 and 1963 these were subjected to the same programme of pollinations as that carried out on the naturally-occurring hybrid. The results were identical: neither selfing, pollination

with one another, with *M. guttatus*, nor with *M. luteus* produced a single seed. The sole plant (R1) of the reciprocal cross gave the same results.

Pollen from four flowers of each of these 15 plants and of the hybrid R1 was examined and the results (Table 2) agree very closely with those from the naturally-occurring hybrid.

Other effects of pollination were observed. When hybrid plants with a very low proportion of full pollen grains were selfed there was no observable swelling of the ovaries or inflation of the calyces. But when those having higher proportions of full pollen grains (e.g. H2, H6 and H7) were selfed there was often a marked enlargement of both capsule and calyx. Pollination of the synthesized hybrid plants with *M. guttatus* also produced the same effects, but to an even greater degree; while pollination with *M. luteus* resulted in the most pronounced effects of all. The results, summarized in Table 3, suggest that these effects, which were also observed in the naturalized hybrid plants, may be due to hormone action following pollination.

TABLE 3. Capsule development (mean of length $\times$ breadth in mm) in hybrid *Mimulus* after pollination with pollen from different sources

Pollen source:		
<i>M. luteus</i>	<i>M. guttatus</i>	Hybrid
44.8	26.2	17.0

Variation in the synthesized hybrid plants

The plants of the synthesized hybrid grown to maturity exhibited considerable variation in several morphological characters. In flower colour and density of pubescence they showed varying degrees of intermediacy between the parents, but the length of the hairs was usually less than half those of *M. guttatus*; in some cases the pubescence was so short and sparse as to be easily overlooked—as indeed it seems to have been in many specimens of the naturalized hybrid, which have consequently often been mistaken for *M. luteus*.

Stature, leaf-size and corolla-size were frequently much larger than in either of the parents, but about a dozen of the 55 hybrid plants were markedly lacking in vigour; although grown under the same conditions as the others, some of these only attained a stature of 5 to 8 cm and either bore minute flowers or failed to come into flower at all.

DISCUSSION AND CONCLUSIONS

The experimental pollinations have shown that the cross *M. guttatus* ♀ $\times$ *M. luteus* ♂ occurs readily and gives a reasonably good seed-set, from a proportion of which highly variable F₁ plants result; the majority are large and vigorous. These F₁s are completely sterile and are identical with the naturalized sterile plants, which are therefore presumed to be of the same parentage.

The reciprocal cross *M. luteus* ♀ $\times$ *M. guttatus* ♂ appears to be very difficult to obtain, only one plant being produced out of many such pollinations; but this single plant was very vigorous and morphologically identical with the others. Like them, too, it was completely sterile.

The synthesized hybrid plants also proved to be as winter-hardy as the naturalized ones. All the cultures were left outside throughout the severe weather conditions of the winter of 1962–63; whilst all the plants of *M. luteus* died, those of *M. guttatus* and both lots of the hybrid survived and grew vigorously in the following summer. This may well be the explanation of the widespread occurrence of the hybrid in the absence of the *M. luteus* parent. The reason for its presence in so many places is problematic: whether it is due to its deliberate production by nurserymen in the past, or to accidental crossing when both species were grown in the same gardens.

LOCALITIES FROM WHICH PLANTS OF THE HYBRID *MIMULUS GUTTATUS* × *LUTEUS* HAVE
BEEN SEEN

- V.c. 3, SOUTH DEVON: near Bridestow, 1953, N. Y. Sandwith (NMW); near Lydford, 1939, D. P. Young (herb. D. P. Young).
 V.c. 17, SURREY: Shere, 1935, D. P. Young (herb. D. P. Young).
 V.c. 35, MONMOUTH: Llanover Forest, Abercarn, 1954, R. E. Stumbles (NMW).
 V.c. 40, SHROPSHIRE: Oswestry, 1954, Miss Vera Gordon (herb. V. Gordon).
 V.c. 45, PEMBROKE: Aberfelin, Trevine, 1954, Mrs. M. Barnes (NMW).
 V.c. 46, CARDIGAN: Eglwys Fach, 1961, P. M. Benoit.
 V.c. 48, MERIONETH: Harlech, 1960, R. H. Roberts & P. M. Benoit.
 V.c. 49, CAERNARVON: Llanllechid, 1960, R.H.R.; Nant y Garth, 1960, R.H.R.; near Groeslon, 1960, R.H.R.; Tregarth, 1959, Mrs. I. Roberts (herb. R. H. Roberts); Gerlan, Bethesda, 1961, R.H.R.; same, 1954, Miss V. Gordon (herb. V. Gordon); near Waun Fawr, 1962, R.H.R.; near Penmachno, 1962, M. Morris; Cwm y Glo, Llanberis, 1941, R. D. Tweed & N. Woodhead (herb. Univ. College of N. Wales, Bangor).
 V.c. 50, DENBIGH: Llangollen, 1954, Miss V. Gordon (herb. V. Gordon).
 V.c. 52, ANGLESEY: near Pentraeth, 1961, R.H.R.
 V.c. 66, DURHAM: Teesdale, 1958, Miss U. K. Duncan (herb. U. K. Duncan). This had been determined as the putative hybrid by D. McClintock.
 V.c. 89, EAST PERTHSHIRE: bank of R. Tay, near Dunkeld, 1958, D. P. Young (herb. D. P. Young).
 V.c. 90, ANGUS: Wester Denoon, Sidlaw Hills, 1958, Miss U. K. Duncan (herb. U. K. Duncan).
 V.c. 97, WESTERNESS: Dalwhinnie, 1954, H. J. M. Bowen (herb. H. J. M. Bowen).
 V.c. 105, WEST ROSS: near Applecross, 1957, Miss V. Gordon (herb. V. Gordon).
 V.c. 108, WEST SUTHERLAND: Lochinver, 1961, Miss V. Gordon (herb. V. Gordon).

OTHER HYBRID PLANTS

Two specimens of *Mimulus* sent to me by Miss U. K. Duncan (Tarfside, Glen Esk, Angus, v.c. 90; near Fettercairn, Kincardine, v.c. 91) and one sent by Dr. D. P. Young (River Tay, near Dunkeld, East Perthshire, v.c. 89) had copper-coloured flowers with few or no small dots in the throat of the corolla; the calyces and pedicels were also minutely, but rather densely pubescent, and their pollen had a high proportion of empty grains. From their morphology these plants appeared to be the hybrid *M. guttatus* × *cupreus*.

Similar specimens, except that they possessed a petaloid calyx, had been collected by Mr. R. C. Palmer and Mr. W. Scott (near Scalloway, Shetland, v.c. 112) and by Miss V. Gordon (near Inverkirkaig, West Sutherland, v.c. 108). Miss Gordon (*in litt.*) informs me that this plant occurs in several localities in Sutherland.

In 1962 a rooted piece of the Scalloway plant was obtained and some observations were made on it during the following summer. Pollen from 6 flowers was found to have from 50% to 60% of full grains—a much higher proportion than in that of the *M. guttatus* × *luteus* hybrid. Ten flowers were selfed and the resulting seed-set found to be extremely low: from 0 to 3 seeds per capsule. Only twelve seeds were obtained altogether, but these germinated fairly readily and the seedlings were transplanted into sterilized soil. Some of these seedlings had small and malformed cotyledons, while some lacked chlorophyll. None of them made any growth beyond the cotyledon stage, and even those with normal, green colouring had all died within a fortnight of germination. The evidence so far available thus favours the view that all these plants possessing copper-coloured flowers and a very short pubescence are also of hybrid origin, the presumed parents in this case being *M. guttatus* and *M. cupreus*. Nevertheless, the artificial synthesis of this hybrid is desirable before any final pronouncement can be made on them.

ACKNOWLEDGMENTS

I wish to record my thanks to Mr. P. M. Benoit for his helpful comments and for obtaining much living material for me; to Mr. M. Morris, Llandudno, and Mr. Walter Scott, Scalloway, who also sent me living material of *Mimulus* species and hybrids. Thanks are also due to Dr. H. J. M. Bowen, Miss U. K. Duncan, Miss Vera Gordon, Mr. R. C. Palmer and Dr. D. P. Young; to the Keepers of the herbaria at the National Museum of Wales, Cardiff, and at the Botany Dept., University College of Wales, Bangor; and to the authorities of the British Museum (Natural History) for assistance in checking some references. Lastly, to my daughter, Anne Roberts, whose insistence on obtaining a specimen of the Harlech hybrid first aroused my interest in it.

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STUDIES ON *ALCHEMILLA FILICAULIS* BUS. SENSU LATO AND *A. MINIMA* WALTERS. III. *ALCHEMILLA MINIMA*

By MARGARET E. BRADSHAW

Department of Extra-Mural Studies, University of Durham

ABSTRACT

By transplant experiments and by growing seed progenies, it has been shown that *A. minima* differs from the dwarf ecogenodemes of *A. filicaulis* in several morphological characters, in habit and in ecological requirements. The chromosome numbers of both are within the same range, $2n = c. 103-108$. *A. minima* occurs on Whernside and Ingleborough in north England and is endemic. The dwarf ecogenodemes of *A. filicaulis* are known from the north Pennines only and may also be endemic.

INTRODUCTION

The third taxon in this critical group within the *A. vulgaris* aggregate is *A. minima* Walters. This small plant is very similar to the dwarf ecogenodemes of *A. filicaulis*, *sensu lato*, found in close-grazed montane grassland in the north Pennine hills (Bradshaw 1963a, p. 316). Leaves from field collections of both are shown in Fig. 1. The plants are difficult to separate in the field and it was hoped that the diagnostic characters could be better established by cultivation experiments. Also, *A. minima* was known only from Ingleborough, yet dwarf *A. filicaulis* plants are plentiful in other hill areas. Cultivation experiments were needed to show if any of these plants were referable to *A. minima*.

MORPHOLOGY AND HABIT

The morphological characters of *A. minima* are most clearly appreciated when compared with the dwarf ecogenodeme of *A. filicaulis*. Transplants of both from the field were grown in pots and boxes (as described by Bradshaw, 1963a, p. 308) for one year under similar conditions in the Botanic Garden at Durham. Some differences in the general appearance can be seen in Plate 2 and measurable differences are given in Tables 1 and 2.

TABLE 1. Measurements of plants cultivated in pots

Characters	<i>A. minima</i> (25 plants)	<i>A. filicaulis</i> dwarf ecogenodeme (29 plants)
1. Petiole length: lamina length	0.8 ± 0.03	1.16 ± 0.03
2. Lobe length: lamina length	0.51 ± 0.01	0.4 ± 0.009
3. Depth of incision between lobes: lamina length	0.21 ± 0.02	0.14 ± 0.006

(a) *Rhizome and habit*

The rhizomes are more slender in *A. minima* and longer because of the longer internodes. In *A. minima* the leaves are more or less prostrate giving a plant a few centimetres high; in *A. filicaulis* the leaves are more erect, so that the length of the petiole gives an approximate measure of the height of the plant (Table 2).

PLATE 2



Plants from closely grazed grassland after 9 months cultivation. Top row : *A. minima* from Ingleborough area. Bottom row : *A. filicaulis* from Mickle Fell and Moor House National Nature Reserve.

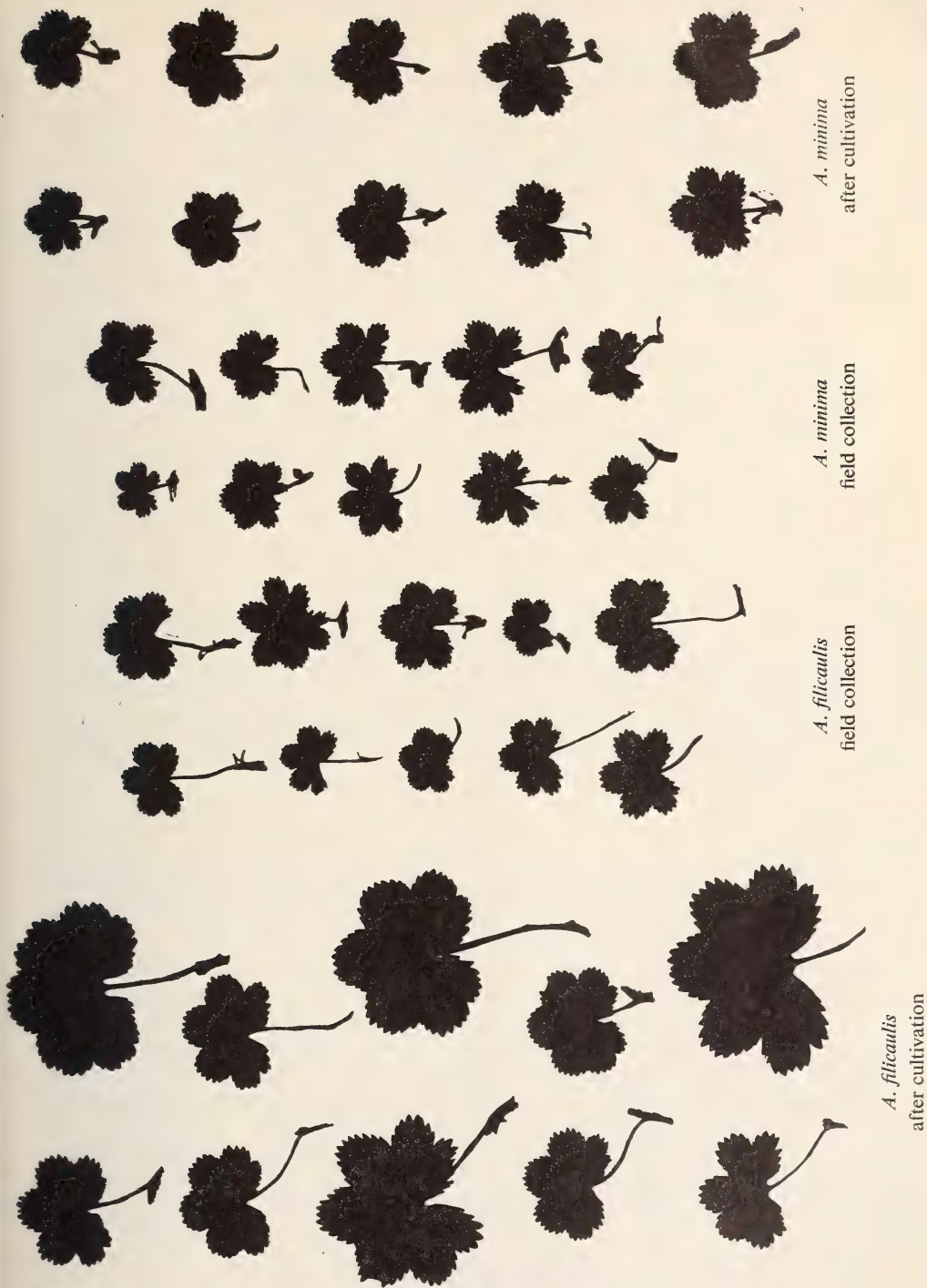


Fig. 1. Single leaves collected from twenty plants—ten of each species—before and after cultivation. The leaves are arranged in the same order in each set ($\times 1$).

(b) *Stipules and base of the petioles*

In *A. minima* these are usually without the wine-red pigment usually found in *A. filicaulis*.

TABLE 2. Measurements of plants cultivated in boxes.

Characters	<i>A. minima</i> (10 plants)	<i>A. filicaulis</i> dwarf ecogenodeme (3 × 10 plants)
1. No. of shoots	4.7 ± 0.45	5.7 ± 0.45 7.3 ± 0.44 6.4 ± 0.67
2. Length of petiole (cm)	1.9 ± 0.17	10.0 ± 0.40 8.7 ± 0.40 9.2 ± 0.39
3. Breadth of leaf (cm)	2.3 ± 0.18	5.1 ± 0.10 4.7 ± 0.19 4.4 ± 0.21
4. No. of inflorescences	15.7 ± 2.22	3.8 ± 0.39 1.9 ± 0.47 3.2 ± 0.66

(c) *Leaf lamina*

In *A. minima* the leaves are usually blue-green, and the lamina of mature leaves tends to be recurved and rather stiff with lobes which are V-shaped in cross section. *A. filicaulis* is less blue, often pure green, and the lobes are more open and the lamina flatter and not stiff. These differences can be seen in Fig. 2. The leaves of *A. minima* are much smaller with five full lobes, while in *A. filicaulis* another pair of basal lobes is more frequently well developed. The longer lobes of *A. minima* have 9(11) teeth on the median lobe while *A. filicaulis* has 11(13).

(d) *Indumentum*

The indumentum of the upper and lower surfaces of the leaf lamina were scored separately in five classes, one being almost glabrous, five very hairy. The flower-stems were scored in seven grades, six being least hairy and 0 most hairy (Bradshaw 1963a, p. 306). The hair characters of *A. filicaulis* have been considered in the first paper of this series. Dwarf ecogenodemes of subsp. *filicaulis* and subsp. *vestita* are known, and some of the former were almost glabrous when collected in the field. The leaves of *A. minima* were almost all class I on the upper surface and in only one case were the leaves more hairy (classes 3 and 4 respectively). An analysis of the hairiness of the flower-stem comparable with that of *A. filicaulis* was difficult because of the smaller number of internodes in *A. minima*, four or five against six or more. The flower-stems of 25 plants of *A. minima* were examined. In all cases the first internode was glabrous (this is often so in *A. filicaulis*) and frequently the second also. The whole flower-stem in ten plants was grade 6, the same as subsp. *filicaulis*; those of the other plants were hairy throughout, 12 were placed in grades 0-3, and three in grades 4-5. Clearly there is variation in the indumentum similar to that in *A. filicaulis*.

CHROMOSOME NUMBERS

Chromosome counts were obtained of pollen-mother-cells of two plants of *A. minima* from different localities on Ingleborough (c. 34/750747). These were as follows: $2n = c. 105$ and $c. 108$ for one plant, and for the other $2n = c. 103$, $c. 98$ and $c. 99$ (the last two values

TABLE 3. Associates of *Alchemilla minima*.

The figures indicate cover/abundance on the Domin scale in quadrats 25 cm × 25 cm in area. × = present in the same community near the quadrat. + = present in the quadrat.

Localities	Localities													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Ingleborough, 34/714733, 950 ft, W aspect														
2-7 Ingleborough, c. 34/721753, 800 ft, NNW aspect														
8-9 Whernside, c. 34/734798, c. 1,600 ft, SE aspect														
10-14 Ingleborough, c. 34/737745, c. 2,000 ft, S and W aspect														
<i>Alchemilla glabra</i>	-	-	1	-	1	-	-	1	-	-	-	-	x	-
<i>A. minima</i>	+	2	1	1	1	1	3	2	1	+	3	3	3	3
<i>A. xanthochlora</i>	-	-	x	1	-	-	-	-	-	-	-	-	-	-
<i>Achillea millefolium</i>	-	-	1	-	-	-	1	-	2	+	2	2	1	2
<i>Bellis perennis</i>	+	2	1	-	1	-	-	2	2	+	-	4	4	2
<i>Cardamine pratensis</i>	-	-	-	-	-	-	-	1	-	-	-	2	2	1
<i>Carex caryophylla</i>	+	-	-	-	-	1	-	-	3	-	3	3	3	-
<i>C. panicea</i>	+	5	5	5	7	2	-	-	2	-	-	-	-	-
<i>Campanula rotundifolia</i>	-	-	-	-	-	1	-	-	-	+	-	2	1	2
<i>Cerastium holosteoides</i>	-	-	1	-	1	-	-	1	1	+	2	2	2	3
<i>Erophila verna</i>	-	-	-	-	-	-	-	-	-	+	1	-	-	-
<i>Euphrasia officinalis</i>	+	1	-	-	1	1	1	2	1	+	1	2	1	2
<i>Galium sternerii</i>	-	-	-	-	-	-	-	-	-	+	1	2	1	3
<i>G. verum</i>	-	1	-	-	1	1	-	-	-	-	-	-	-	-
<i>Leontodon autumnalis</i>	+	2	2	1	2	2	2	2	3	-	-	-	-	-
<i>Lotus corniculatus</i>	+	-	-	-	-	1	-	-	-	-	-	-	2	-
<i>Luzula campestris</i>	-	-	1	-	-	1	1	1	1	+	4	-	-	1
<i>Plantago lanceolata</i>	+	-	2	1	2	2	2	3	4	-	-	1	2	-
<i>Potentilla erecta</i>	+	-	1	1	-	2	-	-	-	+	-	-	-	-
<i>P. sterilis</i>	-	-	-	1	-	-	-	-	1	+	2	2	1	-
<i>Poterium sanguisorba</i>	+	-	-	-	-	x	x	-	-	-	-	-	-	-
<i>Prunella vulgaris</i>	+	2	2	1	2	2	2	3	2	-	-	3	2	-
<i>Ranunculus acris</i>	+	1	-	-	-	-	-	1	-	+	-	2	2	2
<i>R. bulbosus</i>	-	-	-	-	-	-	1	-	-	-	2	-	3	2
<i>R. repens</i>	-	-	2	1	-	1	-	-	-	-	-	-	-	-
<i>Rumex acetosa</i>	-	-	-	-	-	-	-	-	-	-	2	-	-	3
<i>Sagina procumbens</i>	-	-	1	-	-	-	1	-	-	+	2	2	2	1
<i>S. nodosa</i>	-	1	1	-	1	-	-	-	-	-	-	-	-	-
<i>Taraxacum</i> spp.	-	1	-	1	1	1	-	-	-	-	-	-	-	-
<i>Thymus drucei</i>	+	-	-	1	-	-	-	2	-	+	3	3	3	4
<i>Trifolium repens</i>	+	1	2	1	1	-	2	2	-	+	2	2	3	3
<i>Veronica chamaedrys</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	1
<i>Viola riviniana</i>	-	-	-	-	1	-	-	1	-	-	1	-	-	2
<i>Agrostis tenuis</i>	4	3	-	3	3	4	7	4	4	-	4	5	5	-
<i>Anthoxanthum odoratum</i>	-	-	-	-	-	-	3	3	3	-	-	-	2	-
<i>Briza media</i>	3	2	1	2	1	2	-	-	-	-	-	4	-	-
<i>Cynosurus cristatus</i>	3	1	2	2	-	2	5	4	4	-	x	-	3	2
<i>Deschampsia cespitosa</i>	3	-	2	1	3	2	-	-	-	4	1	-	4	3
<i>Festuca ovina</i>	5	5	5	8	7	8	7	7	7	8	9	7	8	9
<i>Helictotrichon pratense</i>	-	-	-	-	-	-	-	-	-	5	-	-	-	3
<i>Koeleria cristata</i>	-	2	-	-	-	2	-	-	-	+	-	-	-	4

Additional species occurring in one quadrat only: *Alchemilla glaucescens* (5), *A. filicaulis* subsp. *vestita* (1), *Hypochaeris radicata* (1), *Juncus effusus* (14), *Leontodon hispidus* (1), *Veronica officinalis* (6), *V. serpyllifolia* (14), *Holcus lanatus* (7), *Nardus stricta* (4), *Sieginglingia decumbens* (3).

are probably too low). These are within the range for *A. filicaulis* ($2n = 101-110$) and near the values obtained for a dwarf montane subsp. *vestita* plant from Mickle Fell (35/809244), which were $2n = c. 105$ and $c. 109$ (Bradshaw, 1963b, p. 323).

DISTRIBUTION

So far *A. minima* has been recorded from two mountains only, Ingleborough and Wharfedale (34/77 and 78) in the Craven area. All the dwarf plants collected from other montane pasture areas became larger in cultivation and belong to *A. filicaulis* (Bradshaw 1963a, p. 316). Walters (1949) first recorded *A. minima* from the east side of Ingleborough at about 1,000 ft (310 m) altitude, and around the 2,000 ft contour on Simon Fell. Now, *A. minima* has been found in suitable habitats down to 750 ft (230 m) on the north west slopes of Ingleborough. Recently, more plants were found on Wharfedale at 700 ft (220 m) and 1,000 ft and between 1,600 ft (500 m) and 1,800 ft (560 m). In all the localities *A. minima* plants were plentiful.

ECOLOGY

A. minima appears to be confined to the intensively grazed *Festuca-Agrostis* grassland areas on or just below the limestone strata of the Carboniferous Limestone Series of the Ingleborough district. All habitats were characterized by the high moisture content of the soil. At the lower altitudes (700 ft– $c. 1,400$ ft) this is maintained by seepage from flushes below the limestone; above this ($c. 2,000$ ft) presumably the higher humidity and rainfall are sufficient since *A. minima* grows amongst the limestone boulders where surface water is absent.

In all cases the soil was a moist, slightly sticky, dark-brown peaty loam. The lower and wetter habitats were less acidic (pH 6.5–7.3) than those at $c. 2,000$ ft (pH 5.2–6.1). No doubt, this is due to the more base-rich flushing by water from the limestone.

The associated species are listed in Table 3. *Festuca ovina* was present in all the sample areas and *Agrostis tenuis*, *Cynosurus cristatus*, *Trifolium repens*, *Prunella vulgaris*, *Plantago lanceolata* and *Euphrasia officinalis* agg. were present in most. The characteristic blue-green appearance of the lower habitats is caused by the high frequency of *Carex panicea*; *Leontodon autumnalis* is a constant species and the only records of *Poterium sanguisorba* are at these lower altitudes. *Carex panicea* is absent from the higher altitudes but several other species are more common there: these are *Achillea millefolium*, *Bellis perennis*, *Cerastium holosteoides*, *Sagina procumbens* and *Thymus drucei*.

CONCLUSIONS

This work fully supports Walters' (1949) original treatment of *A. minima* as a distinct species. The cultivation experiments have emphasized the diagnostic characters which he described, and revealed some other contrasts with the dwarf plants of *A. filicaulis*; these are set out in Table 4. Although typical plants can be identified with a fairly high degree of confidence, plants are found which are less distinct (cf. Fig. 1) and can be determined with certainty only after cultivation.

Details of the ecological preferences and associated species of *A. minima* have been given. Apparently suitable habitats in closely grazed *Festuca-Agrostis* grassland are abundant in the Pennines and may be found elsewhere. Only a relatively small number of these have been examined, and the recent discoveries of *A. minima* some miles from the early localities on Ingleborough suggests that it may be more widespread, at least in the Craven district. Some similar habitats in the north Pennines are occupied by the dwarf ecogenodeme of *A. filicaulis*. Curiously, no plants of *A. filicaulis* were collected from the populations on Ingleborough although *A. filicaulis* does occur in other habitats in the area. This raises interesting points about the evolution and history of these two species. These will be considered in relation to other members of the *A. vulgaris* aggregate in the fourth paper of this series.

TABLE 4

Character	<i>A. minima</i>	dwarf <i>A. filicaulis</i>
<i>Rhizome</i>	long and slender, little branched, internodes long	short and thicker, often much branched, internodes short
<i>Base of plant and stipules</i>	not wine-red	wine-red, sometimes rather faint
<i>Petioles</i>	usually about length of leaf lamina	longer than leaf lamina
<i>Lamina</i>	usually blue-green; lamina pleated and recurved (lobes half open, V-shaped in cross section)	not so blue, usually pure green; whole lamina flat
<i>Lobes</i>	usually 5, $\frac{1}{2}$ radius of lamina, deep incision between lobes	usually 7, less than $\frac{1}{2}$ radius of lamina, shallow incision between lobes
<i>Teeth on median lobe</i>	usually 9	usually 11
<i>Flower-stems</i>	several, very slender, usually with 5 internodes	few, less slender, usually with 6 internodes
<i>Indumentum of whole plant</i>	variable, usually less hairy than <i>A. filicaulis</i> subsp. <i>vestita</i>	variable, subsp. <i>filicaulis</i> , subsp. <i>vestita</i> and intermediate states

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BOOK REVIEWS

Flora of the British Isles. A. R. Clapham, T. G. Tutin and E. F. Warburg. *Illustrations, Part III, Boraginaceae—Compositae*. Drawings by Sybil J. Roles. Pp. 115, 8½ × 11½ in. Cambridge University Press, 1963. Price 32s. 6d.

Miss S. J. Roles's illustrations to 'CTW' are by now familiar to British botanists. This is the third of four parts, covering the remaining dicotyledonous families. The drawings, arranged four to a page, are designed as a companion to the descriptions in the *Flora*. '... The intention is to provide a visual impression of the habit, and a selection of the chief features of the plants ...' Almost all have been made from fresh specimens.

These drawings are less detailed than either Miss Ross-Craig's much more ambitious series, or the illustrations to R. W. Butcher's *New Illustrated British Flora*; indeed, from their stated intention, they cannot fairly be compared with either. A fairer comparison is with Fitch & Smith's illustrations for Bentham & Hooker's flora. The policy of drawing from living specimens has resulted in a freshness and naturalness lacking from many of Fitch's drawings. It has its pitfalls: several of the plants look wilted (e.g. *Asperugo*, *Galium debile*) and in other cases the specimen chosen seems poor or even quite untypical (e.g. *Cymbalaria muralis*, *Linaria arenaria*). In trying to portray habit Miss Roles has attempted a difficult task. Some of the drawings are notably successful; the *Pinguicula* spp., *Origanum*, most of the *Lamium* spp., the *Plantago* spp., *Viburnum opulus*, *Sonchus asper*, *Chrysanthemum segetum* and many others are instantly recognizable. In some other cases the habit is not well caught (e.g. *Galium saxatile*, *Stachys sylvatica*, *Bartsia alpina*, *Dipsacus fullonum*), and sometimes the distinguishing characters of related species are not well brought out (e.g. *Leontodon hispidus* and *L. taraxacoides*, some *Euphrasia* spp.), perhaps most often through a combination of unselectiveness and understatement. To capture the character of a plant at this scale may demand an approach akin to caricature; one is often driven to admire the effectiveness and economy of Fitch's little sketches carried out in a much less flexible medium.

A set of illustrations like these is inevitably a compromise, in which clarity and detail (and to some extent accuracy) are set against portability and cost. Are the illustrations to be used to assist identification in the field, or are they to be studied at leisure at home or in the herbarium? It is possible to have the worst of both worlds, and one wonders if the right compromise has been chosen here. For anyone who simply wants help in identification there is much to be said for a book like Fitch's illustrations, or Thommen's useful *Taschenatlas der Schweizer Flora*, which crams over 3,000 thumb-nail sketches of Swiss plants into a single cheap pocketable volume.

Nevertheless, Miss Roles's drawings will be found an invaluable companion with a vasculum of plants at the end of the day, and they will give much pleasure besides. The drawings themselves are essentially accurate, and their delicate style is admirably set off by good paper, and excellent typography and layout. This is altogether an attractive volume.

M. C. F. PROCTOR

North Atlantic Biota and their History. Edited by Askill Löve and Doris Löve. Pp. xii + 430, with 13 plates and about 180 figs. and tables in the text. Pergamon Press, Oxford. 1963. Price £5 net.

This is the report of a symposium held at the University of Iceland, Reykjavik, under the auspices of the University of Iceland and the Museum of Natural History, in July 1962.

The book contains an introduction followed by 27 papers read at the symposium. More than half of these are devoted to studies of higher plants, and the contributors include such well-known workers as T. W. Böcher, E. Dahl, K. Faegri, E. Hulten, Askill and Doris Löve, J. A. Nannfeldt and R. Nordhagen. The papers cover a variety of topics but the main theme is the study of species, seemingly identical, which occur on both sides of the Atlantic Ocean. Considerable attention is paid, also, to the geological interpretations of the north Atlantic climates of the past.

Professor Hultén's contribution on phytogeographical connections of the north Atlantic is based on a study of distribution maps of all plants known to occur in Iceland, Greenland, Spitzbergen, Jan Mayen, Bear Island and the Faeroe Islands. These are arranged into 24 groups, e.g. Circumpolar, or near circumpolar species which do not occur in Greenland or central Europe; circumpolar plants occurring in Greenland but lacking in central Europe, etc. An analysis of this data leads to the conclusion that phytogeographical conditions around the north Atlantic give poor support to the hypothesis that a land-bridge could have existed in Quaternary or late Tertiary times.

In his paper, Professor Nannfeldt endeavours to illustrate the closer floristic connections of the Scandes with Iceland and Scotland than with the Alps. Dr E. Dahl discusses plant migrations across the north Atlantic Ocean including plants transported across the ocean by man. The western amphi-atlantic element in Europe and the eastern amphi-atlantic element in America, the long-distance dispersal hypothesis and the theory of a land connection between Europe and America are also reviewed.

Doris Löve contributes a fascinating paper on the dispersal and survival of plants. Very few species are really adapted for long-distance dispersal. Such mammals as polar bears and foxes subsist mainly on animal food and are thus excluded as possible plant dispersers. Birds travel freely between land masses and are active as transporters for both ingested and externally carried seeds and plant fragments—ducks, geese and swans in particular are mentioned. A table gives interesting data on the various species of birds and their food plants, together with geographical information on nesting and winter areas. It is concluded, however, that there is a relatively small chance for any large numbers of plants to have been dispersed by birds between North America and the British Isles, and the hypothesis that *Sisyrinchium* and *Eriocaulon* were introduced into Ireland from North America attached to the bodies of pink-footed geese is disputed on the grounds that the American and Irish plants are quite distinct species. Dispersal by wind, and by sea currents are also discussed. The author's conclusion is that the flora of the north Atlantic area is old, well established, and mostly relict from a time preceding the Pleistocene Ice Age.

O. Gjaerevoll in dealing with the survival of plants in nunataks in Norway during the Pleistocene glaciation refers to the strange distribution of *Artemisia norvegica*—the Urals, southern Norway and a single locality in Scotland. Other Arctic species selected for discussion include *Papaver radicum* subsp. *subglobosum*, *Arenaria humifusa*, *Draba crassifolia*, *Saxifraga aizoon*, *Potentilla hypoarctica* and *Carex scirpoidea*. This unusual concentration of rare species in southern Norway is used to illustrate the argument that there must have been quite extensive ice-free areas in that part of the country.

E. Einarsson reviews the elements and the affinities of the Icelandic flora. Between 430 and 440 species of vascular plants are considered to be native to Iceland, about 97% of these are found in Scandinavia, and c. 85% are found also in the British Isles. It is concluded that more than half of the Icelandic species have a Boreal distribution, whereas Arctic-Alpine species comprise of c. 33% of the flora.

There are many other interesting papers dealing not only with higher plants, but with the maximum extent of the Pleistocene glaciation, palynology and geology.

The entire work is of a very high standard and is well printed on excellent paper. It is an essential work of reference to botanists interested in the phytogeography of the north Atlantic area.

D. H. KENT

Drawings of British Plants. Part XVIII, Compositae (4). Stella Ross-Craig. 76 plates. G. Bell & Sons Ltd., London, 28 March 1963. Price 10s. 6d.

Part eighteen of Stella Ross-Craig's series of drawings deals with the remaining ten genera of the family Compositae. Owing to their asexual means of reproduction the species of two of these genera, *Hieracium* and *Taraxacum*, are notoriously difficult taxonomically. In her introduction to *Hieracium* Miss Ross-Craig does not mention apomixis but writes: 'The variation within the species of *Hieracium* can sometimes be so great that I think many of the specific names which have been proposed for the variants could quite happily be forgotten.' It is unfortunate that the authoress did not seek advice from a specialist in the most difficult group. As it is, her selection of species, her identification of the species chosen, and her nomenclature and citation of authors all leave very much to be desired.

In the latest list of British Hieracia (Sell & West in Dandy, 1958), 234 species in 17 sections are listed. That list follows closely the Monograph by Pugsley (1948), the cited specimens in which Miss Ross-Craig has used for her illustrations. In the book under review, 20 species have been selected to illustrate the genus. The section *Alpina*, which is mainly confined to the mountains of Scotland, is represented by four species, the section *Vulgata* subsect. *Eu-Vulgata* and the section *Sabauda* by three species each, and nine other sections by one species each. The very large groups of the section *Vulgata*, namely subsections *Bifida*, *Glandulosa*, *Sagittata* and *Caesia*, in which are placed a very large percentage of the British *Hieracia*, are represented by only one species of the subsection *Glandulosa*. No species at all are given for the sections *Oreadea*, *Alpestrina*, *Auriculina*, *Collina* and *Praealtina*. The three latter groups contain only introduced species, but the widespread *H. brunneocroceum* could lay much greater claim to inclusion than the very rare introduced *H. amplexicaule* of the section *Amplexicaulia*. I can make nothing of the order in which the species are arranged, the oddest thing being the putting of *H. amplexicaule* between two species of the section *Vulgata*.

A close examination of the individual plates reveals several points of criticism, some general and some detailed. The relative sizes of the capitula seem to give the wrong impression, as anyone can clearly observe if

they compare those of *H. calenduliflorum*, *lachenalii* and *pellucidum* (? *exotericum*) with the actual plants. Colours are notoriously difficult to describe, but those given for the leaves and ligules rarely fit in with my idea of the living plant. In *H. holosericeum*, *lingulatum* and *anglicum* the tips of the ligules are usually ciliate. In *H. holosericeum* the parallel-sided involucre bracts are not emphasized. The illustration of *H. pellucidum* seems to be a better fit for one of the *exotericum* aggregate. That of *H. vulgatum* may be of that species but it is a very uncharacteristic example of a widespread and easily recognizable plant. The leaves are too deeply dissected and are certainly never glaucous. In the plate of *H. lachenalii*, Fig. F. seems to be an entirely different plant (? species) from the rest of the figures which are characteristic of the plant they are meant to represent. The example of *H. tridentatum* is what Dr C. West and I would call *H. calcaricola* (F. J. Hanb.) Roffey. *H. tridentatum* Fries sensu stricto does not occur in the British Isles. Pugsley distinguished *H. perpropinquum* and *H. bladdonii* on whether the eglandular or glandular hairs were dominant on the involucre bracts. All intermediates are possible and both extremes can be found on the same plant, and for this reason these species were lumped by Dr C. West and myself in Dandy's Check List. These illustrations do not even show the two extremes and are clearly referable to the same taxon, the correct name for which is *H. perpropinquum* (Zahn) Druce.

The genus *Taraxacum* has not yet received a similar treatment to that of *Hieracium* in this country, and the four species here shown represent the four main groups of microspecies recognized by Continental botanists. *T. officinale* and *T. laevigatum* are excellent illustrations of microspecies within two of these groups. That of *T. palustre* is a composite one. The plant in the foreground probably belongs to the aggregate because of its broad involucre bracts, which are, however, only loosely appressed. The two leaves in the background are characteristic of *T. palustre* (Lyons) DC. sensu stricto. It would be interesting to know to which plant the dissected parts belong. *T. spectabile* seems from the involucre bracts to be correctly named, although the leaves appear to be those of a late-flowering, and therefore uncharacteristic, example.

The species of the other genera are excellently illustrated and show clearly how this group of plants, which prove especially difficult for the beginner, can be identified much more easily by a careful examination of the dissected parts. In these species, also, the relative sizes of the capitula are much better shown, for example in the three species of *Hypochaeris*.

The standard of these drawings is high and it is difficult to find fault with the artist; indeed, if the parts of the plants had not been so meticulously drawn the above comments could not have been made.

P. D. SELL

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A REVISION OF THE BRITISH SPECIES OF *HIERACIUM* SECTION *ALPESTRIA* [FRIES] F. N. WILLIAMS

By P. D. SELL and C. WEST

The Botany School, Cambridge

For the following account we have attempted to examine all the available herbarium material of the British species of the Section *Alpestris* and to consult all the relevant literature.

We are grateful to the authorities in charge of the British Museum (Natural History) (BM), Royal Botanic Garden, Edinburgh (E), Royal Botanic Gardens, Kew (K), University College Leicester, University of Liverpool (LIVU), Marlborough College (MACO), University of Oxford (OXF), University of Sheffield and the South London Botanical Institute (SLBI) for the loan of specimens from their herbaria; to C. J. Cadbury, A. G. Kenneth, J. E. Lousley, R. C. Palmer, Miss C. M. Rob, W. Scott and N. D. Simpson for loans from their private herbaria and for information about the plants *in situ*; to Dr. Carl E. Alm of Uppsala for information on the type material of *H. dovrense*; to Erik Almquist of Uppsala for general information on the section in Scandinavia; and to N. Y. Sandwith for checking the latin descriptions. We are grateful also to the authorities of the British Museum (Natural History) for the photograph of the specimen of *H. hethlandiae* which is in their herbarium, to F. T. N. Elbourn and Miss J. Chenery for taking the remainder of the photographs, which are of specimens in CGE, and especially to Professor H. Godwin who has made available a grant from the 'Brooks Fund' towards the cost of their publication.

Section *ALPESTRIA* [Fries] F. N. Williams (1902) 82; F. J. Hanb. in Bab. (1904) 263; W. R. Linton (1905) 71; Pugsley (1948) 219 (includ. Series *Dovrensis*, Series *Protracta* pro parte exclud. type, Series *Subfoliosa* and Series *Spectabilia*); A. R. Clapham in A. R. Clapham, T. G. Tutin and E. F. Warburg (1952) 1144; ed. 2 (1962) 907 (Lectotype species *H. dovrense* Fries).

Hieracium—*Archhieracium*—*Pulmonaria*—*Alpestris* Fries (1862) 102.

Section *Prenanθοidea* group species *H. carpathicum* Besser in Zahn (1921) 809.

Plants without basal leaves, with basal leaves withered at the time of flowering, or rarely with basal leaves at the time of flowering. Cauline leaves usually fairly numerous, 2–19, rarely thickened at the margins, at least the upper ± rounded at the base and *semi-amplexicaul.* Inflorescence cymose-paniculate. Capitulas *dark*, with *broad*, ± *obtus*e phyllaries, which are usually almost without stellate hairs. Cypselas *dark*. Flowering in July and August.

The species of the Section *Alpestris* are most closely allied to those of the Sections *Prenanθοidea* and *Foliosa*. They can be distinguished from the former by their darker cypselas and usually fewer leaves, and from the latter by their fewer cauline leaves, longer internodes and by the leaves having less thickened margins.

About 200 species have been described in this Section, five from Greenland, 22 from Iceland, three from the Faeroes, 18 from the British Isles (one of which also occurs in the Tatra Mountains) and the remainder from Scandinavia. At least another five species from the mountains of Central Europe should also be included in this Section, but in that region the distinction between the species of the Section *Alpestris* and the Section *Prenanθοidea* is not clear.

In the British Isles all except five of the eighteen species are confined to the Shetland Isles, where they are endemic. Of the remainder, *H. dovrense* is locally abundant in Scandinavia and occurs in one isolated locality in Sutherland; *H. carpathicum* is locally distributed in the Tatra Mountains and also occurs in a few isolated localities in Perth and

Forfar; *H. dewarii* is an endemic species, rather widespread in central and southern Scotland; *H. solum* is endemic to a single locality in Kintyre; while *H. mirandum* is endemic to a single locality in mid-west Yorkshire.

In the Shetlands they are, with one exception, restricted to coastal localities inaccessible to sheep. From the field experience of several botanists the one exception, *H. vinicaule*, occurs, sometimes in quantity, in places easily reached by grazing sheep. This probably accounts for the fact that this species is the most widespread of the Section *Alpestris* in the Shetland Isles. In Scandinavia they are apparently widespread and often abundant in grassland and under trees in mountainous regions.

Pugsley (1948) divided the British species of the Section *Alpestris* into four Series, all of which are *nomina nuda*. These Series are almost entirely artificial, and we fail to understand why the species were so grouped. In our opinion no useful purpose is served by subdividing the Section, although some species are much more closely allied than others. *H. attenuatifolium*, *dilectum*, *hethlandiae*, *northroense*, *pugsleyi*, *subtruncatum* and *vinicaule* have many characters in common. *H. carpathicum*, *dewarii* and *mirandum* are also closely allied and are very distinct from the rest; in fact they closely approach the Section *Foliola*. *H. australis* and *dovreense* have several characters in common, but the six remaining species, *H. breve*, *gratum*, *praethulense*, *difficile*, *solum* and *zetlandicum* have no close allies in the British Isles.

Until recently the study of the Shetland species of the Section *Alpestris* was based mainly on the collections made by W. H. Beeby and by G. C. Druce. The definition of the species and varieties made by Beeby is clear and precise, and the identification of his specimens consistent. On the other hand, an examination of the specimens in Druce's herbarium suggests that he did not understand the taxonomy of the group. Moreover, some of the species, according to the labels attached to the specimens, are recorded from localities where they have never been seen by other botanists. Also, Druce (1928) 71, no. 419: 1635d, published without a diagnosis and without annotating a specimen the name *H. crocatum* var. *ronasii* from 'Zetland', which presumably refers to a taxon in this Section. One cannot even guess to which taxon he is referring since all the taxa described at that time are covered by names in his List, and no new taxon from Ronas Voe (assuming he is describing a plant from that locality, i.e. *ronasii*) is represented in his herbarium.

Pugsley (1948) based his account of the Section on that of Beeby; we have followed the same course.

In the interests of the conservation of our native flora we should like to point out that the species of this Section, which are very local and in small numbers, should not be collected without good scientific reason. They are well represented in public herbaria, and anyone wishing to become familiar with them should examine the specimens to be found there. The collection at the University of Cambridge (CGE) is the most complete, every British species being represented. Here are deposited all the authors' specimens, including material cultivated in the Botanic Garden at Cambridge.

The descriptions in this paper are based on a more precise terminology than is usual, a key to which will be published at a later date; for example, short, medium and long, when applied to hairs, refer to a definite range of length. As the terminology is that used in general practice, the terms having been only more clearly defined, it has been decided not to hold up the paper until the definitions are published. In all the descriptions the most important characters have been put in *italic* so that they can be read off to give a precise diagnosis.

KEY TO THE SPECIES

- | | |
|--|------------------------|
| 1. Leaves up to four times as long as broad | 2 |
| Leaves more than four times as long as broad | 16 |
| 2. Ligules strongly pilose-tipped | 3 |
| Ligules glabrous | 4 |
| 3. Phyllaries 7-9 mm. long, with few stellate hairs at base | <i>17. dewarii</i> |
| Phyllaries 9-11 mm. long, with numerous stellate hairs especially on the margins | <i>18. carpathicum</i> |

4. Cauline leaves up to five	5
Cauline leaves more than five	10
5. Phyllaries 11–13 mm. long	3. <i>solum</i>
Phyllaries 8–11 mm. long	6
6. Styles yellow when fresh	1. <i>zetlandicum</i>
Styles discoloured	7
7. Leaves less than 2.5 times as long as broad	2. <i>breve</i>
Leaves more than 2.5 times as long as broad	8
8. Leaves dentate; phyllaries densely hairy	7. <i>dovrense</i>
Leaves entire or remotely denticulate; phyllaries sparingly hairy	9
9. Cauline leaves 2–4 (–7), about three times as long as broad	4. <i>gratum</i>
Cauline leaves 4–8, about four times as long as broad	5. <i>difficile</i>
10. Leaves never more than 18 mm. broad	9. <i>hethlandiae</i>
Leaves more than 18 mm. broad	11
11. Styles yellow when fresh	12
Styles discoloured	13
12. Peduncles usually glabrous	8. <i>praethulense</i>
Peduncles usually hairy	13. <i>subtruncatum</i>
13. Leaves not more than 2.5 times longer than broad	2. <i>breve</i>
Leaves more than 2.5 (usually more than 3) times as long as broad	14
14. Leaves ovate, abruptly contracted at the base	16. <i>mirandum</i>
Leaves elliptic, gradually narrowed at the base	15
15. Leaves dentate	7. <i>dovrense</i>
Leaves finely denticulate or subentire	6. <i>australius</i>
16. Plant very hairy; phyllaries 1.5–2 mm. wide	6. <i>australius</i>
Plant less hairy; phyllaries 1–1.5 mm. wide	5. <i>difficile</i>
17. Phyllaries with many unequal glandular and few simple hairs	18
Phyllaries with few glandular and without or with few to numerous simple hairs	20
18. Leaves under 20 mm. broad	10. <i>attenuatifolium</i>
Leaves over 20 mm. broad	19
19. Plant usually under 35 cm. high; leaves usually closely spaced and regularly denticulate, abruptly decreasing in size half-way up the stem	14. <i>northroense</i>
Plant usually over 35 cm. high; leaves usually less closely spaced and less denticulate, gradually decreasing in size up the stem	15. <i>vinicaule</i>
20. Phyllaries with numerous simple hairs	11. <i>pugsleyi</i>
Phyllaries with few or no simple hairs	21
21. Styles yellow when fresh	22
Styles discoloured	23
22. Leaves gradually narrowed at both ends, with an acute apex; peduncles glabrous or with an occasional simple hair	12. <i>dilectum</i>
Leaves usually abruptly narrowed at base, with an obtuse to subacute apex; peduncles with few simple hairs	13. <i>subtruncatum</i>
23. Cauline leaves 9–16	24
Cauline leaves 5–9	25
24. Leaves with long acute apex	12. <i>dilectum</i>
Leaves with obtuse or subacute apex	14. <i>northroense</i>
25. Phyllaries 9–10 mm. long	5. <i>difficile</i>
Phyllaries 10.5–13 mm. long	26
26. Leaves usually broadest in the middle and gradually tapering at both ends	9. <i>hethlandiae</i>
Leaves usually broadest below the middle and with a broader base	3. <i>solum</i>

1. *HIERACIUM ZETLANDICUM* Beeby (1891) 243 (Lectotype: Sand Voe, Northmaven, Shetlands, 4 July 1889, W. H. Beeby no. 1044 (BM)); (1892) 54; F. N. Williams (1902) 126 (exclud. Roeness Voe* et Sutherland loc.); Edmondston (1903) 71; F. J. Hanb. in Bab. (1904) 263 (exclud. Sutherland loc.); W. R. Linton (1905) 73; Beeby (1908) 113; Druce (1922) 499; (1925) 646; Roffey (1925) 29, no. 1199 (but one v.c. only (v.c.112));

* The modern official spelling is 'Ronas Voe'. In this paper we have always given the spelling used by the author in question.

Druce (1928) 70, no. 201 (1619) (but one v.c. only (v.c. 112)); Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 222; P. D. Sell & C. West in Dandy (1958) 127, no. 558: 1 : 170. PLATE 3a.

H. demissum subsp. *zetlandicum* (Beeby) Zahn (1921) 855.

Phyllopodous, or rarely with basal leaves withering at the time of flowering. Stem to 40 (–50 cult.) cm. high, slender, flexuous, often purplish, with numerous, medium to long, soft simple hairs at the base, which become gradually fewer upwards, the uppermost sometimes dark-based, usually stellate-hairy throughout, but sometimes sparingly so or not at all near the base, some plants with an occasional, very short, blackish glandular hair near the inflorescence. *Leaves deep green*, often suffused with purple; the *radical* 3–6; primordial small, subrotund, finely denticulate; the later variable, usually *broadly elliptic*, obtuse-mucronate to acute, narrowed below, *denticulate to shallowly but sharply serrate*, or ovate, obtuse-mucronulate, cuneate-based and denticulate, or in large specimens nearly rhomboidal, acute, cuneate-based and irregularly serrate, the teeth interspersed with denticulations, all with numerous, unequal, short to long, subsetiform simple hairs on both surfaces and on the margins, petioles winged, with few to many long simple hairs; *cauline* 2–4 (–6 cult.); the *lower elliptic to elliptic-lanceolate* or sometimes ovate, acute (occasionally obtuse-mucronate), cuneate-based with a winged petiole, *denticulate to sharply serrate*; the *median ovate to ovate-lanceolate*, acute to acuminate, cuneate- or rounded-based and semiamplexicaul, denticulate (sometimes finely serrate); the upper linear-lanceolate, linear or bractlike; all cauline glabrous or with a few, medium simple hairs above, with medium simple hairs beneath and on the margins, sometimes with sparse stellate hairs on one or both surfaces. *Inflorescence* compactly cymose, with 1–7 (–30 cult.), *often geminate capitula*; *peduncles* short to medium, suberect, with numerous stellate hairs, *numerous short, black glandular hairs* and a few, medium, usually dark-based simple hairs. *Capitula cylindrical in bud*. *Phyllaries* 8–9 (–10 cult.) mm. long, 1–2 mm. wide, incumbent in bud, linear-lanceolate, inner $\pm$ acute, sometimes abruptly narrowed near the apex, pale green, sometimes with darker centre, outer shorter, less acute, blackish-green; all *with scattered stellate hairs, numerous, black, unequal, very short to short glandular hairs* and sometimes an occasional, pale, short, dark-based simple hair. *Ligules* glabrous-tipped, *deep yellow*. *Styles yellow*, becoming discoloured in dried specimens. Margins of the receptacle-pits sharply dentate. Cypsela dark, 3.5–4 mm. long.

H. zetlandicum was originally discovered by W. H. Beeby on fine pasture above Sand Voe, Northmaven, in 1889. Two years later he found it in North Roe in the same parish. In 1908 he remarks that 'it is confined to a tract near North Roe about two by one miles, extending from Burga Taing northwards to Benegarth, but plentiful in many places within this area'. Beeby's records are represented by his exsiccatae nos. 1044, 1082, 1083, 1084, 1649 and 1660, which are to be found in several of the larger herbaria. It has since been collected in this area by R. J. Burdon and by M. L. Wedgwood (1921), G. C. Druce (1921 and 1924), J. E. Lousley (1950), C. West no. 53/10 (1953), N. D. Simpson no 53/760 and A. H. G. Alston (1954), W. Scott (1956) and by C. J. Cadbury and by W. Scott (1961). All the above gatherings have been made in grassy fields near North Roe. C. West noted that much of the area is now cultivated and the distribution of the species may be very restricted. In 1963, W. Scott found it in an entirely new locality, on the west side of Snarra Ness, Mainland.

In 1898 E. S. Marshall identified plants from Farr Bay, Kirtomy and Roeness Voe (Beeby no. 1092) as *H. zetlandicum*. This treatment was followed by F. N. Williams (1902) and F. J. Hanbury (1904). W. R. Linton (1905) pointed out that the Sutherland plant was in his opinion a form of *H. caledonicum* F. J. Hanb., and Beeby (1908) described the Roeness Voe plant as a new species, *H. breve*. K. H. Zahn (1921) considered that the Sutherland plant was intermediate between *H. caledonicum* and *H. scoticum* F. J. Hanb., and J. Roffey (1925) described it as a new species, *H. pseudozetlandicum*. H. W. Pugsley (1948) placed it as a variety under *H. caledonicum*. In our opinion some of the specimens can be referred to *H. scoticum*, others to *H. caledonicum*. It is difficult to understand how this Sutherland plant could ever have been referred to *H. zetlandicum* or even compared with the specimens later described as *H. breve*. As the differences between *H. zetlandicum* and the Sutherland plants had been clearly pointed out by W. R. Linton in 1905, the reason for recording *H. zetlandicum* for two vice-counties by Roffey (1925) and by Druce (1928) is not clear.

H. zetlandicum is quite unlike any other British species, but it is closely allied to the Faeroese *H. ostenfeldii* Dahlst. and *H. hartzianum* Dahlst., and to the Icelandic *H. arrostoecephalum* Omang. *H. ostenfeldii* has a less hairy stem, no simple hairs on the peduncles and phyllaries, and larger, broader and less sharply toothed leaves; *H. hartzianum* has longer petioles, broader and usually more sharply toothed basal leaves, no simple hairs on the peduncles, and more stellate hairs on the phyllaries; and *H. arrostoecephalum* has leaves with more stellate hairs and almost without simple hairs, and more stellate and simple hairs on its narrower, more acute phyllaries. These differences are small, and it would be interesting to bring the four species under cultivation in the same environment. In cultivation *H. zetlandicum* becomes much

larger and more robust, its leaves more numerous and more deeply toothed and the petioles longer. The inflorescence is more ample and the peduncles usually have more simple hairs. It may be noted that Beeby (1891) remarks: "The taller plants mentioned occurred towards the bottom of the hillside; and one specimen found quite at the bottom reached the height of 16 inches and bore 10 flowers; this was growing on a patch of waste ground and was evidently abnormal." Thus it seems that the dwarf, slender plant found in the typical habitat could be rather different if found in a more favourable situation. It should be noted, however, that the majority of its characters are constant and that it is sharply demarcated from all except the three species mentioned above.

2. *HIERACIUM BREVE* Beeby (1908) 112 (Lectotype: rocks, north side of Roeness Voe, Mainland, Shetlands, 9 July 1889, W. H. Beeby no. 1043 (BM)); Druce (1922) 499; Roffey (1925) 29 no. 1194; Druce (1928) 70 no. 196; Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 226; P. D. Sell & C. West in Dandy (1958) 127 no. 558: 1: 174. PLATE 3b. [*H. zetlandicum* sensu E. S. Marshall & Shoolbred (1898) *J. Bot. (Lond.)* 36, 172 (quoad Beeby no. 1092); sensu F. N. Williams (1902) 126 (quoad Beeby no. 1092).]

Aphyllipodous or with basal leaves withering at the time of flowering.* Stem 15–33 (–40 cult.) cm. high, robust or slender, markedly striate, with dense, long simple hairs especially below, those of the upper part dark-based, with a few stellate hairs above, without glandular hairs. *Leaves deep green*, sometimes becoming copper-coloured with age; the radical usually few, or occasionally up to 9; the primordial subrotund, subentire, cuneate-based to a broad, winged petiole; the *later* more or less *broadly elliptic to elliptic-rhomboidal*, obtuse-mucronulate to acute, *remotely denticulate or occasionally with a few, shallow, acute, patent teeth*, abruptly contracted to a rounded or cuneate base, petioles broadly winged; the *cauline* 4–11 (–13 cult.), the *lower ovate-lanceolate to ovate*, rarely ovate-rhomboidal, obtuse to acute, *denticulate or with 2–3, short, acute, patent teeth on each side*, cuneate-based, subpetiolate or sessile, the upper smaller, ovate-lanceolate, acute, toothed as lower, the base rounded and semi-amplexicaul; *all with straight, medium, bulbous-based, subsetiform simple hairs on both surfaces and the margins* (in cult. specimens sometimes very few), and on the petioles where they are similar but longer. Inflorescence compactly cymose (in cultivated specimens the branches more elongate), with 2–6 (–13 cult.) capitula, aeladium with medium peduncle; peduncles medium, suberect, with few stellate hairs, fairly numerous, short, patent simple hairs and occasionally a few, very short glandular hairs. *Phyllaries* 8–10 mm. long, 1.75–2 mm. wide, incumbent in bud, blackish-green, inner with paler margins, linear-lanceolate, obtuse, rarely with a few stellate hairs at base, *with numerous, very short, glandular hairs*, sometimes with a few, short simple hairs. Ligules yellow, glabrous tipped. *Styles discoloured*. Margins of the receptacle pits long-dentate. Cypsela dark, 3–3.5 mm. long.

H. breve was first collected by W. H. Beeby (nos. 1043 and 1092) on the north side of the Roeness Voe, Shetland, in 1889 and was referred by E. S. Marshall and F. N. Williams to *H. zetlandicum* Beeby. Beeby, however, realized it was not his *H. zetlandicum*, and described it as a new species. It was seen in 1920, in the same locality, by G. C. Druce who states that he saw two plants. There is a single specimen in Herb. Druce which is, however, atypical in having a nearly glabrous upper surface to the leaves and a long branching inflorescence. It matches well a cultivated specimen of Beeby's, and it is possible that Druce brought back a root and cultivated it. In general appearance these cultivated specimens resemble *H. zetlandicum*, but in detail they are very different. It was rediscovered after a long search by W. Scott in 1963. No species that at all resembles *H. breve* has been seen.

3. *Hieracium solum* P. D. Sell & C. West, sp. nov. PLATE 4a.

Holotype: Loch an Dughail, Kintyre, v.c. 101, Grid Ref. 16/805806, 11 July 1962, A. G. Kenneth (CGE).

In Sectione Alpestribus nulli speciei valde affinis.

Planta pseudophyllipoda. Caulis ad 50 cm. altus, flexuosus, fere purpureus, basi pilis paucis medio-cribus vel longis pallidis interdum nigribasibus simplicibus, superne stellatis dispersis, glanduliferis nullis vestitus. *Folia caesia*, interdum purpureo-tincta; basalia late elliptica, anguste elliptica vel oblonga, obtusa, subintegra, basi cuneata, sessilia, semiamplexicaulia; *caulina* 3–8, *interdum ramos abortivos ex axillis emittentia, lanceolata, acuta, subintegra, basi rotundata sessilia semiamplexicaulia; omnia in marginibus et raro in pagina pilis dispersis, pallidis, mediocribus vel longis, simplicibus vestita, et subtus secus costam et raro in pagina pilis dispersis, pallidis, mediocribus vel longis simplicibus vestita, interdum pilis simplicibus carentia*, interdum marginibus puberulis, interdum supra vel utrinque pilis stellatis dispersis induta. Anthela compacta

* Rarely phyllipodous.

cymosa, nonnunquam ramos ex axillis foliorum cauliorum superiorum emittens, capitulis 3-7 (-11), acladio pedunculo mediocri usque brevi praedito; pedunculi suberecti, mediocres vel longi, pilis stellatis, raro simplicibus vel glanduliferis brevissimis solitariis vestiti. *Squamae* 11-13 mm. longae, 1.5-2 mm. latae, in gemmis incumbentes, atro-virides, interiores marginibus pallidioribus, lineari-lanceolatae, obtusae, pilis stellatis paucis dispersis, aliis simplicibus dispersis obscuris mediocribus, aliis glanduliferis brevissimis nigris dispersis vestitae. Ligulae luteae, glabrae. Styli obscuri. Cypselam non vidimus.

Pseudophyllopodous. Stem to 50 cm. high, flexuous, usually purplish, with a few, medium to long, pale, sometimes dark-based simple hairs at the very base, with scattered stellate hairs above, without glandular hairs. *Leaves caesious*, sometimes purple-tinged; the basal broadly elliptic, narrowly elliptic or oblong, obtuse, subentire, cuneate to a sessile, semiamplexicaul base; the *cauline* 3-8, often with abortive branches in the axil of the leaves, lanceolate, gradually tapering from a rounded, sessile, semiamplexicaul base to a long acute apex, subentire, with scattered pale, medium to long simple hairs on the margins and midrib, rarely beneath, sometimes without simple hairs, sometimes with puberulous margins, sometimes with scattered stellate hairs on one or both surfaces. Inflorescence compactly cymose, often with branches from the axils of the upper cauline leaves, with 3-7 (-11) capitula, acladium with short or medium peduncle; peduncles suberect, medium to long, with stellate hairs, occasionally with a solitary, very short simple or glandular hair. *Phyllaries* 11-13 mm. long, 1.5-2 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, obtuse, with a few scattered stellate hairs, with scattered dark, medium simple hairs and scattered, very short, black glandular hairs. Ligules yellow, glabrous. Styles discoloured. Cypselas not seen.

This very distinct species, which has no close allies, is known only from the type locality and Cruach Lusach nearby. In both localities it is very scarce. Although it is placed between *H. breve* and *H. gratum*, the only character it has in common with these two species is its few cauline leaves.

The epithet *solum* is applicable in two senses, first because this species has no close allies, secondly because its only known localities are isolated ones for a species belonging to the Section *Alpestris*.

4. *HIERACIUM GRATUM* P. D. Sell & C. West (1955) 236 (Based on *H. demissum* var. *pulchelliforme* W. R. Linton); in Dandy (1958) 127 no. 558: 1 : 169. PLATE 4b.

[*H. pulchellum* sensu Beeby (1889-1890) 35; sensu F. N. Williams (1902) 162; sensu Edmondston (1903) 72; sensu F. J. Hanb. in Bab. (1904) 263.]

H. demissum var. *pulchelliforme* W. R. Linton (1905) 73 (Lectotype: Unst, Shetland, 16 August 1886, W. R. Linton in Herb. W. R. Linton (LIVU)); Druce (1922) 499; Roffey (1925) 29 no. 1198b; Druce (1928) 70 no. 200b.

H. dovrense subsp. *demissum* var. *pulchelliforme* (W. R. Linton) Beeby (1908) 114.

H. demissum subsp. *demissum* var. *pulchelliforme* (W. R. Linton) Zahn (1921) 855.

H. pulchelliforme (W. R. Linton) Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 221; non *H. pulchelliforme* Dahlst. ex Omang (1944) *Nytt. Mag. Naturvidensk* (Oslo), **84**, 151.

[*H. pulchellum* var. *vestitum* Lindeb., nomen in Herb.]

Phyllopodous or with basal leaves withering at time of flowering. Stem 15-35 (-40) cm. high, slender, flexuous, markedly striate, usually purple below, with long, pale, wavy simple hairs below, becoming nearly glabrous upwards, but usually with some simple hairs at the nodes, with scattered stellate hairs throughout, without glandular hairs. *Leaves* pale green, often suffused beneath and tinged above with purple; the *radical* few, soon dying off; the primordial when present broadly elliptic, obtuse-mucronulate, with a small denticulation on each side, cuneate to a winged petiole; the *lateral* narrowly to broadly elliptic or ovate-lanceolate with an obtuse-mucronulate to subacute apex, with up to 4 sharp, patent denticulations on each side; $\pm$ attenuate to winged petioles; the *cauline* 2-4 (-7), rapidly decreasing in size, the lower elliptic to lanceolate, obtuse-mucronulate to acute, toothed as basal, narrowed to winged, semiamplexicaul petioles; the median ovate-lanceolate or lanceolate, obtuse to acute, the apex sometimes tapering from near the middle, abruptly contracted to a narrow, sessile, semiamplexicaul base, toothed as lower; the upper lanceolate or ovate-lanceolate, acute, apex tapering from the middle, entire or with up to 3 denticulations on each side; all with long, pale, subsetiform simple hairs on both surfaces and on the margins, the upper cauline sometimes only sparingly so, and sometimes sparsely stellately hairy beneath. Inflorescence compactly cymose, with 1-6 capitula, sometimes with one or two branches from the upper leaf-axils; peduncles usually long, slender and suberect, sometimes with several bracts, with stellate hairs, with or without a very occasional short simple hair or very short glandular hair. *Phyllaries* 9-11 mm. long, c. 1.5 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, obtuse or occasionally acute, with a few stellate hairs

near the base, usually sparingly covered with short to medium, pale, dark-based simple hairs, and slender, very short, dark glandular hairs, sometimes, however, the simple hairs are numerous, sometimes nearly absent. Ligules yellow, glabrous. Styles discoloured. Margins of the receptacle pits fimbriate-dentate. *Cypsela* dark, 2.5–3 mm. long.

H. gratum was first found by W. H. Beeby (no. 608) and W. R. Linton near Burrafirth, Unst, Shetlands, in 1886. It was sent to Lindeberg, who referred it to *H. pulchellum* Lindeb. var. *vestitum* Lindeb. The varietal name does not seem to have been published and is only to be found on herbarium sheets. H. Dahlstedt was of the opinion that it was not *H. pulchellum* Lindeb., but a form very closely allied to *H. demissum* (Strömfelt) Dahlst. In 1905, W. R. Linton described it as a new variety, *pulchelliforme*, of *H. demissum*, which was raised to specific rank by H. W. Pugsley in 1946. As this name was a homonym we were forced to give it a new one, *H. gratum*, chosen because of the pleasing appearance of the plant.

This species has been re-collected by W. A. Shoolbred (1892), F. J. Hanbury (1894), G. C. Druce (1920), R. J. Burdon (1921), J. E. Lousley (1950), C. West no. 53/13 (1953), R. C. Palmer (1956), C. J. Cadbury (1960) and W. Scott (1962).

In our opinion this species bears little resemblance to either *H. pulchellum* or *H. demissum*. It shows no close affinity to any British species, but is closely allied to the Icelandic *H. elegantiforme* Dahlst. It differs from that species, however, in having nearly glabrous, not hairy, peduncles and larger flowers.

In 1953 it was sparingly distributed on steep, grassy slopes on both sides of the Burrafirth.

5. *Hieracium difficile* P. D. Sell & C. West, sp. nov. PLATE 5a.

Holotype: Bank of stream above the Bay of Okraquoy, Mainland, Shetlands, v.c. 112, Grid. Ref. 41/4431, 17 July 1964, R. C. Palmer, N. D. Simpson and C. West (CGE).

Ab *H. australiore* (Beeby) Pugs. pilis paucioribus vestitis squamisque angustioribus differt.

Folia basalia florendi tempore marcescentia vel delapsa. Caulis ad 70 cm. altus, flexuosus, purpureus praesertim subtus, pilis vestitus aliis simplicibus longis flexuosis interdum nigribasibus ubique sed supra tantum dispersis, aliis stellatis ubique, glanduliferis nullis. *Folia* mediocriter viridia, interdum purpureo-tincta; *basalia late elliptica*, obtuso-mucronulata, *subintegra*, e basi ad petiolum brevem alatum attenuata, utrinque et in marginibus pilis simplicibus densis, mediocribus, pallidis, subsetiformibus vestita; *caulina 4–8, remota, a basi caulis sursum gradatim minora*, interdum ramos abortivos ex axillis emittentia; *inferiora elliptica, acuta vel longe acuta, remote et leviter denticulata, sensim ad basem sessilem semiamplexicaulem attenuata* vel petiolo alato semiamplexicaule, ut folia basalia vestita sed pagina superiore pilis simplicibus paucioribus induta; *superiora lanceolata, longe acuta*, e basi rotundata, sessilia semiamplexicaulia, utrinque pilis simplicibus mediocribus dispersis et interdum aliis stellatis vestita. Anthela anguste et compacte cymosa, capitulis 3–12, acladio pedunculo mediocri praedito; pedunculi suberecti, pilis stellatis, interdum pilo unico simplici brevi nigribasi et nonnunquam pilis glanduliferis brevissimis perpaucis obscuris vestiti. *Squamae* 9–10 mm. longae, 1–1.5 mm. latae, in gemmis incumbentes, atro-virides, interiores marginibus pallidioribus, lineari-lanceolatae, obtusae vel subacutae, basi pilis stellatis dispersis, *alioquin pilis glanduliferis brevibus vel brevissimis obscuris dispersis et nonnunquam aliis simplicibus solitariis brevibus nigribasibus vestitae*. Ligulae luteae, glabrae. Styli obscuri. *Cypsela* obscura, circa 4 mm. longa.

Basal leaves withering before or at the time of flowering. Stem to 70 cm. high, flexuous, purplish especially below, with long, wavy, pale, sometimes dark-based simple hairs throughout, but only scattered above, with scattered stellate hairs throughout, without glandular hairs. *Leaves* medium green, sometimes purplish tinged; the *basal broadly elliptic*, obtuse-mucronulate, *subentire*, attenuate to a short winged petiole, with dense medium, pale, subsetiform simple hairs on both surfaces and the margins; the *cauline 4–8, widely spaced and gradually decreasing in size*, sometimes with abortive branches in the axils of the leaves; the *lower elliptic, acute to long acute, remotely and shallowly denticulate, gradually narrowed to a broad, sessile semiamplexicaul base* or with a winged, semiamplexicaul petiole, hairs as on basal but fewer in number on the upper surface; the *upper lanceolate, gradually tapering from a rounded, sessile, semiamplexicaul base to a long acute apex*, with scattered, medium simple hairs and sometimes with stellate hairs on both surfaces. Inflorescence narrowly and compactly cymose, with 3–12 capitula, acladium with medium peduncle, peduncles suberect, with stellate hairs, sometimes with an occasional, short, dark-based simple hair and a very short, dark glandular hair. *Phyllaries* 9–10 mm. long, 1–1.5 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, obtuse to subacute, with scattered stellate hairs at the base, *with scattered short and/or very short, dark glandular hairs, and an occasional, short, dark-based simple hair*. Ligules yellow, glabrous. Styles discoloured. *Cypsela* dark, about 4 mm. long.

This species was discovered by W. Scott in 1962, and collected later that year by R. C. Palmer. In 1964 R. C. Palmer, N. D. Simpson and C. West examined the colony and obtained additional material. We have given it the specific epithet *difficile*, not only because of the difficulty in placing it in its correct

position in the Section *Alpestris*, but also because the variation in hair clothing, even on the same plant, makes it difficult to provide a precise diagnosis. For example, the leaves of the holotype have stellate hairs on both surfaces whereas the leaves of the other specimens have not.

Normal plants of *H. difficile* closely resemble *H. australis*, but differ by being less hairy and having narrow phyllaries. A plant from this population, which seems to us to be conspecific, has a basal rosette and closely resembles *H. gratum* in appearance, but it is immediately distinguishable by its more numerous, less denticulate cauline leaves.

6. *HIERACIUM AUSTRALIUS* (Beeby) Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 224. PLATE 5b.

[? *H. crocatum* sensu Tate (1866) 6.]

[*H. dovrense* sensu Beeby (1889–1890) 35; sensu F. N. Williams (quoad Shetland loc. exclud. Beeby no. 1151) (1902) 161; sensu Edmondston (1903) 72; sensu F. J. Hanb. in Bab. (1904) 264; sensu W. R. Linton (quoad Shetland loc.) (1905) 72.]

H. dovrense subsp. *demissum* var. *australius* Beeby (1908) 114 (Lectotype: Rocks, Loch of Cliff, Unst, Shetlands, 27 July 1886, W. H. Beeby no. 609 (BM)).

H. demissum var. *australius* (*australe*) (Beeby) Druce (1922) 499; Roffey (1925) 29 no. 1198c; Druce (1928) 70 no. 200 c [1621].

[*H. polycomum* sensu Dahlst. (quoad Ronas Voe loc.) (1926 for 1925) *Rep. Bot. Soc. & Exch. Cl. Brit. Isles*, 7, 997.]

[*H. polycomatum* sensu Druce (quoad Ronas Voe et Cliva Hill loc.) (1928) 71 no. 236.]

Aphyllopodous or with basal leaves withering at the time of flowering. Stem to 65 cm. high, usually robust, markedly striate, purplish below, usually with long, pale simple hairs below, sometimes throughout, the hairs often deciduous above, with a few stellate hairs just below the inflorescence, without glandular hairs. Leaves pale green, sometimes with purplish spots; the *radical* soon drying up and dropping off, *elliptic to broadly elliptic*, obtuse-mucronate to acute, *denticulate*, narrowed below to winged petioles, with pale, medium, subsetiform, bulbous-based hairs on both surfaces, the margins and petioles; *cauline* 5–12 (–21 cult.), *gradually decreasing in size, the lower more or less elliptic*, obtuse-mucronate to acute, *subentire or sharply denticulate*, attenuate to a winged petiole, clothed as basal, the *median very variable, elliptic, lanceolate or oblong-lanceolate* (sometimes curved in the shape of a crescent), acute, sometimes gradually narrowed from the middle, *usually with sharp denticulations*, gradually narrowed to a semiamplexicaul base, hair-clothing as on lower, but sparser, *some specimens with abortive branches growing in the axils of the leaves*, the upper ovate-lanceolate, gradually narrowed from a rounded base to an acute apex, denticulate or sometimes with a few sharp teeth, usually semiamplexicaul, nearly glabrous above otherwise as lower, the uppermost sometimes with scattered stellate hairs beneath. Inflorescence compactly cymose, in cultivation laxer and cymose-corymbose, with 2–10 (–80 cult.) capitula, the median acladium subtended by the branches; *peduncles* suberect, stellately hairy, *with an occasional, short, dark-based simple hair*. Phyllaries 9–10·5 mm. long, 1·5–2 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, obtuse, with a few stellate hairs near the base, *with many, very short, pale and dark, glandular hairs, and few to many, usually short, rarely medium, pale, dark-based simple hairs, sometimes without simple hairs*. Ligules yellow, glabrous. Styles discoloured. Margins of the receptacle pits long-dentate. Cypsela dark, 3–3·5 mm. long.

The first record of this species was probably that of Tate (1866), who recorded as *H. crocatum* plants from Burra-firth and Loch-a-Cliff* which were almost certainly this species. The earliest specimens we have seen, however, are those collected in 1886 at Loch-a-Cliff by W. H. Beeby (no. 609), who named them *H. dovrense*. In 1908, however, it was recognized as being distinct from that species, and was described by W. H. Beeby as a new variety, *australius*, of *H. dovrense* subsp. *demissum*. It has subsequently been found in that area by W. H. Beeby no. 859 and 861 (1887), E. F. Linton set no. 156 (1891), F. J. Hanbury (1894), R. J. Burdon and G. C. Druce (1920 and 1921), J. E. Lousley (1950), C. West no. 53/12 (1953) and R. C. Palmer and W. Scott (1962). There are specimens of this species from Ronas Voe collected by G. C. Druce (OXF) labelled *H. polycomum*, and from Cliva Hill in 1920 and 1921 (BM) by the same collector labelled *H. polycomatum* var. *thulense*.

H. australis is quite distinct from *H. dovrense* Fries, *H. demissum* (Strömfelt) Dahlst., and *H. polycomum* Dahlst. (*H. polycomatum* (Zahn) Druce) with which it has been confused. The only species closely allied to *H. australis* is *H. difficile*.

* The modern official spelling is Loch of Cliff.

7. *HIERACIUM DOVRENSE* Fries (1848) 128 (Provisional lectotype: Norveg. centr. a Dovre in Finmarkiarn copiose, M. N. Blytt, sent out as *H. cydonaeifolium* in Fries Set 11 no. 12 (BM)); E. S. Marshall & Shoolbred (1898) 172; F. N. Williams (1902) 161 (quoad Ben Loyal* loc.); W. R. Linton (1905) 72 (quoad Ben Laoghal* loc.); Roffey (1925) 29 no. 1190 (one v.c. only); Druce (1928) 70 no. 192 (1617) (one v.c. only); Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 221; P. D. Sell & C. West in Dandy (1958) 127 no. 558; 1: 168. PLATE 6a.

H. boreale β *latifolium* Blytt (1838) 304 (Lectotype: Lierne ved Drivstuen, 1835, M. Blytt no. 110 (O)).

H. dovrense var. *vulgare* Lindeb. in Blytt (1874) 668.

H. dovrense subsp. *eudovrense* Omang in Blytt (1906) 760.

H. carpathicum subsp. *dovrense* (Fries) Zahn (1921) 810) (exclud. all Brit. loc. except Ben Laoghal).

Aphyllopodous or with basal leaves withering at the time of flowering. Stem to 50 cm. high, robust, flexuous, slightly purple tinted below, with long, pale simple hairs throughout, sometimes sparsely, sometimes densely, sometimes the hairs deciduous, sometimes with a few stellate hairs above, with an occasional, very small glandular hair. *Leaves* pale green, radical few (in British specimens seen, soon disappearing); primordial elliptic, obtuse-mucronulate, slightly denticulate, attenuate to the petiole; the later (from Scandinavian specimens) elliptic, obtuse-mucronulate, remotely denticulate to coarsely dentate, attenuate to winged petioles which are broadened below, midrib very prominent, nearly glabrous above, with a few, pale, medium simple hairs below, margins and petioles with medium, pale simple hairs; *cauline* 4–8, slowly decreasing in size upwards, the lower and median elliptic, obtuse-mucronulate to acute, denticulate to sharply and irregularly dentate, the teeth ascending mammilliform, the lower attenuate below to winged semi-amplexicaul petioles, the median to a sessile or abruptly contracted semiamplexicaul base, clothing as radical, the upper lanceolate, acute to acuminate, denticulate or shallowly dentate, cuneate to a sessile, semiamplexicaul base, glabrous except on the midrib below. Inflorescence rather compactly cymose, usually with 3–9 (–12) capitula, *accladium* geminate, *peduncles* medium, suberect, slender, stellately hairy, otherwise variable in clothing with few to numerous, short to medium, dark-based simple and very short, black glandular hairs. *Phyllaries* 9–11 mm. long, 2–2.5 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, obtuse, sparingly stellately hairy with a tuft at the apex, with many, short to medium, dark-based simple and very short, black glandular hairs. *Ligules* yellow, glabrous. *Styles* discoloured. *Margins* of the receptacle pits long-dentate. *Cypselas* dark, 2–2.5 mm. long in Scandinavian specimens, cypselas from British plants not seen.

H. dovrense was described by E. Fries in 1848 from several alpine localities in Norway, particularly in the Dovre area. He states that he has seen a specimen of this species from Scotland, but the specimen has not been traced. In 1896 E. S. Marshall and W. A. Shoolbred gathered specimens at Glen Roy, Inverness, which were identified as *H. dovrense*. These were later sent out in Linton's Set no. 46 under that name. They are, however, *H. dewarii* Syme. The following year Marshall and Shoolbred collected the true plant on Ben Loyal, which is its only known British locality. It has subsequently been seen by J. E. Raven in 1952 and by C. West in 1953. Specimens collected by W. H. Beeby and F. J. Hanbury in Unst, Shetland, were identified as *H. dovrense*, but they belong to a different species, *H. australius* (Beeby) Pugsley. Specimens collected by E. S. Marshall at Tain in 1890 and labelled *H. dovrense* are *H. subrude* (A.T.) A.T.

The typification of *H. dovrense* Fries is rather complicated. There is no specimen that can be regarded as a type in Fries' own herbarium at Uppsala. At Oslo there are four syntypes of *H. boreale* ? var. *latifolium* Blytt, which is cited in the synonymy of Fries' original account. Although these specimens are all typical *H. dovrense*, there is no evidence on the sheets that they were seen by Fries. Fries' *Exsiccatae* Herb. Norm. XI : 12 sent out as *H. cydonaeifolium* is cited by him in his original account of *H. dovrense*, and can be regarded as type material. All the specimens we have seen of this set number are badly damaged, but they are in our opinion certainly referable to the taxon regarded as *H. dovrense*. We provisionally select the sheet in the British Museum (Nat. Hist.) as the lectotype, but recommend that should a better specimen be found, a fresh designation should be made.

K. H. Zahn (1921) describes seven subspecies of his *Grex H. dovrense*, all of which come from Scandinavia. We have not seen specimens of these, but from the descriptions they seem to differ little from *H. dovrense* Fries in its typical form. No British species is closely allied to *H. dovrense*.

* Ben Loyal, not Ben Laoghal, appears to be the correct modern spelling for the name of this mountain.

8. *HIERACIUM PRAETHULENSE* Pugsley (1948) 226 (Holotype: rocks on north side of Roeness (Ronas) Voe, Mainland, Shetlands, 3 August 1891, W. H. Beeby no. 1115 in Herb. F. J. Hanbury (BM)); P. D. Sell & C. West in Dandy (1958) 127, no. 558:1:175. PLATE 6b.

[*H. auratum* sensu Beeby (1892) 55.]

H. auratum var. *thulense* F. J. Hanb. (1894) 232 (Lectotype: rocks on north side of Roeness Voe, Mainland, Shetlands, 3 August 1891, W. H. Beeby no. 1115 in Herb. F. J. Hanbury (BM)); F. J. Hanb. in Bab. (1904) 267; W. R. Linton (1905) 89; Beeby (1908) 115.

[*H. aestivum* subsp. *crocatum* sensu Zahn (quoad Shetland loc.) (1922) 922.]

H. crocatum var. *thulense* (F. J. Hanb.) Druce (1928) 71, no. 245e (cf. *Rep. Bot. Exch. Cl. Brit. Isles* 8, 879 and 880 (1929 for 1928)).

[*H. praethulense* Pugsley in A. R. Clapham (1946) 346 nom. nud.]

Hypophyllopodous or aphyllpodous or with basal leaves withering at the time of flowering. Stem to 60 cm. high, usually rather slender but some large plants robust, flexuous, markedly striate, purplish below, sometimes throughout, with long, pale simple hairs throughout, but decreasing in density upwards, sometimes without simple hairs except at the very base, with scattered stellate hairs in the upper half, without glandular hairs. *Leaves* pale green, often suffused with purple; the *radical* few or absent, *usually broadly elliptic and sometimes almost subrotund*, apex rounded or obtuse, remotely denticulate, narrowed (sometimes abruptly) to winged petioles, *with scattered, medium simple hairs or glabrous above*, with long simple hairs beneath and on the margins; the *cauline* 7–12 (–16) (in cultivation with numerous other leaves on the branches), the *lower variable, elliptic, ovate or oblong-lanceolate*, obtuse-mucronulate to acute, *remotely denticulate*, attenuate to a winged petiole or abruptly narrowed to a sessile, semiamplexicaul base, *clothed as basal, the median elliptic or lanceolate, acute, remotely denticulate, with a rounded or subcordate semiamplexicaul base, glabrous above*, with few simple hairs beneath, the margins with simple hairs or scaberulous; the upper ovate-lanceolate to lanceolate, gradually narrowed to an acute apex, entire or with an occasional denticulation, base rounded or subcordate, semiamplexicaul, glabrous above, with few simple and stellate hairs beneath, margins ciliate or scaberulous. *Inflorescence* compactly cymose (in cultivation cymose-corymbose), with 2–9 (–100 cult.) capitula, with medium acaudium; the *peduncles* slender, suberect, medium to long, sparingly stellately hairy and *sometimes with a few, pale, short simple hairs, without glandular hairs*. *Phyllaries* 9–10 mm. long, (1–) 1.5–2 mm. wide, incumbent in bud, blackish-green, inner with paler margins, linear-lanceolate, obtuse, with scattered stellate hairs, *few to many, very short to short glandular hairs and occasionally a few, short simple hairs intermixed*. Ligules yellow, glabrous. *Styles* yellow, sometimes discoloured when dry. Margins of the receptacle pits shortly and irregularly dentate. *Cypsela* dark, 4–4.5 mm. long.

H. praethulense was first found by W. H. Beeby in 1889 (nos. 1041 and 1042), and re-collected by him in 1891 (nos. 1108, 1109, 1111, 1112, 1114, 1115 and 1116). It has since been collected by G. C. Druce (1920), J. E. Lousley (1950), C. West no. 53/8 (1953), C. J. Cadbury (1960 and 1961) and W. Scott (1961 and 1963). It is a frequent plant on the north side of Ronas Voe and near Mavisgrind.

In 1892 Beeby called it *H. auratum* Fries; two years later F. J. Hanbury described it as a new variety, *thulense*, of that species. It was included under *H. aestivum* subsp. *crocatum* by Zahn, and both Roffey and Druce transferred the varietal name *thulense* to *H. crocatum* Fries. Pugsley quite rightly gave the plant specific status.

In general appearance it resembles the Icelandic *H. phrixoclonum* Omang, but that species differs in having fewer cauline leaves, more glandular hairs on the peduncles, dark styles and smaller achenes. It is also closely allied to the Icelandic *H. halfdanii* Oskarss. from which it differs in being more hairy throughout and in having numerous fine glandular hairs on the peduncles.

In cultivation, *H. praethulense* often becomes a very large plant with a widely spreading inflorescence with many capitula. It then has a superficial resemblance to *H. latobrigorum* (Zahn) Roffey (*H. auratum* auct.), which is perhaps the reason why Beeby and Hanbury originally placed it under that species. The shape and clothing of its phyllaries, however, are very different. The leaves in cultivated plants are far less amplexicaul than in the wild plant, a point which suggests that one of the characters on which the Section *Alpestris* is based may be artificial.

The plants which Druce recorded as *H. polycomum* Dahlst., and which Pugsley referred to *H. praethulense*, are in fact *H. australis* (Beeby) Pugsley.

9. *HIERACIUM HETHLANDIAE* (F. J. Hanb.) Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 224; P. D. Sell & C. West in Dandy (1958) 127 no. 558: 1: 171. PLATE 7a.

[*H. truncatum* sensu Beeby (1892) 55.]

H. dovrense var. *Hethlandiae* F. J. Hanb. (1894) 232 (Lectotype: rocks at the foot of Cliva Hill, near Brae, Mainland, Shetlands, 14 August 1891, W. H. Beeby no. 1107 in Herb. F. J. Hanbury (BM)); F. J. Hanb. in Bab. (1904) 264; W. R. Linton (1905) 72; Druce (1922) 499 (exclud. Burn of Quoys loc.).

[*H. dovrense* sensu F. N. Williams (1902) 162 (quoad W. H. Beeby no. 1151).]

H. dovrense subsp. *humidorum* var. *Hethlandiae* (F. J. Hanb.) Beeby (1908) 114.

H. aestivum subsp. *crocatum* subvar. *Hethlandiae* (F. J. Hanb.) Zahn (1922) 923.

H. crocatum forma *Hethlandiae* (F. J. Hanb.) Roffey (1925) 29, no. 1243.

H. crocatum var. *Hethlandiae* (F. J. Hanb.) Druce (1928) 71, no. 245c. (1635).

Aphyllopodus or with basal leaves withering at the time of flowering. Stem to 40 cm. high, slender, flexuous, purplish below, often throughout, with long, pale simple hairs only at the very base and then often only sparingly, with $\pm$ numerous stellate hairs especially above, without glandular hairs. *Leaves* 5–9, *caesious medium green*, often purple-tinted especially beneath and on the margins, the *upper rapidly decreasing in size*; the *lowest broadly elliptic*, $\pm$ obtuse, *subentire*, attenuate to short, winged, semiamplexicaul petioles, glabrous or with pale, medium, subsetiform, bulbous-based simple hairs above and on the margins, petioles with medium, pale, simple hairs; the *lower cauline narrow-elliptic, gradually narrowed at both ends, apex acute, denticulate*, with short winged petioles, or sessile and semiamplexicaul, glabrous or with pale, medium simple hairs on both surfaces and the margins; the *median as lower, but sometimes broader and more rounded at the base with a long acute apex*, sessile, glabrous or nearly so on both sides, margins puberulous, or with a few, short simple hairs; the *upper gradually narrowed to an acute, apiculate tip from a broad, rounded, semiamplexicaul base*, glabrous except for a few stellate hairs below. *Inflorescence* compactly cymose, with 2–4 capitula, acladium with medium peduncle; *peduncles* medium, suberect, slender, stellately hairy, *usually without simple hairs, without glandular hairs*. *Phyllaries* 10·5–12 mm. long, 1·5–1·75 mm. wide, incumbent in bud, blackish-green, inner with paler margins, linear-lanceolate, obtuse, with stellate hairs scattered over the whole surface, *with very short to medium, dark glandular and some short to medium, dark simple hairs*. Ligules yellow, glabrous. Styles discoloured. Margins of the receptacle pits long-dentate. Cypsela dark, 3–5 mm. long.

This species was first described as a variety of *H. dovrense* Fries by F. J. Hanbury (1894), from material collected by W. H. Beeby (no. 1107) at Cliva Hill. It was later placed by some authors under *H. crocatum* Fries. It is a rare plant, and has only been collected since by W. H. Beeby no. 1151 (1896), R. J. Burdon (1920), G. C. Druce (1920 and 1921), J. E. Lousley (1950), C. West no. 53/4 (1953) and C. J. Cadbury and W. Scott (1960). A sheet in Herb. Mus. Brit. (BM), collected by R. J. Burdon at Roeness Voe on the 28 July 1920, contains a mixed gathering of two plants of this species and one of *H. vinicaule*. *H. hethlandiae* needs to be refound at this locality. Both W. H. Beeby (1908) and G. C. Druce (1922) remark that it grows in some plenty on Cliva Hill rocks, but C. West (1953) found that much of the cliff had been blasted away for road repair, and that the plant might be in danger of extinction. In 1960 Cadbury and Scott saw eight plants. Druce (1922) identified plants from the Burn of Quoys as *H. hethlandiae*, but we consider these plants to be a distinct species, *H. dilectum*.

H. hethlandiae does not seem to be closely allied to any of the British species of the Section *Alpestris*. It was likened to the Scandinavian *H. dovrense* subsp. *humidorum* Almq. ex Elfstrand by Elfstrand, but that taxon, although closely allied to *H. hethlandiae*, differs in its long-petioled lower leaves, smaller capitula and markedly pale-edged phyllaries. *H. hethlandiae* has a superficial resemblance to *H. sparsifolium* Lindeb. (*H. pseudoprotractum* Pugsley), which grows with it; it can easily be separated, however, by its broad-based, semi-amplexicaul leaves and different clothing of the inflorescence.

10. *Hieracium attenuatifolium* P. D. Sell & C. West, sp. nov. PLATE 7b.

Holotype: Laxo Burn, Mainland, Shetlands, August 1953, C. West no. 53/1 (CGE)

[*H. demissum* var. *pulchelliforme* sensu Druce (1925) 646.]

Ab *H. dilecto* P. D. Sell & C. West, *H. pugsleyi* P. D. Sell & C. West et *H. subtruncato* Beeby squamis capitulorum pilis glanduliferis densis indutis distinguitur.

Planta aphyllopoda. Caulis ad 90 cm. altus, flexuosus, $\pm$ purpureus, pilis simplicibus longis pallidis superne saepe deciduis, per bases pilorum decidorum trunciformes tandem scaberulus, aliis stellatis paucis, glanduliferis nullis. *Folia caulina* 6–15, saturate vel pallide viridia, saepe purpureo-tincta; *ima late elliptica*, rotundo-obtusum-mucronulata, *subintegra vel remote denticulata, basi cuneata vel in petiolum attenuata; inferiora elliptica, interdum late elliptica*, obtusum-mucronulata vel subacuta, *remote denticulata vel raro dente levi acuto solitario praedita, basi gradatim in petiolum late alatum angustata; media anguste ad late elliptica*,

±*acuta*, *remote denticulata vel raro dentibus levibus acutis paucis praedita*, *basi angustata vel abrupte contracta*, *sessilia*, *semiamplexicaulia*; superiora lanceolata vel lineari-lanceolata, *acuta*, *subintegra vel bracteiformia*; inferiora et media utrinque et in marginibus pilis simplicibus mediocribus pallidis, praeterea media raro subtus pilis stellatis paucis, superiora raro pilis simplicibus paucis et utrinque pilis stellatis dispersis vestita cum marginibus costisque puberulis. Anthela laxa cymosa, capitulis 2–7 (ad 13 cult.), acladio pedunculo longo praedito; pedunculi vulgo longi, pilis stellatis dispersis, saepe aliis simplicibus numerosis mediocribus nigribasibus, aliis glanduliferis paucis brevissimis atris vestiti. *Squamae* 10–12 mm. longae, 1·5–2 mm. latae, in gemmis incumbentes, *exteriore atro-virides*, *brevissimae*, *triangulato-ovatae*, *mediae marginibus pallidioribus*, *lanceolatae*, *interiores valde pallidae et angustiores*, omnes obtusae, pilis stellatis paucissimis, aliis glanduliferis inaequalibus brevissimis usque mediocribus nigris, aliis simplicibus paucis mediocribus obscuris vestitae. Ligulae pallide luteae, glabrae. *Styli lutei*, in sicco obscuri. Alveoli receptaculi margine breviter dentati. *Cypselae* obscurae, 4·5–5 mm. longae.

Aphyllopodous. Stem to 90 cm. high, flexuous, ±purple, with long, pale simple hairs above, often becoming scaberrulous from the bases of the deciduous hairs, with a few stellate hairs, without glandular hairs. *Cauline leaves* 6–15, deep or pale green, often suffused with purple; the lowest broadly elliptic, rounded-obtuse-mucronulate, *subentire to remotely denticulate*, *cuneate- or attenuate-based to winged petioles*; the lower elliptic, sometimes broadly, obtuse-mucronate to subacute, *distantly denticulate or occasionally with one or more sharp teeth, gradually narrowed below to broad winged petioles*; the median narrow to broadly elliptic, ±acute, *distantly denticulate or rarely with a few, sharp, shallow teeth, narrowed or abruptly contracted to a sessile, semiamplexicaul base*; the upper lanceolate to linear-lanceolate, acute, subentire or bractlike; the lower and median with medium, pale simple hairs on both surfaces and the margins, the median occasionally with a few stellate hairs beneath, the upper with or without an occasional simple hair, with scattered stellate hairs on both surfaces, margins and veins puberulous. Inflorescence loosely cymose, with 2–7 (–13 cult.) capitula, acladium with a long peduncle; peduncles mostly long, with scattered stellate hairs, usually with numerous, medium, dark-based simple hairs and an occasional very short to short, dark glandular hair. *Phyllaries* 10–12 mm. long, 1·5–2 mm. wide, incumbent in bud, the outer blackish green, very short, triangular-ovate, the median with paler margins, lanceolate, the inner similar to the median but paler and rather narrower, all obtuse, with very few stellate hairs, numerous, unequal, very short to medium, dark glandular and a few, medium, dark simple hairs. Ligules pale yellow, glabrous. *Styles* yellow, darkening when dry. Margins of receptacle pits shortly dentate. *Cypselae* dark, 4·5–5 mm. long.

G. C. Druce was the first person to mention this species from the Laxo Burn, after his third visit to the Shetlands in 1924, and we have seen three sheets containing eight very poor specimens which he gathered. In his *Additions to the Flora Zetlandica* (1925), Druce refers this plant to *H. demissum* var. *pulchelliforme* W. R. Linton, and his specimens are so labelled. This species bears not the slightest resemblance to *H. gratum* P. D. Sell and C. West (= *H. demissum* var. *pulchelliforme* W. R. Linton).

In 1953, C. West no. 53/1, found it growing in abundance on the grassy banks of the Laxo Burn, where it has since been collected by N. D. Simpson no. 53/762 (1954), W. Scott (1956) and C. J. Cadbury (1962).

In 1954 Simpson (no. 54/291) gathered it from sea cliffs at West Burra-firth, Sandsting, where it was collected again by W. Scott in 1963. The plants from Sandsting differ from those of the Laxo Burn in having slightly narrower phyllaries clothed with slightly longer glands, but these differences are negligible. Plants collected by W. Scott at Boust, Sandness, 29 July 1962, seem to belong to this species, but they have fewer leaves and apparently darker styles.

H. attenuatifolium is closely allied to *H. subtruncatum* Beeby, *H. pugsleyi* P. D. Sell & C. West and *H. dilectum* P. D. Sell & C. West. From these three species it can be distinguished by the dense glandular hairs on its phyllaries, on which there are only a few simple hairs.

We have called it *attenuatifolium* because it can readily be distinguished from *H. subtruncatum* Beeby, which it strongly resembles in appearance, by the narrower more attenuate bases of the leaves.

11. *Hieracium pugsleyi* P. D. Sell & C. West, sp. nov. PLATE 8a.

Holotype: grassy banks of burn, Weisdale, Mainland, Shetlands, August 1953, C. West no. 53/14 (CGE).

Ab *H. subtruncatum* Beeby squamis capitulorum pilis simplicibus numerosis vestitis, ab *H. attenuatifolio* P. D. Sell et C. West capitulis minoribus, squamis capitulorum pilis glanduliferis sparsis et forma foliorum basali differt, praeterea ab *H. dilecto* P. D. Sell et C. West caulibus pedunculisque pilis simplicibus praeditis et internodiis longioribus distinguitur.

Planta aphyllopoda. Caulis ad 60 cm. altus, gracilis, flexuosus, purpureus, perpilosus, pilis longis pallidis simplicibus, superioribus nigribasibus, superne pilis stellatis paucis, nonnunquam glanduliferis sparsis brevissimis vestitus. *Folia caulina* 8–12 (–15), pallide viridia, praecipue infra purpureo-tincta; *inferiora*

elliptico-oblonga ad oblonga, obtuso-mucronata ad subacuta, *subintegra ad minute denticulata*, basi in petiolum brevem alatum attenuata; *media elliptico-oblonga ad oblonga*, $\pm$ acuta, *subintegra ad regulariter denticulata*, basi rotundata, sessilia, *semiamplexicaulia*; superiora lanceolata ad ovato-lanceolata, acuta, subintegra, basi rotundata, sessilia; omnia utrinque et in marginibus pilis pallidis mediocribus simplicibus vestita, superiora inferne pilis stellatis paucissimis vestita. Anthela cymosa, nonnunquam ramos longos foliosos ex axillis foliorum caulinarum emittens, capitulis 3–9 (–22), acladio pedunculo brevi usque mediocri praedito, ramis gracilibus suberectis; pedunculi breves usque mediocres, nonnunquam geminati, pilis aliis stellatis paucis, aliis simplicibus numerosis mediocribus basi obscuris, aliis glanduliferis raris brevissimis obsiti. Squamae 9–10 mm. longae, 1·5–1·75 mm. latae, in gemmis incumbentes, atro-virides, nonnunquam apicibus rubescentibus, interiores marginibus pallidioribus, lanceolatae, obtusae, pilis aliis stellatis rarissimis, aliis simplicibus numerosis mediocribus basi obscuris, aliis glanduliferis paucis vel multis brevissimis obscuris vestitae. Ligulae luteae, glabrae. Styli lutei. Alveoli receptaculi margine breviter dentati. Cypsela obscura, 3–3·5 mm. longae.

Aphyllopodus. Stem to 60 cm. high, slender, flexuous, purple, with dense, long, pale simple hairs throughout, those of the upper half with dark bases, with few, scattered stellate hairs, sometimes with a few very short glandular hairs. *Cauline leaves* 8–12 (–15), pale green suffused with purple especially on the lower surface; the lower elliptic-oblong to oblong, obtuse-mucronate to subacute, subentire to minutely denticulate, base attenuate to a short, winged petiole; the median elliptic-oblong to oblong, $\pm$ acute, subentire to regularly denticulate, base rounded, sessile, *semiamplexicaul*; the upper lanceolate to ovate-lanceolate, acute, subentire, with a rounded, sessile base; all with pale, medium simple hairs on both surfaces and the margins, the uppermost with very few stellate hairs beneath. Inflorescence cymose, sometimes with long leafy branches in the leaf-axils, with 3–9 (–22) capitula; acladium with short to medium peduncle, with slender, suberect branches; peduncles short to medium, sometimes geminate, with scattered stellate hairs, numerous, medium, dark-based simple hairs and a few, very short glandular hairs. *Phyllaries* 9–10 mm. long, 1·5–1·75 mm. wide, incumbent in bud, blackish green, sometimes reddish at the tip, the inner with paler margins, linear-lanceolate, obtuse, with very few stellate hairs, numerous, medium, dark-based simple hairs and few or many, very short, dark glandular hairs. Ligules yellow, glabrous. Styles yellow. Receptacle pits shortly dentate. Cypsela dark, 3–3·5 mm. long.

This species was discovered by C. West (no. 53/14) in 1953 on grassy banks by the Weisdale Burn, Mainland, Shetlands, where it was re-collected in 1961 by C. J. Cadbury and in 1962 by W. Scott. It has also been collected at the Laxo Burn, Lunnasting by N. D. Simpson (no. 54.762) in 1954, and near Otters Wick, Yell, by C. J. Cadbury and by R. C. Palmer in 1961. In 1963, W. Scott collected it at the Burn of Laxdale near Cunningsburgh and at Tumblin, Sandsting.

It is closely allied to *H. subtruncatum* Beeby, *H. attenuatifolium* P. D. Sell & C. West and *H. dilectum* P. D. Sell & C. West. From *H. subtruncatum* it differs in having numerous simple hairs on the phyllaries, from *H. attenuatifolium* by its smaller heads, less glandular hairy phyllaries, and differently shaped basal leaves, and from *H. dilectum* by its hairy stems and peduncles and its longer internodes.

It is thought appropriate to dedicate this plant to the late Mr. H. W. Pugsley, whose contributions to our knowledge of the British species of *Hieracium* are outstanding.

12. *Hieracium dilectum* P. D. Sell & C. West, sp. nov. PLATE 8b.

Holotype: Burn of Quoys, Catfirth, Mainland, Shetlands, August 1953, C. West no. 53/2 (CGE).

[*H. dovrense* var. *hethlandiae* sensu Druce (quoad Burn of Quoys loc.) (1922) 499.]

Ab *H. attenuatifolio* P. D. Sell et C. West et *H. pugsleyi* P. D. Sell et C. West squamis capitulorum sparsius vestitis differt, praeterea ab *H. subtruncato* Beeby foliis longioribus angustioribus acutioribus distinguitur.

Planta aphyllopoda. Caulis ad 55 cm. altus, flexuosus purpureusque, raro glaber, plerumque pilis simplicibus paucis (raro numerosis) mediocribus pallidis praesertim in nodis, aliis stellatis dispersis, superne pilis glanduliferis brevissimis paucis vestitus. Folia caulina 9–16 (–20), pallide viridia, saepe purpureo-tincta praesertim inferne; inferiora longa anguste elliptica vel interdum linearia, obtuso-mucronulata vel subacuta, regulariter remoteque denticulata, basi in petiolum brevem late alatum attenuata, *semi-amplexicaulia*; *media longa*, anguste elliptica vel interdum linearia, acuta, remote denticulata, interdum dente acuto parvo praedita, basi breviter angustata vel cuneata vel rotundata, *semiamplexicaulia*, sessilia; superiora longe lanceolata, longe acuta, remote denticulata vel integra, sessilia, basi rotundata, *semiamplexicaulia*; omnia glabra vel utrinque et in marginibus pilis simplicibus paucis usque nullis pallidis, mediocribus vestita, interdum costa subtus dense pilosa, media atque superiora saepe pilis stellatis utrinque dispersis induta. Anthela laxa cymosa, capitulis 1–10, acladio pedunculo mediocri usque longo praedito; pedunculi mediocres usque longi, suberecti, pilis stellatis dispersis, interdum scaberuli et raro pilo simplici pallido mediocri vestiti. Squamae

9–11 mm. longae, 1·25–1·5 mm. latae, in gemmis incumbentes, atro-virides, mediae et interiores marginibus pallidioribus, lineari-lanceolatae, obtusae, pilis stellatis dispersis, aliis simplicibus brevibus vel brevissimis obscuris dispersis, aliis glanduliferis brevibus vel brevissimis obscuris dispersis vestitae. Ligulae luteae, glabrae. Styli lutei vel obscuri. Alveoli receptaculi margine dentato-fimbriati. Cypsela obscura, 4–4·5 mm. longa.

Aphyllopodous. Stem to 55 cm. high, flexuous, purple, rarely glabrous, usually with a few (rarely more numerous), pale, medium simple hairs especially at the nodes, with scattered stellate hairs and a few very short glandular hairs above. Cauline leaves 9–16 (–20), pale green, usually suffused with purple, especially below; the lower narrowly elliptic or sometimes linear, obtuse-mucronulate to subacute, regularly and remotely denticulate, attenuate below to short, broad-winged, semi-amplexicaul petioles; the median narrowly elliptic or sometimes linear, acute, remotely denticulate with an occasional small sharp dentation, shortly narrowed to a cuneate or rounded, semiamplexicaul, sessile base; the upper long-lanceolate, long-acute, remotely denticulate or entire, sessile with a rounded, semiamplexicaul base; all glabrous or with few to many, pale, medium simple hairs on both surfaces and the margins, sometimes with very numerous simple hairs on the midrib beneath, the median and upper often with scattered stellate hairs on both surfaces. Inflorescence loosely cymose with 1–10 capitula, acladium with medium to long peduncle, peduncles medium to long, suberect, with scattered stellate hairs, sometimes scaberulous and occasionally with a solitary, pale, medium simple hair. Phyllaries 9–11 mm. long, 1·25–1·5 mm. broad, incumbent in bud, blackish-green, the median and inner with paler margins, linear-lanceolate, obtuse, with scattered stellate hairs, scattered short or very short, dark simple hairs, and scattered very short or short, dark glandular hairs. Ligules yellow, glabrous. Styles yellow to discoloured. Margins of the receptacle pits fimbriate-dentate. Cypsela dark, 4–4·5 mm. long.

This species was first collected in 1908 in the ravine of the Burn of Quoys, Catfirth, Mainland, Shetlands, by W. H. Beeby (no. 1664). Although Beeby does not mention this plant in any of his papers on the Shetland *Hieracia*, a specimen in his herbarium is labelled *H. dovrense* var. *hethlandiae* F. J. Hanb. A plant of this same gathering in Herb. E. S. Marshall (CGE) is similarly labelled, and the Burn of Quoys is given as a locality for *H. hethlandiae* in Druce's *Flora Zetlandica*.

In 1953 C. West (no. 53/2) collected a series of specimens from this locality, as did W. Scott in 1956, and these were identical with Beeby's plant. The same plant was collected by C. West (no. 53/15) from the Laxo Burn in 1953. In 1959 W. Scott found it on rocks one-and-a-half miles north-east of West Burrafirth, Sandsting, where it was re-collected by C. J. Cadbury in 1960. Cadbury also collected it in two other localities, the Burn of Crookadale, Catfirth, Mainland, in 1960 and 1961, and near the South Wick of Sound, near Setter, Yell, in 1961. In 1962 W. Scott found it on rocks above the Bay of Brenwell, near Sandness, and in 1963 at Channer Wick in south Mainland. A plant collected on 29 July 1961 by R. C. Palmer from sea cliffs at the West side of Whale Firth, near Grimister, Yell, differs only in having few (six), widely spaced cauline leaves. The plants from Crookadale have narrower (almost linear) leaves than those from the other localities; this character is retained in cultivation.

H. dilectum is very different from *H. hethlandiae* (F. J. Hanb.) Pugsley and has a closer affinity with *H. subtruncatum* Beeby, *H. attenuatifolium* P. D. Sell & C. West and *H. pugsleyi* P. D. Sell & C. West. It can be distinguished from *H. pugsleyi* and *H. attenuatifolium* by the sparse indumentum of its phyllaries, and from *H. subtruncatum* by its longer, narrower and more pointed leaves.

The use of the epithet *dilectum* for this beautiful plant needs no explanation.

13. *HIERACIUM SUBTRUNCATUM* Beeby (1908) 114 (Lectotype: near the sea, Hamar Voe, Northmaven, Shetlands v.c. 112, 10 August 1891, W. H. Beeby no. 1105 in Herb. F. J. Hanbury (BM)); Druce (1922) 500; Roffey (1925) 29, no. 1192; Druce (1928) 70, no. 194; Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 225; P. D. Sell & C. West in Dandy (1958) 127, no. 558:1:173. PLATE 9a.

[*H. friesii* sensu Beeby (1892) 55 (exclud. Loch of Cliff loc.); sensu Roffey (1925) 29, no. 1224 (quoad Shetland loc.); sensu Druce (1928) 71, no. 226 (quoad Shetland loc.).]

[*H. truncatum* sensu F. J. Hanb. in Bab. (1904) 264; sensu W. R. Linton (1905) 75 (quoad Shetland loc.).]

[*H. rigidum* var. *friesii* sensu W. R. Linton (1905) 82 (quoad W. H. Beeby no. 1040); sensu Beeby (1908) 115; sensu Druce (1922) 500 (exclud. Loch of Cliff loc.).]

[*H. carpathicum* subsp. *truncatum* sensu Zahn (1921) 811 (quoad Shetland loc.).]

[*H. levigatum* subsp. *friesii* sensu Zahn (1922) 887 (quoad Shetland loc.).]

H. subtruncatum var. *glussburnense* Pugsley (1948) 225 (Holotype: Banks by the Gluss Burn, near Ollaberry, Mainland, Shetlands v.c. 112, 5 July 1889, W. H. Beeby no. 1040 (BM)).

Aphyllopodous. Stem to 75 cm. high, flexuous, usually purplish below, sometimes throughout, usually with pale, medium to long simple hairs throughout, those above dark-based, often densely so below, sometimes only sparingly so or scaberulous, with scattered stellate hairs throughout, sometimes more dense near the inflorescence, without glandular hairs. *Cauline leaves* 8–20, gradually decreasing in size, pale to medium green, often suffused with purple; the lowest broadly elliptic or oblong, obtuse, subentire or denticulate, narrowed (sometimes abruptly) to a sessile base or occasionally shortly petiolate, with numerous, pale, sub-setiform, bulbous-based, medium simple hairs on both surfaces and the margins; the median lanceolate to oblong, subacute, denticulate or with a few shallow teeth intermixed, contracted to a rounded, semi-amplexicaul base, clothed as lower except that the hairs are fewer, the upper surface is sometimes glabrous, and the lower surface sometimes has scattered stellate hairs; the upper lanceolate to ovate-lanceolate, often gradually narrowed from the middle to an acute apex, denticulate, sometimes with a simple shallow tooth, base broad, rounded and semiamplexicaul, clothed like the median. Inflorescence narrowly and laxly cymose with 1–13 capitula, acaudium with a long peduncle, peduncles long and slender, suberect, with few to numerous stellate hairs, few to numerous, usually dark-based, medium simple hairs, sometimes only the dark bases remaining, and occasionally a few, very short, dark glandular hairs. *Phyllaries* 9–11 mm. long, c. 1.5 mm. wide, incumbent in bud, blackish-green, inner with paler margins and often reddish tipped, linear-lanceolate, obtuse, without stellate hairs, usually with a few, very short, dark glandular hairs and solitary, dark, very short simple hairs. Ligules yellow, glabrous. *Styles* yellow. Margins of the receptacle pits shortly dentate. Cypselas dark, 3.5–4 mm. long.

This species was originally collected on the banks of the Eala Water,* Northmaven, by W. H. Beeby in 1891 and 1896, and is represented by his exsiccatae nos. 1105, 1106, 1153 and 1154. It was referred by M. Elfstrand and E. F. Linton to the Scandinavian *H. truncatum* Lindeb. In 1908, however, Beeby, on the advice of W. R. Linton, described it as a new species, *H. subtruncatum*. It is indeed very different from *H. truncatum*, which has a nearly glabrous stem and foliage, petiolate basal leaves and a more spreading inflorescence. Later gatherings from this locality have been made by G. C. Druce (1920 and 1921), M. L. Wedgwood (1921), J. E. Lousley (1950), C. West no. 53/6 (1953), A. H. G. Alston, and N. D. Simpson no. 54/745 (1954), and W. Scott (1956). In 1953 C. West found this species on the banks of a stream on the north side of Ronas Voe, and W. Scott sent us a specimen from the same locality in 1957. There is a sheet in the Oxford herbarium from Cliva Hill, collected by G. C. Druce in 1921; and W. Scott found it near there at Islesburgh in 1963. Beeby (1902) quotes Hanbury as having identified a plant from Cliva Hill as *H. truncatum*, but the Beeby specimen in *Herb. Mus. Brit.* is *H. hethlandiae*. W. Scott collected a specimen in 1959 along the NE arm of the Mangaster Voe, which is probably this species, and another collected nearby in 1963 which is certainly it. In 1963 W. Scott found it at Channer Wick, which extends its range to the southern part of Mainland, and in the same year collected it at Hamna Dale, near Lunning, Lunnasting.

In 1889 and 1891 Beeby collected specimens from the banks of the Gluss Burn, near Ollaberry, Mainland (nos. 1040 and 1104) which, together with the Eala Water plant, were referred by Hanbury to *H. friesii* Hartm. When Beeby described *H. subtruncatum*, however, the Gluss Burn plant, on the advice of W. R. Linton, was left under *H. friesii*. Here it remained until Pugsley (1948) pointed out its affinities with *H. subtruncatum*, and described it as variety *glussburnense* of that species. It has more recently been gathered by C. West no. 53/16 (1953), and by A. H. G. Alston and N. D. Simpson no. 53/746, and from their fine series of specimens we consider that it is distinguishable from the type only in the insignificant character of having fewer and shorter simple hairs on the stem and peduncles. The amount of purplish colouring is very variable in plants from all populations of *H. subtruncatum*.

In 1892 (*J. Bot. (Lond.)* 47, 51) A. Ley recorded a plant from the Mellte Glen, Brecon as *H. truncatum* forma. This plant was brought to Ley in an undeveloped state and grown by him in his garden. No specimens gathered in the wild state exist, but we have seen the cultivated specimens. They are certainly neither *H. subtruncatum*, Beeby nor *H. truncatum* Lindeb., and do not match any described British species. Until wild material is available it is difficult to say whether it is, in fact, a new species. *H. truncatum* sensu F. B. W. White (1898) 203 according to his specimen in BM is *H. suberocatum* (E. F. Linton) Roffey.

H. subtruncatum is closely allied to *H. pugsleyi* P. D. Sell & C. West, *H. attenuatifolium* P. D. Sell & C. West and *H. dilectum* P. D. Sell & C. West. From *H. pugsleyi* and *H. attenuatifolium* it differs by the sparser indumentum of its phyllaries, and from *H. dilectum* by its shorter, broader and less pointed leaves.

No extra-British species that is closely allied to *H. subtruncatum* has been seen, *H. truncatum* Lindeb. being easily distinguishable, as mentioned above, while *H. friesii* Hartm. which is quite different, is perhaps best placed in the Section *Tridentata*.

* The modern official spelling is Eela, not Eala.

14. *HIERACIUM NORTHROENSE* Pugsley (1948) 228 (Holotype: hillside, North Roe, Northmaven, Shetlands, 30 July 1891, W. H. Beeby no. 1085 (SLBI) (the label also contains the date 11 August 1891 and no. 1086)); P. D. Sell & C. West in Dandy (1958) 127, no. 558:1:177. PLATE 9b.

[*H. crocatum* sensu Beeby (quoad North Roe loc.) (1892) 55.]

H. crocatum var. *congestum* Beeby (exclud. no. 1634) (1908) 115 (Lectotype: hillside, North Roe, Northmaven, Shetlands, 30 July 1891, W. H. Beeby no. 1085 (SLBI); Druce (exclud. Holm in Burga Water loc.) (1922) 500; Druce (1928) 71 no. 245e.

H. congestum (Beeby) Roffey (1925) 29, no. 1246, non Freyn (1891) *Oest. Bot. Zeit.*, **41**, 56.

[*H. northroense* Pugsley in A. R. Clapham (1946) 34 nom. nud.]

Aphyllopodous or with basal leaves withering at the time of flowering. Stem 17–35 (–45) cm. high, flexuous, with numerous, pale, medium simple hairs at the base, usually less numerous above or scaberulous, with scattered stellate hairs, without glandular hairs. Leaves pale to medium green, often reddish-purple on the margins and veins; the basal elliptic, obtuse, regularly denticulate, attenuate to a short, winged petiole; the cauline (7–) 9–15, suddenly decreasing in size about half-way up the stem; the lower lanceolate to broadly elliptic, obtuse to acute, with numerous, fine, closely placed denticulations, narrowed to a semiamplexicaul base; the upper linear-lanceolate to lanceolate (to ovate-lanceolate in cultivation), subacute to acute, denticulate as the lower, base sessile, rounded and semiamplexicaul; all with short to medium, pale simple hairs below and on the margins, the lower sometimes have them above, all with numerous stellate hairs on the lower surface, the upper with stellate hairs on both surfaces. Inflorescence cymose, laxly so in cultivation, with 2–9 (–20 cult.) capitula, a cladium with a medium peduncle; peduncles medium to long, suberect, with scattered stellate hairs, with a few, very short, dark glandular hairs and occasionally a few, pale, medium simple hairs. Phyllaries 9–11 mm. long, 1·5–2·0 mm. wide, incumbent in bud, green with a dark centre, lanceolate, obtuse, with scattered stellate hairs, with a few, very short or short, dark glandular hairs and sometimes a few pale, medium simple hairs in a row down the centre and at the base. Ligules yellow, glabrous. Styles discoloured. Margins of the receptacle pits shortly dentate. Cypselas dark, about 3·5 mm. long.

H. northroense was discovered by W. H. Beeby in 1891 (nos. 1085 and 1086). There is no specimen to prove that Druce saw it on his visits to the Shetlands, even though he states (1922, p. 466) that he had re-gathered all Beeby's critical plants. In the last few years several botanists have searched carefully for it without success. In 1959, however, C. J. Cadbury collected seeds from a plant growing at North Roe which he sent to us to cultivate. The plants cultivated from this seed in the Botanic Garden at Cambridge flowered freely in 1961, 1962 and 1963. They were *H. northroense*. The colony found by C. J. Cadbury has since been examined by R. C. Palmer, W. Scott, N. D. Simpson and C. West, and additional material obtained.

It is very closely allied to *H. vinicaule*, but differs in its more dwarf, compact habit, more numerous denticulate shorter leaves, which are less drawn out at the apex, and in its paler, less densely clothed phyllaries. The specimens cultivated by Beeby in 1894 and by us in 1961 and 1962 were taller, the leaves even broader in proportion to their length, and the denticulations more pronounced. Our cultivated specimens in 1963, however, exactly matched Beeby's original wild material.

15. *HIERACIUM VINICAULE* P. D. Sell & C. West (1955) 236 (based on *H. vinaceum* (Beeby) Pugsley, non Johansson & Samuelsson); in Dandy (1958) 127, no. 558:1:176. PLATE 10a.

[*H. crocatum* sensu Beeby (quoad 3 loc. north shore Roeness Voe) (1892) 55.]

[*H. strictum* sensu W. R. Linton (quoad W. H. Beeby no. 1156) (1905) 85.]

H. crocatum var. *vinaceum* Beeby (1908) 115 (Lectotype: Roeness Voe, Northmaven, Shetlands, 1891, W. H. Beeby no. 1087 (BM)); Druce (1922) 500; (1928) 71, no. 245f.

H. strictum var. *humilius* Beeby (1908) 115 (Lectotype: Gelli Burn, Hillswick, Northmaven, 13 August 1896, W. H. Beeby no. 1156 (SLBI)); Druce (1922) 500; Roffey (1925) 29 no. 1237b; Druce (1928) 71 no. 239b.

H. congestum forma *vinaceum* (Beeby) Roffey (1925) 29 no. 1246.

[*H. platylepium* sensu Druce (1928) 71, no. 246.]

H. vinaceum (Beeby) Pugsley in A. R. Clapham (1946) 346; (1948) 227; non Johansson & Samuelsson (1923) *Dalarnes Hieracia Silvaticiformia* 90.

Aphyllopodous. Stem to 70 cm. high, flexuous, purple below, sometimes throughout, usually with scattered, pale, medium simple hairs throughout, with few stellate hairs especially above, sometimes with a few, very short, dark glandular hairs near the inflorescence. Leaves all cauline, 10–19 (–30 cult.), medium or



(a) *Hieracium zelandicum* Beeby.



(b) *Hieracium breve* Beeby.

HERBARIUM OF THE
UNIVERSITY OF CALIFORNIA
JANUARY 1951
C. WEST

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JANUARY 1951
C. WEST



Herb. Univ. Calif.
BRITISH ISLES
Hieracium solum P. D. Sell & C. West
V. 312. Locality and Habitat:
Loch an Duibhail,
Kintyre,
Glas. 10/10/86.
11/7/1982.
Stems discoloured. Leaves glaucous.
Stems and leaves
Call. A.D. Smith. No.

(a) *Hieracium solum* P. D. Sell & C. West. Holotype.



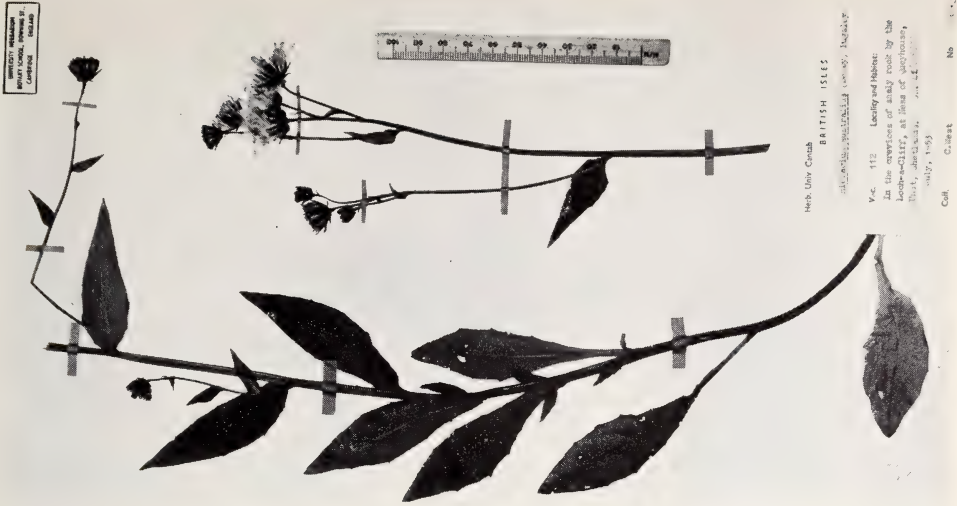
Hieracium gratum P. D. Sell & C. West
Determiner 1987
Herb. Univ. Calif.
BRITISH ISLES
Hieracium gratum P. D. Sell & C. West
V. 312. Locality and Habitat:
Grassy ditches by the shore, Flacka, Shetland,
Barwick, Shetland, 10/10/86.
11/7/1982.
Call. C. West. No. 55/15.

(b) *Hieracium gratum* P. D. Sell & C. West.



Herb. Univ. Canada
BRITISH ISLES
Hieracium difficile P.D. Sell & C. West
V. 112 Locality and Habitat:
Road of stream above the Bay of
St. John's, Newfoundland, St. John's,
Canada, 17/7/1964.
Coll. P.D. Sell & C. West. No.
C. West.

(a) *Hieracium difficile* P. D. Sell & C. West. Holotype.



Herb. Univ. Canada
BRITISH ISLES
Hieracium australis (Beeby) Pugsley
V. 112 Locality and Habitat:
In the crevices of rocky rock by the
roadside, at base of mountain,
St. John's, Newfoundland, Canada,
17/7/1964.
Coll. P.D. Sell & C. West. No.
C. West.

(b) *Hieracium australis* (Beeby) Pugsley.

Herb. E. S. Marshall
Presented 1919

HERBARIUM
BRITISH MUSE, LONDON
No. 1111

Hieracium praetulaense (L.)
P. D. 1911
Determined by P. D. 1911
R. H. S. 1911

Great Britain, V.C. *praetulaense*

Hieracium praetulaense
R. H. S. 1911

W. H. BEERY, A.L.B.
No. 1111

17. 8. 1891

(see *Journal of Botany* for 1919)
det. on *Herbarium of Oxford* (det. 1919)

Hieracium praetulaense (L.)
det. on *Herbarium of Oxford* (det. 1919)

(b) *Hieracium praetulaense* Pugsley.

HERBARIUM
BRITISH MUSE, LONDON
No. 1111

Herb. Univ. Camb. BRITISH MUSE

Hieracium dovrense Fries

V. 1. 192

Locality and Notes
Rocky cliff edges on the north
face of Mount Dovre, 1,500 ft., near Logdalen,
Norway

Col. J. H. Davis
6/12/92 No

(a) *Hieracium dovrense* Fries.



(a) *Hieracium hehlandiae* (F. J. Hanb. Pugsley, Lectotype.



(b) *Hieracium attenuatifolium* P. D. Sell & C. West, Holotype.

HERBARIUM
JANUARY 1900, JOURNAL
LONDON



Herb. Univ. Camb. *HERACIUM*
BRITISH ISLES
Hieracium pugsleyi P. D. Sell & C. West
V.c. 112 Locality and Habitat:
Grassy banks of the Resolva Burn,
Mainland, Shetland. Gr. 4/5/50/527
Aug., 1953. Stylee yellow.
Coll. C. West No. 53/4

(a) *Hieracium pugsleyi* P. D. Sell & C. West. Holotype.

HERBARIUM
JANUARY 1900, JOURNAL
LONDON



Herb. Univ. Camb. *HERACIUM*
BRITISH ISLES
Hieracium dilectum P. D. Sell & C. West
V.c. 112 Locality and Habitat:
Grassy banks of the Burn of Quoys,
Orkney, Shetland. Gr. 4/4/50/53
Aug., 1953
Coll. C. West No. 53/2

(b) *Hieracium dilectum* P. D. Sell & C. West. Holotype.



Herp. Univ. Calif.

BALTIMORE VALLEY

Hieracium subtruncatum Beeby

V-4. 112 Locality and Habitat:

Wet meadow of the farm of the SJA

near the University, Baltimore

1911. 1. 11. 11.

1911. 1. 11. 11.

1911. 1. 11. 11.

(a) *Hieracium subtruncatum* Beeby.



Great Britain, Va. Richmond.

Hieracium northroense Pugsley

Richmond, Va. (1911. 1. 11. 11.)

Richmond (Va.)

30. 7. 1891

W. H. BEEDY, ALE

NO. 1013

1. 1. 11. 11.

Hieracium northroense Pugsley

Richmond (Va.)

1911. 1. 11. 11.

1911. 1. 11. 11.

(b) *Hieracium northroense* Pugsley.

dark green, slowly decreasing in size upwards; the lower narrow-elliptic to elliptic-oblong, $\pm$ acute, obscurely denticulate or with an occasional shallow tooth, attenuate below to short or medium, narrowly winged petioles, with sparse, pale, short to medium simple hairs on both surfaces, the margins and the petioles; the median and upper lanceolate, linear-oblong or narrow elliptic, subacute to acute, subentire to shallowly and remotely denticulate or occasionally dentate, abruptly or gradually narrowed below to a semiamplexicaul base, clothed like the lower except that simple hairs are sometimes absent on the upper surface, and stellate hairs are frequent below and rare above, and the margins are sometimes only scaberulous. Inflorescence narrowly and laxly cymose, with 2–42 (–350 cult.) capitula, with long, slender, suberect branches exceeding the medium peduncled accladium; peduncles medium to long, suberect, with scattered stellate hairs, and with dark-based, short to medium simple hairs and very short, dark glandular hairs in varying proportions, one or the other type of hair sometimes absent. *Phyllaries* 9–10.5 mm. long, 1.25–1.5 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, sometimes narrowed above but always obtuse, with few scattered stellate hairs, with $\pm$ numerous, very short to short, dark glandular hairs and usually a few, medium, dark-based simple hairs. Ligules yellow, glabrous. Styles discoloured. Margins of the receptacle pits shortly dentate. *Achenes* dark, 4–4.5 mm. long.

H. vinicaule was first found in 1891 by W. H. Beeby (nos. 1087, 1088 and 1089) at Roeness (Ronas) Voe, Northmaven, and referred to *H. crocatum* Fries. A sheet of no. 1088, now in Herb. Hanbury (BM), was sent to Elfstrand, who identified it as *H. angustum* var. *platylepium* Dahlst. In 1908 Beeby described it as a variety, *vinaceum*, of *H. crocatum* Fries, and Druce accepted this treatment. Roffey considered it to be a form of *H. congestum* (Beeby) Roffey. It has since been collected in this locality by R. J. Burdon and G. C. Druce (1920), J. E. Lousley (1950), C. West no. 53/5 (1953), A. H. G. Alston and N. D. Simpson no. 54/731 (1954), R. Palmer (1955), W. Scott (1956) and C. J. Cadbury (1961).

In 1896 Beeby collected specimens (no. 1156) around Hillswick, and yet others (no. 1633) by the Hamari Water, which Dahlstedt suggested were a form or variety of *H. strictum* Fries. Beeby then named the plants *H. strictum* var. *humilius*, this treatment being accepted by both Druce and Roffey. Further material has been collected from these localities by C. West no. 53/17 (1953), R. Palmer (1956) and W. Scott (1956).

Pugsley (1948), after examining all the available material of *H. crocatum* var. *vinaceum* and *H. strictum* var. *humilius*, united them under the specific name, *H. vinaceum*. On comparing material from these localities we found that it could be separated into two groups, but that no clear-cut characters could be found that would distinguish them. The leaves, even in dried specimens, seemed to be a slightly different colour, while var. *humilius* had a more strict stem and more regularly denticulate leaves; however, a series of specimens from the two areas must be consulted before these small differences can be appreciated. In the few cultivated specimens we have seen, the var. *humilius* retains its characters while var. *vinaceum* looks much more like var. *humilius*. In view of this, and of the fact that the characters they have in common are much greater than their differences, we have followed Pugsley in uniting them as one species. We have given the plant a new name because *vinaceum* had already been used for another species belonging to an entirely different Section. The epithet *vinicaule* was chosen because of the wine-coloured stems of many of the plants.

The range of *H. vinicaule* has recently been greatly extended. In 1958 W. Scott found this species near Muckle Roe Bridge, in 1960 R. C. Palmer found it at Swining Burn, Lunnasting, in 1961 W. Scott found it in Yell at the lower end of North Burn, in 1961 C. J. Cadbury found it at North Roe, Mainland, and in 1963 W. Scott found it at Kels Wick, Lunnasting. Specimens collected by R. C. Palmer in 1960 on a holm in the Loch of Lumbister, Yell, probably belong to this species, but show slight differences in leaf shape and type of inflorescence.

This is the tallest of the Shetland species of *Alpestria*, and although Pugsley gives the number of capitula as 2–4 (–9), C. West found that this number is often exceeded. In fact, a plant seen by the roadside near Hillswick, had 19 cauline leaves and 42 capitula. In cultivation at Cambridge, plants were produced with 30 cauline leaves and over 350 capitula.

In its natural habitats *H. vinicaule* grows on steep grassy slopes of burns and sometimes near roadsides.

The only closely allied species is *H. northroense*, from which it can be distinguished by its taller habit, less denticulate, longer leaves, and by its darker, more hairy phyllaries.

16. *Hieracium mirandum* P. D. Sell & C. West, sp. nov. PLATE 10b.

Holotype: By aqueduct near Well House, Stean, Mid-W. Yorks., v.c. 64. Grid. Ref. 44/0774, 29 July 1962, Miss C. M. Rob (CGE).

Ab *H. dewarii* Syme ligulis glabris, foliis ovatis, pedunculis pilis glanduliferis carentibus differt.

Planta foliis basalibus florendi tempore marcescentibus. Caulis ad 38 cm. altus, flexuosus, inferne purpureus, ubique pilis simplicibus longis pallidis, superne paucioribus nigribasibus pilosus, pilis stellatis

glanduliferisque nullis. *Folia* mediocriter viridia, inferne caesia; *basalia elliptica vel ovata*, subacuta, *denticulata*, *basi in petiolum mediocrum anguste alatum attenuata*, utrinque et in marginibus pilis simplicibus mediocribus pallidis dispersis vestita; *caulina* 6–7, *ovata*, subacuta vel acuta, *denticulata vel dentibus paucis brevibus praedita*, *inferiora basi cuneata petiolis brevibus*, *superiora basi rotundata*, sessilia, *semiamplexicaulia*, superne glabra, inferne et in marginibus pilis simplicibus mediocribus pallidis paucis vestita. Anthela compacte cymosa, capitulis 3–5, acladio pedunculo mediocri praedito; *pedunculi* suberecti, mediocres, *pilis stellatis densis*, aliis simplicibus numerosis nigribasibus mediocribus, *glanduliferis nullis vestiti*. *Squamae* 9–10 mm. longae, 1·5–2 mm. latae, in gemmis incumbentes, atrovirides, interiores marginibus pallidioribus, lineari-lanceolatae, obtusae, *praecipue basi pilis stellatis paucis*, aliis *glanduliferis brevibus et brevissimis atris*, necnon aliis simplicibus paucis brevibus nigribasibus vestitae. *Ligulae* luteae, glabrae. Styli obscuri. Cypselam non vidimus.

Basal leaves withering at the time of flowering. Stem to 38 cm. high, flexuous, purplish below, with pale, long simple hairs throughout, those above fewer and dark-based, without stellate or glandular hairs. *Leaves* medium green, caesious below; *the basal elliptic or ovate*, subacute, *denticulate*, *attenuate to a medium*, *narrowly winged petiole*, with scattered, pale, medium simple hairs on both surfaces and margins; *the cauline* 6–7, *ovate*, subacute to acute, *denticulate or with a few shallow teeth*, *the lower cuneate with a short petiole*, *the upper rounded*, sessile, *semiamplexicaul*, glabrous above with few, pale, medium simple hairs below and on the margins. Inflorescence compactly cymose, with 3–5 capitula, acladium with medium peduncle; *peduncles* suberect, medium, *with dense stellate hairs and numerous*, *dark-based*, *medium simple hairs without glandular hairs*. *Phyllaries* 9–10 mm. long, 1·5–2·0 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, obtuse, *with occasional stellate hairs mainly at the base*, with very short to short, dark glandular hairs and a few, short, dark-based simple hairs. *Ligules* yellow, glabrous. Styles discoloured. Cypselas not seen.

This species is known only from two plants taken from the type locality, which is so remote from any other locality for an Alpestrian species that the specific epithet *mirandum* has been used. It was searched for in 1963 and 1964 without success. However, in view of the distinctness of the plant, and of the remoteness of the locality from that of any other species of the Section *Alpestris*, we have described it from what we should otherwise have considered to be insufficient material.

It is most closely allied to *H. dewarii*, from which it can be distinguished by its glabrous ligules, ovate leaves, and peduncles without glandular hairs.

17. *HIERACIUM DEWARII* Syme (1878 for 1876) 23 (Lectotype: Linmill, Clackmannan, July 1876, J. T. Boswell-Syme in Herb. Boswell-Syme (BM)); (1879) 211; F. B. W. White (1898) 203; F. N. Williams (1902) 162; F. J. Hanb. in Bab. (1904) 265; W. R. Linton (1905) 73; Druce (1928) 70 no. 197 (1620); Roffey (1925) 29 no. 1195; W. Young (1936) 92; Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 229; A. R. Clapham in A. R. Clapham, Tutin, T. G. & E. F. Warburg (1952) 1145; ed. 2 (1962) 907; P. D. Sell & C. West in Dandy (1958) 128, no. 558:1:178. PLATE 11a.

[*H. dovrense* sensu F. N. Williams (quoad Glen Roy loc.) (1902) 161; sensu W. R. Linton (quoad Glen Roy loc.) (1905) 72.]

H. carpathicum subsp. *dewarii* (Syme) Zahn (1921) 812.

Basal leaves withering before or at the time of flowering. Stem to 110 cm. high, flexuous, occasionally purplish below, with long, pale simple hairs throughout, less densely so above, the upper sometimes dark-based, with scattered stellate hairs above, usually without glandular hairs, but occasionally with a very short glandular hair near the inflorescence. *Leaves* 6–20, all except the lowermost widely spaced, gradually decreasing in size, medium green, midrib prominent; *the lowermost broadly elliptic or obovate*, obtuse-mucronulate to acute, entire or remotely denticulate, *attenuate to winged petioles*; *the lower and median similar to the lowermost but never obovate*, and *the petioles are either short or absent*; the upper ovate or ovate-lanceolate, acute to long acute, entire or denticulate, with a rounded, sessile, semiamplexicaul base; indumentum variable, usually very hairy on both surfaces and the margins with pale, subsetiform, medium simple hairs, but sometimes the hairs are fewer or nearly absent. Inflorescence narrowly and compactly cymose, with –17 (–35 cult.) capitula, acladium with a short to medium peduncle; *peduncles* medium, suberect, with dense stellate hairs, *with more or less numerous dark-based*, *short simple hairs and ± numerous*, *very short*, *dark*, *fine glandular hairs*, the number of simple and glandular hairs, and the proportions of one to the other, varying greatly. *Phyllaries* 9–10 mm. long, usually c. 1·0 mm. wide, incumbent in bud, blackish-green, the inner with paler margins, linear-lanceolate, obtuse or rarely subacute, *with scattered stellate hairs towards*

the base and on the margins, and with a tuft at the apex, with numerous short or very short, dark glandular hairs and few to many, short to medium, dark-based simple hairs. Ligules yellow, with very short simple hairs at the apex. Styles discoloured. Margins of the receptacle pits fimbriate-dentate. Cypsela dark, 3.5–4 mm. long.

Distribution:

- V.c. 87. W. PERTH: 26/89, Menstrie Glen, 8 August 1882, J. Groves (BM); 26/99, Linmill, 1875, T. Drummond (CGE), 1876, J. B. Syme (BM, CGE), 1876, T. Drummond (BM, OXF), Glen of Sorrow near Dollar, 1876, J. B. Syme (BM) and 1877 (K); 27/42, Am Binnein, 1889, F. J. Hanbury (BM); 27/90, Glen Devon, 1876, J. B. Syme (herb. J. C. Melvill) and 1881 (BM), 1876, T. Drummond (CGE, K), Glen Quay, 1876, J. B. Syme (BM, CGE, OXF) and 1881 (BM, CGE), 1949, J. E. Lousley (K), 1959, P. D. Sell nos. 59/218 and 59/224 (CGE), N. D. Simpson no. 59/086 (herb. Simpson) and C. West (CGE). Lethensdene, Clackmannan, 26 August 1875, T. Drummond.
- V.c. 88. MID-PERTH: 27/32, Strath Fillan, 1891, E. S. Marshall (CGE and herb. J. C. Melvill), 1917, R. J. Burdon (CGE, K, OXF, herb. Univ. Sheffield, YRK), Crianlarich, 1889, E. S. Marshall (CGE), 1891, E. S. Marshall (BM), Glen Falloch, 1889, E. S. Marshall (BM, SLBI), 1914, E. S. Marshall no. 3996 (CGE, E), 1915, H. W. Pugsley (BM); 27/43, Ben Heasgarnich, June 1952, D. McClintock (herb. J. E. Lousley); 27/52, Lochearnhead, 1891, F. Buchanan-White (BM), By the Dochart, 1935, H. W. Pugsley (BM); 27/53, Killin, 1844, C. C. Babington (CGE), 1848, I. B. Balfour (BM), 1888, F. J. Hanbury (BM), 1891, E. S. Marshall (CGE), 1891, E. F. Linton (Set of British Hieracia no. 47) (BM, CGE, K), 1891, W. R. Linton (OXF), 1929, H. W. Pugsley (BM); 27/64, Glen Lyon, 1913, E. S. Marshall (BM, CGE, E), Ben Lawers, 1887, E. S. Marshall (CGE, SLBI), 1888, F. J. Hanbury (BM, OXF), 1900, F. R. Tennant (CGE), 1951, T. G. Tutin (herb. Univ. Leicester); 27/74, Fortingall, 1891, W. R. Linton (LIVU), 1913, E. S. Marshall (CGE), 1913, C. E. Moss (CGE); 27/75, Keltney Burn, 1913, E. S. Marshall (CGE).
- V.c. 89. E. PERTH: 27/55, Loch Rannoch, C. E. Palmer (OXF).
- V.c. 96. E. INVERNESS: 28/70, By the River Spey, Kingussie, coll. unknown (BM).
- V.c. 97. W. INVERNESS: 27/06, Corran near Onich, 1913, N. D. Simpson no. 13/188 (herb. Simpson); 27/17, Glen Nevis, 1887, E. S. Marshall (CGE); 27/27, Choire Coille, 1896, E. S. Marshall and W. A. Shoolbred (as Linton's Set of British Hieracia no. 47) (BM, CGE, herb. Leicester, herb. J. C. Melvill, OXF); 27/28, Glen Roy, 1896, E. S. Marshall and W. A. Shoolbred (as Linton's Set of British Hieracia no. 46) (BM, CGE, E, K, OXF).
- V.c. 98. ARGYLL: 27/12, Dalmally, 1888, G. C. Druce (OXF), 1910, E. S. Marshall (BM, CGE), Loch Awe, 1898, H. J. Riddelsdell (BM); 27/15, west side of Buchaille Etive Beag, 1893, E. S. Marshall (BM, CGE, SLBI); 27/20, Ben Donich, 27 June 1962, A. G. Kenneth; 27/24, Clach Leathad, 1889, F. J. Hanbury (BM); 27/25, near Kingshouse, 1889, E. S. Marshall (BM, CGE), Cam Glen, 1899, C. Bucknall (K).
- V.c. 99. DUNBARTON: 27/20, Arrochar, Loch Long, 1842, C. C. Babington (CGE).

H. dewarii was described in 1878 by J. T. Boswell-Syme from specimens gathered in Perth, Clackmannan, Dunbarton and Stirling. The description is a good one, and all the original specimens belong to the same taxon. A lectotype has been selected from the many syntypes in the Boswell-Syme herbarium. *H. dewarii* seems to have caused little trouble taxonomically, and the great majority of the specimens we have examined have been correctly identified. Before it was described as a new species in 1878 it had been incorrectly referred by J. Backhouse and others to *H. strictum* Fries.

Ley's record (loc. cit.) of *H. dewarii* from an old lime kiln above Chapel-le-Dale, Yorks, is based on weak specimens of *H. latobrigorum* (Zahn) Roffey.

Zahn (1921) considered *H. dewarii* to be a subspecies of *H. carpathicum* grex *H. truncatum* Lindeb., but it is much more closely allied to grex *carpathicum* Besser.

Its usual habitat is on the banks of streams, but occasionally it occurs on rocky ledges.

18. *HIERACIUM CARPATHICUM* Besser (1809) 154 (typification by original description and by constant application of the name to the same taxon. No original specimens traced).
PLATE 11b.

H. dovrense var. *spectabile* E. S. Marshall (1894) 215 (Lectotype: Bank above the Lochsie Burn, in upper Glen Shee, E. Perth, c. 1250 ft, 28 July 1892, E. S. Marshall no. 896 (CGE); F. J. Hanb. in Bab. (1904) 264; F. B. W. White (1898) 203.

H. perthense F. N. Williams (1902) 163 (there is no evidence that Williams ever saw any material, and it is best regarded as a new name for *H. dovrense* var. *spectabile* E. S. Marshall, with the same type); W. R. Linton (1905) 75; Roffey (1925) 29, no. 1196; Druce (1928) 70 no. 198 (1624); Pugsley in A. R. Clapham (1946) 346; Pugsley (1948) 230; P. D. Sell & C. West in Dandy (1958) 128 no. 558:1:179.

H. carpathicum subsp. *perthense* (F. N. Williams) Zahn (1921) 815.

Basal leaves withering before or at the time of flowering. Stem to 90 cm. high, flexuous, sometimes purplish at the very base, with long, pale simple hairs throughout but less dense above, the upper sometimes dark-based, with numerous stellate hairs above, without glandular hairs. *Leaves* 6–17, gradually decreasing in size, dark green, with a prominent midrib; the lowermost broadly elliptic or obovate, rounded-obtusely-mucronulate, entire or remotely and minutely denticulate, attenuate below to short, broadly winged petioles; the lower and median broadly elliptic, elliptic or ovate-lanceolate, obtuse to acute, denticulate to finely, sharply and remotely dentate, sessile, semiamplexicaul; the upper ovate-lanceolate or ovate, acute to long-acute, denticulate or finely and sharply dentate, with a rounded, sessile, semiamplexicaul base; all glabrous or nearly glabrous above, with medium, pale simple hairs on the lower surface and margins, the upper sometimes with scattered stellate hairs on the lower surface. *Inflorescence* narrowly and compactly cymose, with 3–12 (–20 cult.) capitula, acladium with medium to long peduncle; peduncles medium to long, suberect, densely stellately hairy, usually with a few, short to medium, pale, dark-based simple hairs, rarely with a very short dark glandular hair. *Phyllaries* 10–13 mm. long, 1–1.5 mm. wide, incumbent in bud, blackish-green, inner with paler margins, linear-lanceolate, obtuse, stellately hairy, densely so on the margins, sometimes with a slight tuft at the apex, with dense, short to medium, pale, dark-based simple hairs and numerous, very short to short, dark, slender glandular hairs. *Ligules* yellow, with dense, very short hairs at the apex. *Styles* discoloured. *Margins* of the receptacle-pits fimbriate-dentate. *Cypselas* dark, 4–4.5 mm. long.

In 1894 E. S. Marshall described a new taxon, *H. dovrense* var. *spectabile*, from specimens collected in 1892 from two places near Glen Shee, E. Perth. It has since been found there only by J. E. Raven (1953) and P. D. Sell no. 56/38 (1956). On both occasions only a few plants were found.

In 1889 E. F. Linton had collected specimens from Clova which proved to be the same species. It has not been recorded again from that locality.

Cultivated specimens of the original gatherings from both localities were distributed as Linton's Set of British Hieracia no. 72. One of these cultivated gatherings was presumably seen by Williams (1902) when he raised the variety *spectabile* to specific rank, but we can trace no specimen annotated by him. The new epithet *perthense* was used owing to the earlier use of *spectabile* for another species. We have regarded *H. dovrense* var. *spectabile* as the basionym of *H. perthense*, the lectotype of the variety therefore being the lectotype of the new epithet.

All gatherings have been from grassy riversides.

Zahn (1921) placed *H. perthense* under *H. carpathicum* as a subspecies, but we are unable to distinguish it from his subsp. *carpathicum*. The type of *H. carpathicum* cannot be traced, but all material identified as that species which we have examined belongs to the same taxon, and agrees with the description published by Besser.

H. carpathicum is at present known only in a few localities in the Tatra Mountains of east central Europe and at the above-mentioned localities in central Scotland. Such a distribution suggests that morphologically similar plants may have arisen independently in different localities. No closely allied species in the Section is found on the main land-mass of Continental Europe, its closest allies being in Scandinavia. In Scotland it is closely allied to *H. dewari*, from which it can be distinguished by its more dentate leaves, longer capitula and stellately hairy phyllaries.

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FRUIT VARIATION IN *POLYGONUM PERSICARIA* L.

By J. TIMSON

Botany Department, University of Leicester*

ABSTRACT

The variation found in the fruits of *Polygonum persicaria* L. is described and analysed. A possible explanation of the variation is discussed. A new fruit type (tetragonal), believed to be previously unrecorded, is described.

INTRODUCTION

The 'seeds' of *Polygonum persicaria* are in fact the fruits (nuts) which fall from the parent plant with the dead perianth still attached. Styles (1962) found the relationship between the length of the nut and the length of the persistent perianth a useful character in section *Polygonum*, but it would appear to be of no value in section *Persicaria*.

The phenomenon of polymorphism of fruits or seeds is not common. The best-known example outside the *Polygonaceae* is *Rhynchospora*, which has fruits which are usually biconvex and rarely trigonous. In other members of the *Cyperaceae*, e.g. *Carex*, *Eleocharis* and *Schoenoplectus* the number of stigmas and hence the shape of the fruit is used as a species-separating character. Within the *Polygonaceae* only the genus *Polygonum* is recorded as having polymorphic nuts and within this genus polymorphism occurs only in sections *Persicaria* and *Echinocaulon*.

In *P. persicaria* the two fruit shapes found are:

- (i) lenticular or biconvex to planoconvex which arise from flowers with two styles and lenticular ovaries;
- (ii) angular or trigonous with three concave faces which arise from flowers with three styles and trigonous ovaries.

There is no apparent correlation between the position of the flower in the inflorescence and the type of nut produced. Both fruit shapes may be found on the same plant, and although considerable variation has been found in the relative numbers of each type, no plants have been found which have nuts of only one type. This situation may be compared with that found in *P. lapathifolium* in which the percentage of trigonous nuts is always very low and where plants may readily be found on which there are only biconcave nuts (Timson 1963).

METHODS

The length and maximum breadth of the nuts (without perianth) were measured in millimetres to the nearest 0.1 mm, each set of measurements being on a sample of mature nuts usually 50 or more in number. An index was obtained by dividing the length by the breadth. The arithmetic mean, standard deviation, and the range of these measurements were calculated. The average nut weight in mg of a sample was obtained by weighing a known number of nuts, usually 100 and never less than 30.

RESULTS

The averages of the data for all the nuts of *P. persicaria* measured are given in Table 1. From this it is clear that the British and foreign material are essentially similar. The comparative column for *P. lapathifolium* shows that the two species are significantly different in index and in percentage of trigonous nuts (see also Timson 1963). Styles (1962) found that fruit length was a useful character in section *Polygonum* for the separation

* Present address: Department of Chemistry and Biology, Hatfield College of Technology, Hatfield, Herts.

of the species, but the data presented here suggest that it is of little value in section *Persicaria*. In this section the nuts not only show a considerable range of size on a given plant, but also the average lengths for the different species are very similar.

Using nuts collected in 1958 near Ryston, Norfolk, plants were grown from nuts of known shape in similar conditions and the percentages of trigonous nuts determined. This was repeated over three seasons and the results are given in Table 2. From these results it seems that the shape of the nut from which the parent plant has been grown can affect the relative proportions of trigonous and biconvex nuts. The age of the parent plants also seems to affect the relative abundance of trigonous nuts. This was discovered when the nuts of a number of plants which had been allowed to grow old (i.e. leaves dried up, stem very dry and red), in the greenhouse were examined. They were found to be 73 per cent trigonous and 26 per cent biconvex. A third shape, not previously recorded, was present in small numbers (1 per cent)—four-sided with four concave faces (tetragonal).

There are few records in the literature of the weight of nuts of *P. persicaria*. Simmonds (1945) gives 2.3 mg; Korsmo (1934), 2.7 mg; and Pammel (1910), 1.41 mg. It is difficult to compare these figures with those given here because the authors do not say

TABLE 1. Combined data for all fruits measured of *P. persicaria*.

		British	<i>P. persicaria</i> Foreign	Total	<i>P. lapathifolium</i>
Length	mean	2.61	2.05	2.33	2.64
	s.d.	0.11	0.14	0.12	0.13
	range	2.0-3.2	1.7-3.0	1.7-3.2	2.0-3.3
Breadth	mean	2.01	1.99	2.00	2.27
	s.d.	0.12	0.12	0.12	0.13
	range	1.4-2.7	1.5-2.4	1.4-2.7	1.7-2.9
Index	mean	1.31	1.28	1.30	1.17
	s.d.	0.07	0.06	0.07	0.045
	range	1.1-1.6	1.1-1.6	1.1-1.6	1.0-1.5
Shape (%)	biconvex	76	80	78	99.2
	trigonous	24	20	22	(biconcave) 0.8
Average weight	(mg)	2.32	1.93	2.13	2.57

TABLE 2. Changes in the proportions of trigonous nuts in plants grown from nuts of known shape.

Year	From trigonous	% Trigonous From biconvex	From total	% of total from plants grown from trigonous nuts
1958	—	—	24	—
1959	44	26	35	63
1960	60	34	43	64
1961	45	8	26.5	78

whether or not the persistent perianth was removed before weighing. If, as is probable, it was not removed, it is difficult to be sure that only mature nuts have been weighed. For this reason the results given in Table 3 are for mature nuts without perianth.

TABLE 3. Weights of fruits of *P. persicaria*.

<i>Year of growth</i>	<i>Grown in</i>	<i>Shape</i>	<i>Average weight (mg)</i>
Origin: BUDE, CORNWALL			
1959	Nature	Total	2.57
1960	Garden	Biconvex	2.64
"	"	Trigonous	3.22
"	"	Total	2.93
1961	Greenhouse	Biconvex	2.36
"	"	Trigonous	2.61
"	"	Total	2.49
Origin: KEELE			
1959	Nature	Total	1.69
1960	Garden	Biconvex	2.26
"	"	Trigonous	2.74
"	"	Total	2.50
1961	Greenhouse	Biconvex	1.67
"	"	Trigonous	2.96
"	"	Total	2.31

There is considerable variation in the results obtained and it seems probable that the environment of the parent plant is the main factor. Thus nuts harvested in nature where the parent plant is in competition with other plants were usually lighter than those grown in cultivation where the plants were spaced out and competitors removed. Those produced in the garden were usually heavier than those produced in the greenhouse, probably because more space per plant was available in the former. It is clear that the trigonous nuts are normally heavier than the biconvex nuts produced on the same plant.

DISCUSSION

In *P. persicaria* the control of nut shape appears to be complex. The main conclusions emerging from the results are that:

1. It is possible to select to some extent for nut shape;
2. The nuclear genes do not completely control the nut shape, since the three kinds of nut may occur together on one plant.
3. More trigonous nuts are produced as the plant becomes senescent.

From this it seems that the production of trigonous nuts is caused by some interaction between genetic and other factors; possibly their production is favoured by a breakdown of some metabolic mechanism which occurs more frequently during senescence.

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LEAF MEASUREMENTS AND EPIDERMIS IN *POA ANGUSTIFOLIA*

By D. M. BARLING

Biology Department, Royal Agricultural College, Cirencester

ABSTRACT

In *Poa angustifolia* and *P. subcaerulea* leaf-blade length on fertile tillers increases and then decreases to the flag leaf. The third leaf-blade down from the panicle is usually longest. Leaf sheaths increase progressively to the flag leaf. Total leaf length is greatest in the leaf below the flag leaf. The per cent. contribution of sheath in the leaf increases to the flag leaf and sterile tillers show the reverse. Individual tillers may show modified patterns. The leaf blade epidermis of *P. angustifolia* was studied, and the lower of sterile tiller leaves contained none or very few stomata and were of a xeromorphic type, whilst the leaves of the fertile tiller showed stomata increasing in quantity to the flag leaf. Inflorescence initiation is in December–January when the leaves showing the above patterns on fertile tillers are all in the primordial stage.

INTRODUCTION

The leaves are of taxonomic importance in the *Gramineae*, for where floral characteristics of closely related species are very similar, vegetative features are commonly used as aids to identification. There is considerable variation in leaf dimensions in grass species both in the vegetative tiller (Langer 1958), and also in the fertile tiller (Borrill 1959 and 1961a). Leaf blade length is known to be affected by temperature, daylength and other factors (Langer 1954, Stuckey 1942), particularly in the sterile tillers. The variation in fertile tillers was suggested by Evans (1949) to be the result of apical dominance (Meyer & Anderson 1939). Borrill (1959) has suggested that it is due to the development of inflorescence primordia when the longest leaf blade has emerged and that subsequent leaf blades are shorter due to decrease in cell extension, not number. This work has done much to clarify the factors associated with varying leaf blade dimensions in the grasses. The culms of grasses also show considerable variation in internode length with increasing length up the shoot (Evans 1927, Cooper 1956, Barling 1959). Sørensen (1953) has used epidermal characters with species of *Puccinellia* found in Greenland and so have Burr & Turner (1933), Tutin (1955), Melderis (1955), and Borrill (1961b) in other species, whilst Prat's (1932 and 1948) work has thrown much light on the epidermal characteristics of the grasses.

The data presented here are chiefly from transplants of *Poa angustifolia* and *P. subcaerulea* grown in 8-in. pots of calcareous loam immersed in washed gravel at Cirencester (lat. 51° 43' N., long. 1° 57' W.) at an elevation of 440 ft. (130 m), under natural daylength.

STERILE TILLERS

The contribution of leaf blade and sheath to total leaf length in *P. subcaerulea* (Table 1) is typical. In the early part of the season the relative proportion of blade increases up the tiller. This trend may be reversed in leaves formed in the autumn when the blades shorten probably as a result of decreasing photoperiod. The sheaths may also decrease in length later in the season. The blade is always asymmetrical, with a marginal indentation near the apex.

FERTILE TILLERS

The leaf measurements from transplants of *P. angustifolia* and *P. subcaerulea* have shown a characteristic and similar pattern in the relative development of leaf blade and sheath as well as in total length (Table 2). The third leaf blade down from the panicle is usually the longest with progressively shorter blades above and below. However, the

TABLE 1. *P. subcaerulea*: % contribution of blade and sheath to leaf length in early (E) and late (L) growth of sterile tillers.

Origin		Time	Leaves in ascending order			
			1.	2.	3.	4.
Slapton	Sheath	E	55.56	38.04	28.48	22.73
	Blade		44.44	61.96	71.52	77.27
Craig-y-Llyn	Sheath	E	66.51	25.30	22.73	—
	Blade		53.49	74.70	77.27	—
Bwlfa wall	Sheath	L	30.46	25.32	22.73	23.23
	Blade		69.54	73.68	77.27	66.67
Montrose	Sheath	L	80.65	64.10	37.50	28.53
	Blade		19.35	35.90	62.50	61.47

TABLE 2. Average values of leaf and internode lengths for *P. angustifolia* and *P. subcaerulea* (mm.).

		Blade	Sheath	Total	Internode
<i>P. angustifolia</i> (transplants 1958)	F	32.86±2.35	102.29±4.10	135.15±6.81	199.57±9.20
	2	69.43±3.10	93.43±3.25	162.86±6.63	127.71±6.71
	3	81.57±3.90	67.29±3.20	148.86±6.90	70.43±6.80
	4	70.29±3.40	33.71±2.91	104.00±9.50	14.57±1.21
<i>P. angustifolia</i> (wild plants)	F	36.39±2.65	121.74±4.97	162.44±6.63	323.78±11.70
	2	71.13±3.30	114.65±3.98	185.65±6.44	164.70±7.40
	3	92.87±4.21	75.39±3.77	164.09±7.00	73.00±7.01
	4	61.00±6.30	51.78±3.25	112.91±9.09	18.22±0.77
<i>P. subcaerulea</i> (transplants 1958)	F	35.50	96.43	131.93	149.86
	2	70.50	81.50	152.00	79.79
	3	75.64	53.57	129.21	28.71
	4	72.07	41.64	113.71	15.29

pattern within individual tillers is not necessarily constant as sometimes the second or fourth leaf blade is longest. The leaf sheaths consistently increase in length up the culm and, like the blades, show considerable variation in length from plant to plant. The culm itself shows the usual pattern of increasing internode length up to the panicle. The sheaths of the lower nodes are often longer than the internodes above them, whilst those of the top node are normally shorter, though exceptions to the latter are common. The ratio of sheath : blade is lowest at the flag leaf and increases down the fertile tiller (Table 3). Whilst these characteristic patterns are seen in leaf parts, total leaf length is greatest in the leaf above the one with the longest blade (Table 2).

A conspicuous feature of *P. angustifolia* is the difference in leaf characters in a tiller that is sterile in one season and fertile in the next (Barling 1959). The sterile leaves are long and narrow and of a xeromorphic type, whilst those on the fertile tiller are shorter but much broader (Fig. 1).

TABLE 3. Ratio of sheath : blade, and % sheath in the four top leaves of fertile tillers.

	<i>angustifolia</i>		<i>subcaerulea</i>	
	ratio	%	ratio	%
F	0.32	75.68	0.37	73.09
2	0.74	57.36	0.87	53.61
3	1.21	45.20	1.41	41.45
4	2.10	32.41	1.73	36.61

LEAF-BLADE EPIDERMIS IN *P. angustifolia*

In *P. angustifolia* the lower epidermis of the leaf-blade from sterile tillers had cells with folded walls and cork cells throughout the inter-nerve area. The nerves had narrower cells and silica-suberose couples, though there was variation in cell size in the inter-nerve areas. The major feature of the lower epidermis was the absence or limited occurrence of stomata (Fig. 2 and Table 4). The upper epidermis had more or less smooth-walled cells with the stomata in rows and asperites prominent (Fig. 1). Long unicellular hairs or asperites were found in the inter-nerve epidermis.

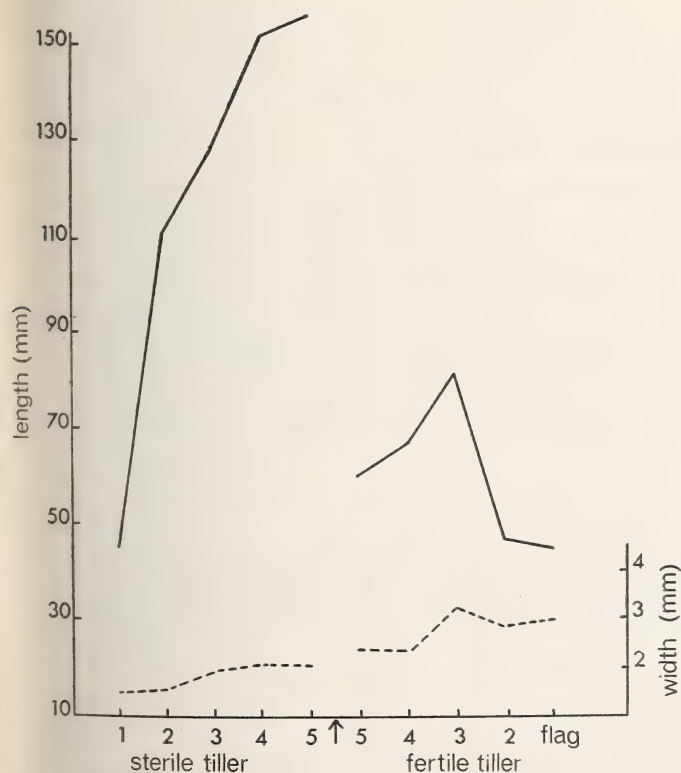


Fig. 1. Leaf blade length and width (broken line) sterile and fertile condition of a tiller of *Poa angustifolia*. ↑ Inflorescence initiation.

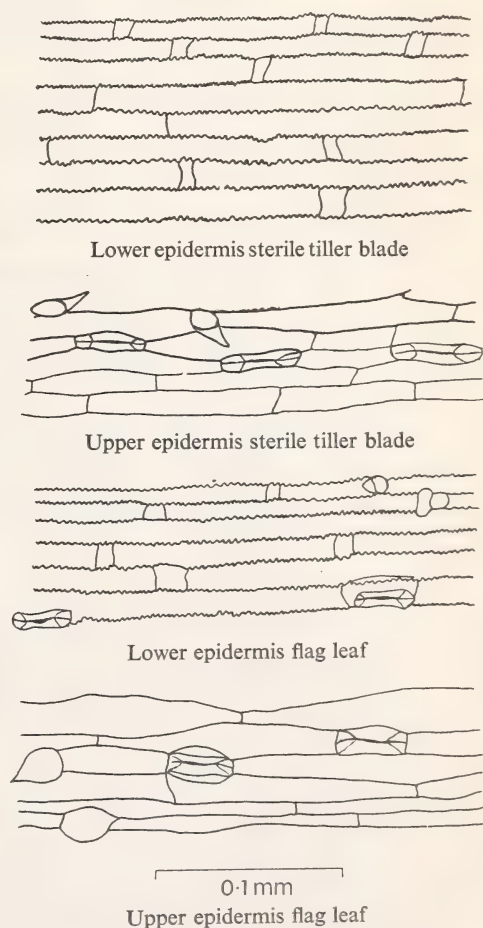


Fig. 2. *Poa angustifolia* leaf blade epidermis. Upper diagrams from sterile tiller leaves. Lower diagrams from flag leaf.

On the fertile tillers, by contrast, the lower epidermis of the flag leaf had numerous stomata (Table 4). The upper epidermis was of the type described for sterile leaves and the leaf margins showed asperities in all cases. As there was such a marked difference in the epidermal characters of the flag leaf blade and sterile tiller blades, this feature was investigated in all the leaves of the flowering tiller. The blade below the flag leaf showed stomata on the lower epidermis, but the third leaf down, which was longest, varied considerably. In some tillers there were abundant and well-distributed stomata, in others they were limited to the region near the mid rib. The fourth leaf down showed very few stomata on the lower epidermis in the majority of cases.

TABLE 4. Stoma density in *P. angustifolia* and *P. subcaerulea* transplants.

		Stomata/0.7 mm ²	
		Upper epidermis	Lower epidermis
<i>P. angustifolia</i>			
Deer Park No. 1	Flag leaf	36.92±3.72	9.96±0.76
	Sterile tiller leaf	63.76±3.68	0.00±0.00
Daneway 18	Flag leaf	58.88±3.16	18.96±0.84
	Sterile tiller leaf	59.08±4.18	0.04±0.04
<i>P. subcaerulea</i>			
Cefn-y-Gyngon	Flag leaf	28.12±1.07	10.20±0.82
	Sterile tiller leaf	46.36±2.78	10.40±0.70

INFLORESCENCE INITIATION

In *P. angustifolia* the inflorescence primordia are first found in late December, but are easier to find in January and February. During this period the field populations tend to lose all foliage through winter burn, and the leaves that emerge on these fertile tillers in spring are to be found as primordia beneath the panicle primordium. The stages of primordial development in *P. pratensis* have been illustrated by Evans (1949). The stages in *P. angustifolia* show that the vegetative apex with its leaf primordia first elongates and develops large folds, whilst later these show deeper folds, the beginnings of branching. At this and subsequent stages the number of potential spring and early summer leaves can be counted and usual numbers are not more than five. Similar features are to be found in *P. subcaerulea*.

DISCUSSION

Borrill (1959) demonstrated the influence of the development of the inflorescence primordia on blade length in *Glyceria*, and noted that there is occasional disturbance by external factors. He found that the primordia developed as the longest leaf emerged, subsequent leaves being shorter, and in the species studied inflorescence initiation occurred in spring. In *P. angustifolia* there is winter initiation and at this time the leaves in the bud are usually four to five in number and are the ones that emerge on the extending culm in spring and early summer. These leaves show the same pattern as found by Borrill, although, unlike the leaves of *Glyceria*, they all emerge after inflorescence initiation.

Leaf-sheath length is closely correlated with increases in stem internode, but total leaf length shows no clear association with inflorescence initiation or internode length. It is also clear that the percentage contribution of the blade and sheath to total leaf length decreases and increases respectively in succeeding leaves. The annual species *Lolium temulentum* (Borrill 1961a) shows similar increases in sheath length, but total leaf length also increases to the flag leaf which is different from that found in the present species which

are, of course, perennials. Probably differing patterns occur in different *Gramineae*, related to timing of inflorescence initiation and perenniality of species.

The epidermis of the lower surface of the narrow leaf blades shows an absence of or very few stomata, and it is reasonable to assume that this is a xeromorphic feature tending to increase its adaptability to dry areas, since the closure of the leaf by folding of the upper surface will effectively reduce water loss. On the fertile tiller, however, the narrow leaf blades with xeromorphic features change to broad leaf blades in which there is a progressive increase of stoma number in the lower epidermis. This reversal of xeromorphic characters is in striking contrast to many dicotyledons, and is possibly associated with the important part played by the leaves of the fertile tiller, particularly the flag leaf, in the filling of the caryopsis, as has been demonstrated in barley (Archbold 1945; Watson *et al.* 1958). Further, these broad leaves of the flowering tiller would be active in British conditions in the relatively moist periods of spring and early summer when water economy is not critical.

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SULPHUR AND THE DISTRIBUTION OF BRITISH PLANTS

By H. J. M. BOWEN

The University, Reading

ABSTRACT

The extent of recent additions of sulphur from fertilizers and atmospheric pollution to British soils is pointed out. Gymnosperms are especially sensitive to sulphur pollution, while crucifers and some other plants are unusually tolerant. It is possible that the diminution of some species, such as *Juniperus communis*, in Britain is a result of atmospheric pollution, as is the spread of many crucifers such as *Cardaria draba*. The distribution maps of many alien crucifers can be correlated with a map of sulphur dioxide pollution. Many native crucifers restricted to coastal habitats may be so restricted because their requirement for sulphur is satisfied by sea-spray.

Sulphur is a common element in the soil which is essential for the growth of plants. During the present century the amount of sulphur in British soils and plants has increased, partly from the use of fertilizers, but more substantially from pollution of the atmosphere. The present note attempts to correlate some recent changes in the distribution of plants with sulphur pollution in Britain, and suggests that further studies of the problem should be made.

SULPHUR IN SOILS

Sulphur is universally present in British soils, largely as the sulphate anion, but there are no data from which a map of sulphur abundance could be drawn. In the north and west of Britain, on soils derived from igneous rocks, sulphur is four or five times more abundant in soils derived from basalt and other basic rocks than it is in granitic soils. It is also unusually abundant in regions where certain minerals are common, as in parts of Cornwall. South and east Britain are mostly covered by soils derived from sedimentary rocks. In these rocks the relative abundance of sulphur increases in the order sandstones, limestones, shales and coal deposits: sulphur deficiency is most likely to occur in sandy soils. Soils unusually rich in sulphur are found near open-cast coal mines and above clays containing the sulphide of iron (iron pyrites). Calcium sulphate or gypsum occurs in large amounts in triassic clays in a narrow band stretching from Watchet in Somerset to Hawton in Nottinghamshire, while strontium sulphate or celestine occurs in a small area near Bristol, including the Avon gorge. Barium sulphate or barytes is found very locally in several parts of Britain, for example, the Derbyshire dales and Ben Bulbin in Sligo.

Sulphur constitutes 4 per cent of the solids in fresh water, and 2.5 per cent of the solids in sea water, so that it must be unusually abundant in salt marshes and on cliffs and beaches exposed to salt spray. Thomas *et al.* (1950) have shown that halophytes usually contain far more sulphur than do other plants.

Agricultural soils are subjected to a steady drain on their sulphur content, since a ton of crop usually contains between 1.5 and 10 kg of sulphur. During the present century most agricultural land in Britain has received heavy dressings of sulphur in fertilizers, either as ammonium sulphate, potassium sulphate or more often as superphosphate, which contains 12 per cent of sulphur from the sulphuric acid used to make it. The amount of sulphur applied to agricultural land in Britain each year is about 130,000 tons, corresponding to 10 kg/hectare. Some artificial soils, such as colliery dumps and railway cinder tracks, contain sufficient sulphur to restrict plant growth.

SULPHUR IN THE AIR

The extent of atmospheric pollution in Britain has been described by Meetham (1956), and the world problem has been summarized by Junge (1963). The pollution arises largely

from burning coal, and to a minor extent from smelting ores and making sulphuric acid. Coal contains from 0.5 to 4 per cent of sulphur, but much of this is oxidized to sulphates which remain in the ash after the coal is burnt. The remainder produces sulphur dioxide, and about five million tons of this gas are set free in Britain every year. As a result all big cities and industrial areas in Britain are surrounded by belts of air polluted with sulphur dioxide, as shown in Fig. 1. Polluted air may contain up to 200 μg sulphur dioxide per cubic metre, as against 1–3 μg in the purest air to be found on the earth today. The mean time each molecule of sulphur dioxide remains in the air before it is absorbed by plants or washed out by rain is 4 days. During this time the gas may be blown well out into the surrounding countryside. The ultimate effect of this pollution is to add between 5 and 400 kg of sulphur to each hectare of soil in Britain every year.

SULPHUR IN PLANTS

Plants need sulphur for many aspects of growth, and absorb it either as the sulphate ion through the roots, or as gaseous sulphur dioxide from the air. Sulphur deficiency has never been reported in Britain, though it is known in Nyasaland and western North America (Wallace 1961): it gives rise to chlorosis of the younger leaves in the same way as a shortage of iron does. Plants suffering from excess of sulphur in the soil are seldom noticed. Excessive amounts of sulphur dioxide in the air are harmful to plants, and markedly reduce their growth rate. The gas causes leaf necrosis and accelerates leaf senescence, and may cause evergreen species such as *Ilex aquifolium* and *Ligustrum vulgare* to become deciduous (Scurfield 1960). There are wide variations in tolerance between different species.

Analytical data for sulphur in plants have been given for example by Beeson (1941), Thomas *et al.* (1950), and Spector (1956). Conifer leaves contain only about 0.1 per cent of the element, grasses contain 0.05–0.2 per cent, while most other Angiosperm leaves contain 0.2–0.4 per cent. Exceptionally large amounts of sulphur are found in species of Cruciferae and the genus *Allium* (0.5–1.5 per cent), halophytes such as *Salicornia* and *Suaeda* (2–3 per cent), and *Cuscuta europaea* (1 per cent); the last finding needs confirmation.

The biochemistry of sulphur compounds in plants has been reviewed by Kjaer (1963). He points out that all species of Cruciferae, together with members of the related families Resedaceae and Capparidaceae, contain thioglucosides (mustard oils), which are responsible for the pungent taste of such well-known condiment plants as radish, horseradish, cress, watercress and the mustards. Species of the genus *Allium* contain no thioglucosides, but instead have a wide range of unusual sulphur compounds, including the lachrymator propenyl-sulphenic acid. Other genera which have been shown to contain unusual sulphur derivatives include *Equisetum*, *Athyrium*, *Pteridium*, *Petroselinum*, *Lactuca*, *Petasites* and *Asparagus*. Much remains to be discovered in this field, but it is clear that the Cruciferae and the genus *Allium* need more sulphur than other plants and are adapted to high concentrations of the element. This implies that these groups may have evolved in regions rich in sulphur, but such speculations will not be followed up here.

SPECIES ABNORMALLY SENSITIVE TO SULPHUR POLLUTION

Sulphur dioxide is known to be absorbed almost entirely by the leaves, but very few studies of chronic exposure of plants have been made (Bleasdale 1959). Hence it is not possible to say which species are most sensitive to sulphur pollution, though it seems that Gymnosperms and grasses are more sensitive than other plants (Katz & Shore 1955, Scurfield 1955, 1960). Since pollution reaches its maximum levels in winter, its effects are usually most severe on evergreen trees, and on herbaceous plants which overwinter with functional leaves. Comparison of Fig. 1 with the distribution maps in the *Atlas of the British Flora* which show records before and after 1930 (Perring & Walters 1962) is suggestive. Unfortunately it is difficult to disentangle the effects of pollution from two other major factors responsible for recent changes in the distribution of British plants—

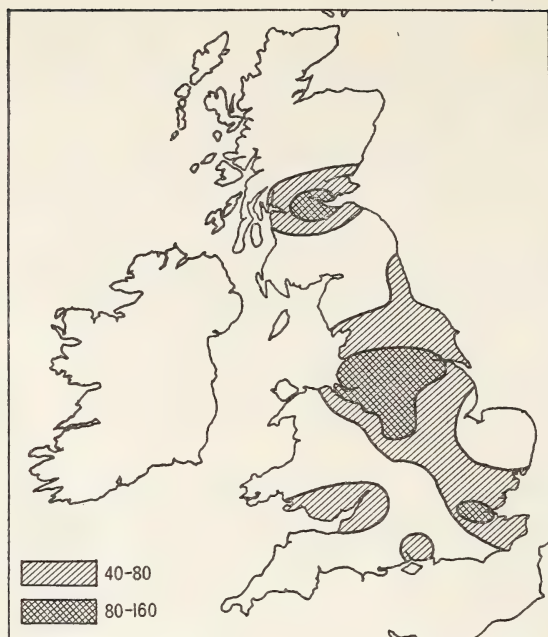


Fig. 1. Average amount of sulphur dioxide in the air in winter, in micrograms per cubic metre. After Meetham (1956).

the rise in mean winter temperatures which has caused many Northern species such as *Lycopodium selago* to retreat northwards or westwards, and the artificial drainage of wet habitats. However, there is sufficient correlation between areas of gross pollution and recent extinction to justify further studies on the following species: *Lycopodium inundatum*, *Juniperus communis*, *Hypericum elodes*, *Radiola linoides*, *Drosera* spp., *Gentiana pneumonanthe*, *Colchicum autumnale*, *Paris quadrifolia*, *Neottia nidus-avis* and *Rhynchospora alba*. The majority of these are plants of bogs or wet heaths, whose decrease may be largely due to drainage. Of the remainder, the Juniper (Fig. 2) has aroused interest because of its unexplained diminution on the Chilterns and in County Durham (Fitter 1964, Heslop-Harrison 1962). The decrease of the three monocotyledonous woodland species has been less spectacular and so has not been commented on. Studies of the chronic effects of sulphur dioxide on these species would be needed to establish whether the correlation is a true one.

SPECIES TOLERANT OF SULPHUR POLLUTION

The maps given in the *Atlas of the British Flora* show that the distributions of the following species are fairly well correlated with regions of industrial pollution: *Artemisia absinthium*, *Barbarea stricta*, *Bunias orientalis*, *Cardaria draba* (Fig. 3), *Descurainia sophia*, *Erucastrum gallicum*, *Erysimum cheiranthoides*, *Lepidium ruderales*, *Rapistrum rugosum*, *Senecio squalidus*, *S. viscosus*, *Sisymbrium altissimum* and *S. orientale*. All of these are plants of waste ground and are commonly found growing on soils containing large amounts of coal-ash, such as railway tracks, yards and refuse-tips, though *Descurainia*, *Erysimum* and *Rapistrum* occur as weeds in arable land as well. All are introduced plants, and one, *Senecio squalidus*, is native to the sulphureous region of Sicily. Rarer plants confined to similar habitats in Britain include *Artemisia verlotorum*, *Astragalus cicer*, *A. odoratus*, *Hirschfeldia incana*, *Rorippa austriaca* and several other crucifers. Five other species (*Cerastium atrovirens*, *Cochlearia danica*, *Corrigiola litoralis*, *Diplotaxis muralis* and

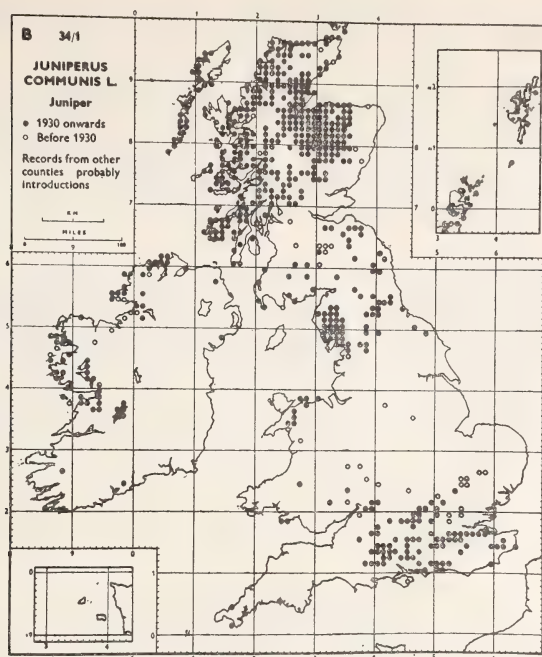


Fig. 2. Distribution map of *Juniperus communis* (Perring & Walters 1962). Note the disappearance since 1930 from polluted regions.

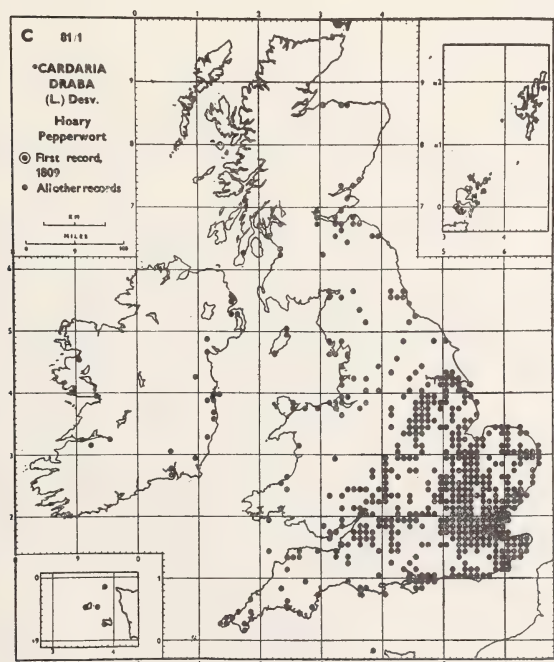


Fig. 3. Distribution map of *Cardaria draba* (Perring & Walters 1962). Most of the records outside polluted regions are from near the coast.

D. tenuifolia) should also be mentioned in this group. They are natives of the sea coast which have spread inland along railway tracks, but have not colonized unpolluted soils to any extent.

All these species can be said to be tolerant of sulphur pollution, and the high percentage of crucifers is noteworthy. As mentioned above, crucifers store much of their sulphur as thioglucosides, but the species of Caryophyllaceae, Papilionaceae and Compositae are believed not to do this. Biochemical examination of *Artemisia*, *Astragalus* and *Corrigiola* for sulphur compounds should be carried out.

FURTHER PECULIARITIES IN THE DISTRIBUTION OF CRUCIFERAE AND ALLIEAE

Sulphur may also be important in maintaining the abundance of some of the bad cruciferous weeds in Britain, such as *Brassica nigra*, *Sinapis arvensis*, *S. alba*, *Raphanus raphanistrum*, *Thlaspi arvense* and *Capsella bursa-pastoris*, as well as the crow garlic, *Allium vineale*. The large amounts of sulphur added to the soil in fertilizers may stimulate cruciferous weeds at the expense of others, and this should be tested experimentally.

In nature, coastal habitats are rich in sulphur and this may account for the high percentage of cruciferous species restricted to the sea-coast. If one compares the British representatives of other large herbaceous families in this respect, as in Table 1, one finds that only Allieae and Caryophyllaceae have a similar proportion of coastal species.

TABLE 1. Proportion of coastal species in various families of British plants.

Family	No. of native species	% of coastal species
Cruciferae	57	26.4
Allieae	8	25.0
Caryophyllaceae	71	18.3
Umbelliferae	53	11.3
Ranunculaceae	36	2.8
Scrophulariaceae	50	2.0
Labiatae	47	0

Coastal habitats are, of course, even richer in chlorine than they are in sulphur, but the two habitats of *Diplotaxis* suggest that the latter element is more important as far as crucifers are concerned.

The question arises as to whether some of our native crucifers and garlics are limited to soils relatively rich in sulphur. This is a difficult problem to which no definite answer can be given. A number of species of *Arabis*, *Cardaminopsis*, *Draba*, *Hornungia* and *Thlaspi*, together with *Allium oleraceum*, *A. schoenoprasum* and *A. sphaerocephalon*, are more or less localized to rocky soils in regions containing unusual minerals. The association of *Arabis stricta*, *Hornungia petraea* and *Allium sphaerocephalon* in the Avon gorge near Bristol may have arisen because of the sulphate minerals there, but there are other possible reasons. The area round Matlock in Derbyshire is noted for the occurrence of *Arabis hirsuta*, *Thlaspi alpestre*, *Draba muralis*, *D. incana*, *Hornungia petraea*, *Cardamine impatiens* and *Allium oleraceum*, as well as the mineral barytes or barium sulphate. However, it also yields minerals containing large amounts of fluorine, lead and zinc, among other elements, and the effects of specific minerals on these plants have not been tested. There is obviously a rich field here for future research.

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THE ASSESSMENT OF THE TAXONOMIC STATUS OF MIXED OAK (*QUERCUS* spp.) POPULATIONS

By A. CARLISLE and A. H. F. BROWN

ABSTRACT

The oaks (*Quercus* spp.) on slate, limestone and peat sites in Roudsea Wood, North Lancashire, were subjected to a taxonomic analysis using both the Hybrid Index and Pictorial Scatter Diagram methods. Both methods showed that *Quercus petraea* (Mattuschka) Liebl. predominates on the slate site, while the oaks on both the limestone and peat sites are very mixed, with a well-developed *Q. robur* L. component. The Hybrid Index method over-estimated the morphological intermediacy of the trees, while the Pictorial Scatter Diagram method under-estimated the *Q. robur* component. The scatter diagrams suggested that hybridization and introgression had occurred between *Q. petraea* and *Q. robur*.

INTRODUCTION

Until recently there has been confusion about the identification of *Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl. in Britain, partly due to contradictions in the literature and partly to the fact that in Britain many of the oaks exhibit intermediate characteristics. Jones' (1959) paper has gone a long way towards clarifying the characteristic morphology of the two species, but even so, apart from the recent work by Cousens (1962a, 1962b, 1963) the descriptions of British oak populations have generally been qualitative. In fundamental work on the autecology and nutrient cycles of oak woodlands, of which this study forms a part, it is essential to have a quantitative description of the individuals and populations if comparisons are to have any real meaning. The present investigation was undertaken to examine two methods of quantitative classification of individual oak (*Quercus* spp.) trees and mixed populations of *Quercus petraea* and *Q. robur*.

SITE DESCRIPTION

The investigation was carried out in Roudsea Wood in North Lancashire (SD(34)/331828). The woodland, which is owned by Mr. R. E. O. Cavendish, covers 116 hectares (287 acres) of which 45.3 hectares (112 acres) are currently leased by the Nature Conservancy.

The mean annual rainfall is 136 cm (53.5 in), and the mean monthly temperature ranges from 4.2 to 14.8° C (Ordnance Survey 1949; Meteorological Office, 1952).

The woodland includes areas of Upper Silurian slates of the Bannisdale series, carboniferous limestone, and peat, with local glacial and fluvio-glacial deposits. The oak populations were examined on all these sites.

The soils on the slate area are well drained brown earths of low base status, generally > 0.5 m deep, with a pH of 3.6–4.3 at a depth of 5–10 cm, and humus of the moder type (Kubiena 1953). The tree cover on these sites is irregular oak high forest, 70–80 years old, and the ground flora is dominated by *Deschampsia flexuosa*.

The soils of the limestone site are well drained, shallow (< 0.5 m) brown earths of higher base status than the slate soils, and are more variable owing to patches of glacial material containing slate debris. The pH at 5–10 cm depth is 4.3–8.0, and the humus type is similar to a mull. The tree cover on the limestone area consists mainly of dense thickets of oak, ash (*Fraxinus excelsior*), birch (*Betula* spp.), and hazel (*Corylus avellana*) coppice, with scattered standards of the first three. This woodland has a rich ground flora dominated by *Mercurialis perennis* and *Brachypodium sylvaticum*.

The peats are deep (> 1 m), poorly drained, contain 10 per cent of ash (550° C) per unit dry (105° C) weight, and have a pH of 3.2–3.8 at 5–10 cm depth. The woodland on the

peats consists of irregular, uneven-aged birch/Scots pine (*Pinus sylvestris*) woodland with scattered oak standards more than 50 years old. The ground flora is dominated by *Calluna vulgaris* and *Vaccinium myrtillus*.

There are no records of planting in Roudsea Wood earlier than 1953, but it is not certain that all the oak is completely natural and indigenous. These woodlands are probably the end product of a number of coppice rotations originating mainly from indigenous, natural maiden trees.

METHODS

Two methods were used to assess the taxonomic status of individuals and populations of oak in the present investigation, both of them being what Anderson (1949) terms 'polygraphic analyses':

I The Hybrid Index (HI) Method;

II The Pictorial Scatter Diagram (PSD) Method.

The main survey of the oak populations in Roudsea Wood was carried out using the HI method. Sub-samples ($n = 20$) of the populations were assessed by both methods.

I. THE HYBRID INDEX METHOD

This method, explained in detail by Anderson (1936, 1949), is useful for describing complex populations where two species have hybridized and backcrossed to produce plants of intermediate morphology (Anderson 1936, Raunkaier 1925, Riley 1938). It consists of calculating for each sample tree a numerical index, which describes the degree to which overall morphology of the individual is typical of one or other of the species.

When frequency distributions of these indices, calculated for a sample of plants from a population, are drawn as histograms, they give a visual description of the extent to which the components of the population are intermediate or typical of the species.

In the present investigation the calculation of the Hybrid Index was modified to permit different numbers of characters being examined in individual sample trees. In the calculation of the ordinary HI for a number of individual plants it is essential to keep the number of characters examined constant, otherwise the indices are not comparable. This is not always possible, and if strictly adhered to could introduce a bias into the sampling. *Q. robur* tends to produce seed more readily than *Q. petraea* (Jones 1959), and if all trees without acorns were rejected from the sample there would be a tendency to sample *Q. robur* more often than *Q. petraea* in a mixed population. In this instance, therefore, a variable number of characters must be accepted, and to overcome this difficulty, the index was calculated as a Percentage Hybrid Index. As many as possible of the selected characters were examined, assigned individually to the three categories *Q. robur*, or intermediate, or *Q. petraea*, and the number of characters in each category summed. These three sums were then calculated as percentages of the total number of characters examined, and the percentages multiplied by the factors 0, $\frac{1}{2}$ and 1 respectively. The summation of these products gave the Percentage Hybrid Index (PHI) which has a range of 0–100 (0 = *Q. robur*, 100 = *Q. petraea*) and is independent of variations in the total number of characters recorded.

The characters used in the estimation of the PHIs of the oaks in Roudsea Wood were based on Jones' definitions (1959). To begin with, 23 characters were examined by two independent workers examining the same set of specimens. Persistent disagreement occurred when attempting to categorize leaf glossiness, colour and texture, and these characters were discarded. The remaining 20 characters are defined in Table 1.

In view of the current lack of knowledge on the relative importance of individual oak characters, no weighting was used in the calculation of the PHI.

Roudsea Wood was divided into three parts, on the basis of the main soil types: slate soils, limestone soils, and peat. A random sample of 118 trees was taken on the slate site, 54 on the limestone, 48 on the peat. More than half the oaks in the wood are on the

TABLE 1. Morphological characters of *Quercus* spp. used in the assessment of percentage hybrid indices.

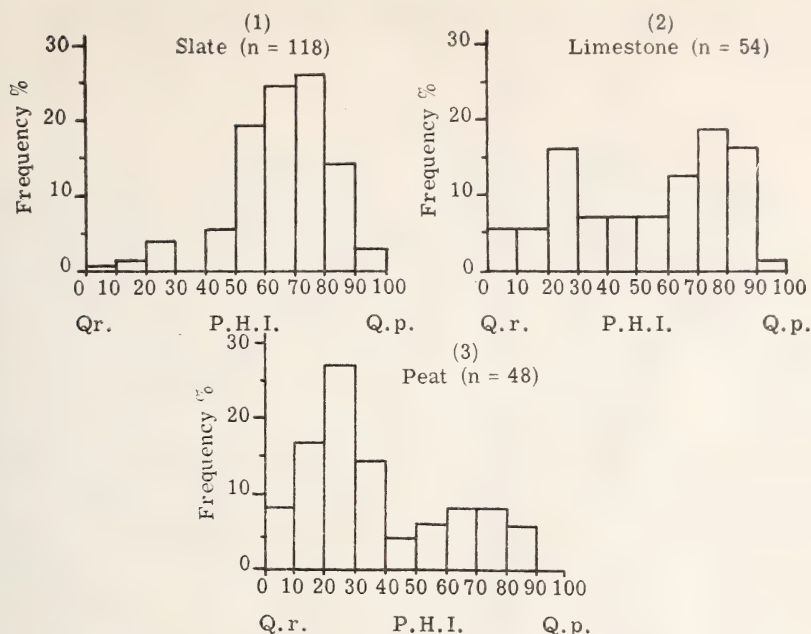
Character	<i>Q. robur</i>	<i>Q. petraea</i>
Stem persistence	Not persistent	Persistent
Angle between branches	> 45°	< 45°
Crown density	Open (foliage in clusters)	Dense (foliage uniformly distributed)
Bark	Thick elongated units	Thin rectangular units
Buds (terminal)		
(a) Size	Small (< 5 mm long)	Large (> 5 mm long)
(b) Form	Obtuse tip	Acute tip
Leaves		
(a) Shape	Obovate, widest in apical third of leaf	Ovate, widest near mid-leaf
(b) Lobe number*	< 5	> 5
(c) Lobe depth	Deep (> 50% of half leaf width)	Shallow (< 50% of half leaf width)
(d) Lobe regularity	Irregular	Regular
(e) Venation	Some veins to the sinuses between lobes	None to the sinuses
(f) Base auricle	Strongly auriculate, with the auricle lobes overlapping the petiole	Cordate, or slightly indented
(g) Petiole	< 7 mm	> 13 mm
(h) Simple hairs on abaxial surface	Few or absent	Abundant
(i) Stellate hairs on abaxial surface	Absent	Present
Acorns		
(a) Colour (when ripe)	Pale fawn	Dark brown
(b) Stripe (when ripe)	Olive green	None
(c) Form	Elongated	Rounded
(d) Peduncle length†	> 30 mm	< 20 mm
(e) Peduncle pubescence	Glabrous	Clustered hairs

* Jones gives the leaf lobe number of *Q. robur* as 3-5 (-6), and for *Q. petraea* as 5-6-8.

† Peduncle length taken as peduncle length to the terminal flower or bract.

slate site, and this area was sampled most intensively. Even so the sample of the trees on the slate site was less than a 10 per cent enumeration. On the limestone and peat more than half the total number of oaks present were sampled. The trees were sampled in the autumns (August to September) of 1961 and 1962. Stem persistence, branch angle, bark form and crown density were all recorded in the field. Ten sample shoots were taken from the upper half of the south side of the crown of each tree, all the shoots being free from shading. Lammas shoots were not included. Acorns were taken where possible, but a tree was not discarded from the sample because acorns were absent. Samples were examined either the same day or the day after collection. Ten leaves were taken at random from the pre-Lammas growth, and as many acorns as possible (up to 10) were examined. Decisions were made as to whether each character was typical of *Q. robur* or *Q. petraea*, or intermediate, and the PHIs calculated (Figs. 1-3).

There was a tendency to regard a character which was only slightly atypical of one or other of the species as intermediate. This was particularly so where a character was defined qualitatively (e.g. leaf lobe regularity, acorn shape). There is therefore a tendency for the PHI method to over-emphasize the intermediate character of a tree.



Figs. 1-3. The frequency distributions of Percentage Hybrid Indices (PHI) of oaks on slate, limestone and peat sites in Roudsea Wood.

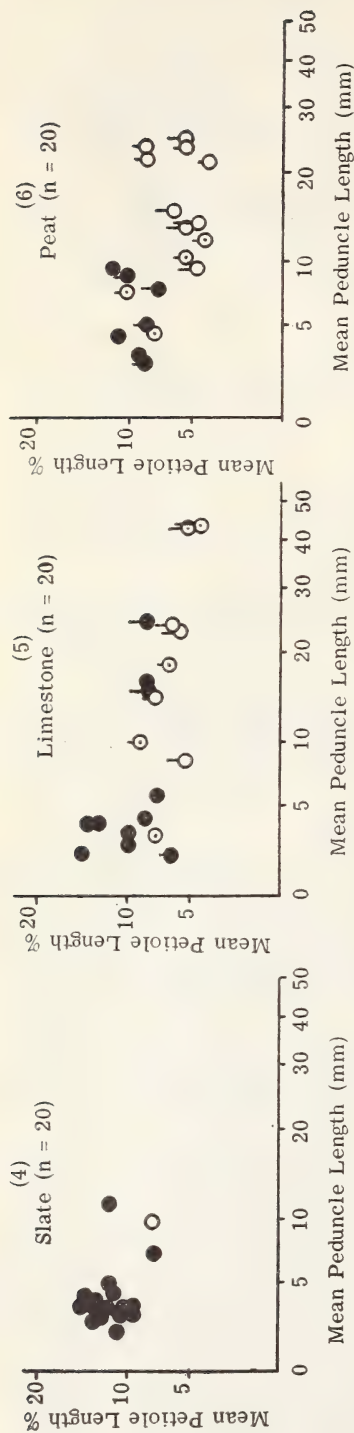
We examined samples from 10 trees twice within a period of a week, and the two PHI estimates differed by a mean of ± 2.6 PHI units with a maximum difference of 6.0 units. The method can, therefore, be repeated with an acceptable degree of error.

II. PICTORIAL SCATTER DIAGRAM

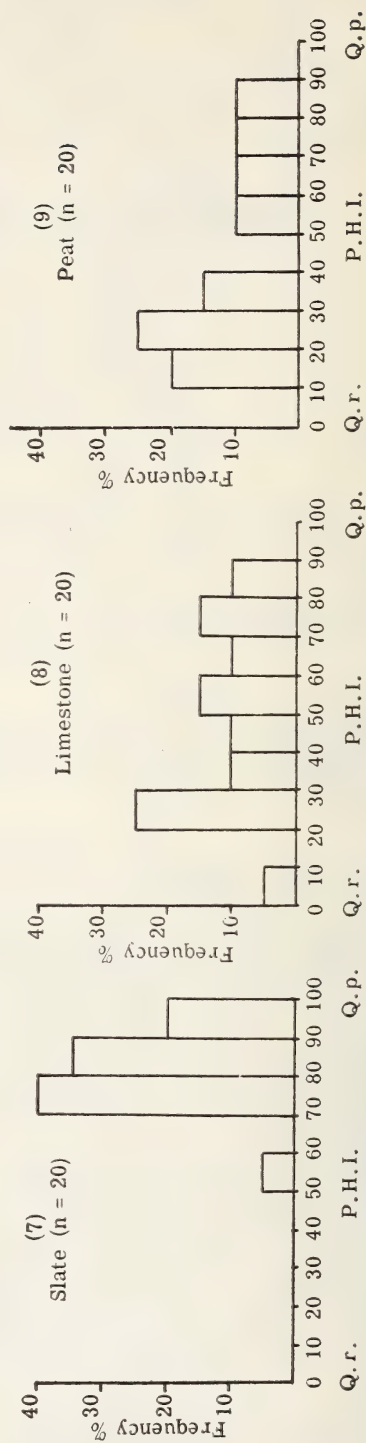
This method, based upon a technique described by Anderson (1949), has been used by Cousens (1962a and b) for surveys of oak populations in Britain. The principle of the method is that when, in a population of two species and their hybrids, two continuously variable morphological attributes by which the species are known to differ are plotted graphically, and each co-ordinate coded for subsidiary characteristics, the resultant scatter diagram gives a visual description of the population. The pattern of the scatter may be interpreted in terms of the degree of hybridization and introgression, and different populations can be compared visually. Points for the two species tend to concentrate in two separate zones, those for individuals with intermediate characteristics lying outside and between these zones.

The Pictorial Scatter Diagram (PSD) method was used on a sample of 20 trees taken at random on each of the slate, limestone, and peat sites. Ten shoots were taken from the upper half of the south side of the crown of each tree. Lammas growth was excluded from the sample. As many acorns as possible (up to 10) were included in each sample. Five leaves were taken from the mid-zone of each of the 10 shoots, mixed, and 10 of these 50 leaves taken at random. The petiole length, total leaf length, leaf auricle type and abaxial stellate pubescence were assessed for these 10 leaves, and the petiole length expressed as a percentage of total leaf length as suggested by Cousens. The acorn peduncle lengths to the first bract or flower were measured and the mean calculated. The mean petiole per cent. and mean peduncle length were plotted on logarithmic paper, and the points coded for leaf auricle type and abaxial stellate pubescence (Figs. 4-6). The same 20 trees were subjected to a PHI analysis (Figs. 7-9).

This PSD procedure differed from that used by Cousens in that 10 leaves per tree



Figs. 4-6. Pictorial Scatter Diagrams for oaks on slate, limestone and peat sites in Roudsea Wood. ●, ○ = stellate pubescence on abaxial leaf surface abundant, sparse and absent respectively. ⊙, ⊖ = leaf auricle well developed, weak and absent respectively.



Figs. 7-9. The frequency distributions of the Percentage Hybrid Indices (PHI) of the oak samples from slate, limestone and peat sites in Roudsea Wood used to construct the Pictorial Scatter Diagrams (Figs. 4-6).

were used instead of two; the mean acorn peduncle length was used instead of maximum peduncle length; and the peduncle stoutness and pubescence were not included in the code on the scatter diagram.

RESULTS

The taxonomic status of the oak populations

The PHI frequency distributions (Figs. 1–3) show differences between the oak populations on the different sites. On the slate site, the oaks are mainly trees with marked *Q. petraea* characteristics, and there are very few *Q. robur*. The oak populations on the limestone and peat are more mixed with modes near both the *Q. robur* and *Q. petraea* ends of the scale. There is a strong *Q. robur* component in the woodlands on the peat site.

The scatter diagrams (Figs. 4–6) also show that the oak populations on the slate, limestone and peat sites are different. On the diagram (Fig. 4) for the slate site, there is a concentration of points in a zone where the mean petiole length per cent. is high and the mean peduncle length low, the leaves having well-developed stellate hairs and no leaf auricles, all of which indicates that most of the trees are *Q. petraea*. There are three intermediate points. This suggests a predominantly *Q. petraea* population containing a few trees with intermediate characteristics. The diagram (Fig. 5) for the limestone site suggests a very mixed population ranging from trees with high mean petiole percentages and low mean peduncle lengths (*Q. petraea*) to trees with low mean petiole percentages and high mean peduncle lengths (*Q. robur*), with many intermediates. The *Q. petraea* trees all have at least a few stellate hairs and no auricle, and all the points in the *Q. robur* zone are associated with trees having well-developed auricles and few or no stellate hairs. The diagram for the peat site shows that while there are a few trees in or near the *Q. petraea* zone on the diagram, and a few more or less in the *Q. robur* zone, most of the trees are intermediate in their petiole and peduncle characteristics. Near the *Q. petraea* zone some of the trees have weakly-developed auricles.

The scatter diagrams reflect the *Q. petraea* component suggested by the PHI frequency distributions, but the former do not suggest as strong a *Q. robur* component as the latter.

As *Q. robur* apparently prefers base-rich fertile soils and *Q. petraea* the more acid, less fertile soils (Jones 1959, Moss 1914), the distribution of the species on the slate and limestone sites in Roudsea Wood, with *Q. petraea* predominating on the slate and a well-represented *Q. robur* component on the limestone, could perhaps be interpreted in terms of these soil preferences. However, it must be remembered that it is possible that some oak has been planted in Roudsea Wood, although there is no evidence of such plantings in the estate records. It seems most unlikely that oak has ever been planted on the peat sites and more likely that the trees have arisen naturally. If any oaks survive at all on these peats, it would be expected that *Q. robur*, with its tolerance of soil waterlogging (Jones 1959) would compete successfully with the *Q. petraea*.

Hybridization and introgression

So far, all the trees with characteristics which are neither markedly those of *Q. petraea* nor *Q. robur* have been termed "intermediates", and no assumptions have been made that they are necessarily due to hybridization. Dengler (1941) suggests that *Q. robur* and *Q. petraea* are able to hybridize to a certain extent, and it is likely that hybridization occurs in field conditions. Cousens (1962a and b) has discussed the possibility of introgression occurring.

The PHI frequency distributions give little information about hybridization and introgression other than showing that the populations are mixed, with many intermediates which may or may not be hybrids. On the other hand, PSDs provide a certain amount of information on this point. The patterns of the scatter diagrams in Figs. 4–6 are similar to those described by Anderson (1949) as being associated with populations of plants where hybridization and introgression have occurred. The scatter diagram for the slate

site suggests a population of *Q. petraea* that is almost pure but slightly introgressed. The other scatter diagrams (Figs. 5–6) suggest strongly introgressed populations, possibly with some F1 hybrids.

These data lend support to Cousens' (1962a and b) view that introgression occurs in British oak woodlands.

A comparison of the Hybrid Index and Pictorial Scatter Diagram methods

Although the two methods give similar general pictures of the taxonomic status of the oak populations in Roudsea Wood, these pictures differ in detail. The closest agreement is in the *Q. petraea* component. The marked *Q. petraea* tendencies of the slate population as shown by the PHI frequency distribution histograms (Figs. 1 and 7) are also reflected by the pronounced concentration of points in the long petiole/short peduncle zone on the PSD in Fig. 4. In the PHI histograms in Figs 2–3 and 8–9 there are indications of a strong *Q. robur* component which are not reflected in the corresponding PSDs in Figs. 5–6. Either the PHI method tends to over-estimate the *Q. robur* component or the PSD method under-estimates it. It has already been mentioned that there is a tendency in the PHI method to over-emphasize the intermediacy of a specimen. It seems unlikely, therefore, that this method will over-emphasize the *Q. robur* (or *Q. petraea*) components, and more likely that the PSD is under-estimating the *Q. robur* component. This under-estimation may well be due to the fact that *Q. robur* apparently is much more variable than *Q. petraea* (Weimarck 1947). This greater variability may extend to the petiole and peduncle lengths, so that unless large numbers of trees are examined, there may not be clear evidence of a concentration of points in any particular zone at the small petiole/long peduncle end of the scale, even though a PHI analysis suggests an almost pure population of *Q. robur*. Cousens (1962a and b) designates concentration centres on his scatter diagrams, using petiole length per cent. and maximum peduncle length. He found that none of the many oak woodlands examined by him was pure *Q. robur*, i.e. not all the points came within the limits of the *Q. robur* concentration centres. It is possible that this apparent absence of pure *Q. robur* woodlands may be due to this method under-estimating the *Q. robur* component. On the scatter diagrams, it will probably be necessary to allow more latitude for *Q. robur* than *Q. petraea* if concentration centres are delineated.

The two methods, when used simultaneously in an oak population survey, provide complementary information. The PHI method is based upon more characters; the histograms give an overall picture of the population. The PSD method, on the other hand, provides information about hybridization and introgression. Where extreme purity of a species is needed, as, for example when seed is needed for autecological studies, the PHI method is to be preferred as it is based on more characters and tends to over-estimate the intermediacy and under-estimate the purity of the trees. For a tree to have a PHI of <10 or >90 it has to be very typical of the species indeed.

Modifications of the oak population survey methods

In future surveys using the PHI method, it will be better to use only the characters of bud size and form; leaf shape, lobe number, lobe depth, lobe regularity, venation, auricle, petiole, abaxial stellate pubescence; and acorn colour, stripe, form and peduncle length (Table 1). The petiole length character should be expressed as a percentage of the total leaf length as suggested by Cousens (1962a and b), and defined as <6.5 per cent for *Q. robur* and >9.5 per cent for *Q. petraea* as suggested by the scatter diagrams in Figs. 4–6. The mean value should be based upon 10 or more leaves taken from the middle of shoots from the south side of the upper half of the crown where possible. The peduncle length should be expressed as the mean length of the peduncle to the first bract or flower, based upon 10 or more peduncles per tree where possible. Tentatively it is suggested that a mean peduncle length of >20 mm is regarded as a *Q. robur* characteristic and <6 mm as a *Q. petraea* characteristic.

The main weakness of both the methods is our lack of knowledge about the variations of the individual characters within pure stands of *Q. petraea* and *Q. robur*. Individual morphological characters may have considerable latitude in the pure species types. If this is so, at least some characters which are now regarded as morphologically intermediate may occur in pure types. At the moment, therefore, estimates of the taxonomic status of these oaks probably under-estimate the purity of the trees. The species are at present defined in terms of multiple qualitative data so that more precise statistical methods of discrimination, such as Fisher's discriminant analysis (Fisher 1950), cannot be used.

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DACTYLORHIZA NEVSKI, THE CORRECT GENERIC NAME OF THE DACTYLORCHIDS

By P. F. HUNT and V. S. SUMMERHAYES

Royal Botanic Gardens, Kew

ABSTRACT

The correct generic name for the dactylorchids (marsh and spotted orchids) is shown to be *Dactylorhiza* Nevski. A list of species of *Dactylorhiza* is given and the subspecies occurring in the British Isles are indicated. Several new combinations at specific and subspecific rank and five new bigeneric hybrid formulae are published for the first time.

In his *Species Plantarum* (939–944, 1753) Linnaeus divided the genus *Orchis* into three parts based on the morphology of the roots, namely: *Bulbis indivisis*, *Bulbis palmatis* and *Bulbis fasciculatis*. Some time later, Necker, in his *Elementa Botanica* (3, 129, 1790), raised these groups to generic level although he actually used the category name ‘species naturalis’ for them. *Orchis* L. was retained for *Bulbis indivisis* whilst *Bulbis palmatis* and *Bulbis fasciculatis* became *Dactylorhiza* Necker.

The next important treatment of the genus was by Klinge, in 1898 (*Acta Hort. Petrop.* 17, 148). He recognized two subgenera, namely *Eu-orchis*, into which he placed the Linnaean *Bulbis indivisis*, and *Dactylorchis* which included *Bulbis palmatis*. This classification was adopted by many later workers, but in 1935, Nevski, in his account of the *Orchidaceae* for the *Flora URSS*, substituted Necker’s name *Dactylorhiza* for the second of Klinge’s subgenera on the ground that it was earlier than *Dactylorchis* Klinge. Nevski also seems to have excluded Linnaeus’s *Bulbis fasciculatis*, at least by implication.

Two years later, however, Nevski evidently decided that the two subgenera were better treated as distinct genera and adopted the generic name *Dactylorhiza*, making a new combination, *D. umbrosa* (Kar. et Kir.) Nevski (*Acta Inst. Bot. Acad. Sci. URSS* ser. 1, 4, 332, 1937). This generic name is obviously based on *Orchis* subgen. *Dactylorchis* Klinge although naturally Nevski attributed it to Necker.

Ten years later still, in 1947, Vermeulen published his well-known *Studies on Dactylorchids* in which he raised Klinge’s subgenus *Dactylorchis* to generic rank as *Dactylorchis* Vermeul., making many of the necessary new combinations. In this book, Vermeulen quite arbitrarily dismissed the name *Dactylorhiza* as not being a synonym of *Dactylorchis* because the two concepts were not co-extensive. It is true that *Dactylorchis* is not identical with *Dactylorhiza* as understood by Necker but this does not preclude the two names from being synonymous. Vermeulen evidently overlooked Nevski’s use of the name *Dactylorhiza* in its narrower sense, which was identical with his concept of *Dactylorchis*.

Unfortunately, owing to the relative obscurity of Nevski’s publication contrasted with the obviously wide distribution of Vermeulen’s book, the generic name *Dactylorchis* has been adopted by some botanists whereas *Dactylorhiza* was almost completely ignored until 1959. In that year Bullock (*Taxon* 8, 46) in a paper recommending the rejection of Necker’s names, cited the case of *Dactylorhiza* versus *Dactylorchis* as an example of the possible confusion arising if this course were not taken.

Necker’s names were arbitrarily designated as unitary specific names and rejected under article 20 of the International Code of Botanical Nomenclature in 1959 but this does not affect the legitimacy of Nevski’s use of the name. *Dactylorhiza* Nevski is validated by reference to Necker’s *description* which was effectively published and by reference to *Orchis* L. subgenus *Dactylorchis* Klinge which also is accompanied by a *description*.

Although Nevski was wrong in using the name *Dactylorhiza* at subgeneric level he was

quite in order when using it for a genus. The correct generic name for the group of *Orchis* designated by Klinge as subgenus *Dactylorchis* is therefore *Dactylorhiza* Necker ex Nevski (or simply *Dactylorhiza* Nevski) which has ten years' priority over *Dactylorchis* Vermeul.

The first worker to follow Nevski was Borsos (*Acta Bot. Acad. Sci. Hung.* 5, 321, 1959) in her "*Dactylorchis fuchsii* et son affinité dans les flores Hongroise et Carpathique". She dealt with the names *Dactylorhiza* and *Dactylorchis* and pointed out that *Dactylorhiza* has priority. She then made several new combinations but unfortunately stated that they were intended to be valid in both *Dactylorhiza* and *Dactylorchis*. This is contrary to article 34 of the Code and consequently none of her names can be accepted as validly published in either genus.

The next year, 1960, Soó summed up the situation to date in his "Synopsis Generis *Dactylorhiza* (*Dactylorchis*)" (*Ann. Univ. Sci. Budap. de Rolando Eötvös nom. sect. Biol.* 3, 335) and made many new combinations in *Dactylorhiza*. Although he clearly accepts *Dactylorhiza* as the correct name he thinks that as *Dactylorchis* has been used by a number of authors it should be conserved.

Unfortunately many of these new combinations do not comply with article 33 of the Code which states that a new combination or a new name is not validly published unless the basionym is clearly indicated with a full and direct reference to its author and original place of publication, including page reference and date. Soó was informed by us of this error and in 1962 he published a separate paper entitled "Nomina Nova Generis *Dactylorhiza*" in order to validate his new combinations and new names.

There seems to be little doubt, in view of the evidence from both morphological and cytological studies and the incidence of hybridization in nature, that Nevski, Vermeulen, Borsos, Soó and others are correct in considering the dactylorchids to belong to a genus distinct from *Orchis* proper which is typified by *O. militaris* L. and contains species such as *O. mascula* (L.) L. The dactylorchids are readily distinguishable by their foliaceous bracts (*Orchis* proper usually has chaffy, membranous bracts), hand-like (palmate) tubers (testicle-like in *Orchis*) and basic chromosome number of 20 (*Orchis* $n = 16, 18$ or 21). The general habit is also different in the two groups, the developing inflorescence in *Orchis* proper being covered by the spathe-like uppermost stem bract until just before the buds open, whereas in the marsh and spotted orchids the apical flower buds of the inflorescences are exposed as soon as the spike appears above ground.

In order to emphasize our acceptance of the existence of a separate genus for the marsh and spotted orchids and of the correct name, *Dactylorhiza*, for this genus, we repeat here the new combinations of all the species that Soó recognizes in *Dactylorhiza*. We are not, however, expressing any opinions as to the status of any of the taxa that do not occur in Britain, nor do we agree entirely with the details of his classification. For various reasons we have found it necessary to make some new combinations ourselves; these include cases where Soó has still not made the combinations in a valid manner. With regard to the British species, which are indicated by asterisks, we have added what we consider to be the subspecies occurring in Britain. We do not think that it is possible at present to recognize varieties in the British species of *Dactylorhiza*. The taxonomic positions of *Orchis francis-druei* Wilmott and of *Dactylorchis majalis* subsp. *cambrensis* Roberts are not yet clear and we have therefore omitted them from this account.

We also give a synonymy of the names used in the *Flora of the British Isles* by Clapham, Tutin & Warburg, edition 1, 1952 (abbreviated as CTW) and in the *List of British Vascular Plants* by Dandy, 1958 (abbreviated as DANDY). We add those of the *Flora of the British Isles* CTW, edition 2, 1962, where the nomenclature or taxonomy differs from that of Dandy. In all these cases we quote the author citations of these synonyms as given in the books cited.

1. DACTYLORHIZA IBERICA (M. Bieb.) Soó.
2. DACTYLORHIZA SAMBUCINA (L.) Soó.
3. DACTYLORHIZA ROMANA (Seb. & Maur.) Soó.

4. **DACTYLORHIZA INCARNATA* (L.) Soó.
Dactylorchis incarnata (L.) Vermeul. DANDY 643/3.
Orchis strictifolia Opiz CTW.
 (a) subsp. *INCARNATA*
Dactylorchis incarnata (L.) Vermeul. subsp. *incarnata* DANDY 643/3/a.
Dactylorchis incarnata (L.) Vermeul. subsp. *gemmana* (Pugsl.) H.-Harrison f. DANDY 643/3/e.
 (b) subsp. *ochroleuca* (Boll.) P. F. Hunt & Summerh., **comb. nov.**
Orchis incarnata subsp. *ochroleuca* (Boll.)
 Schwarz. Mittel. Thüring. Bot. Ges. **1** (1), 94 (1949).
Orchis incarnata L. var. *ochroleuca* Boll. Arch. Ver. Nat. Meckl. 14, 307 (1860).
Dactylorchis incarnata (L.) Vermeul. subsp. *ochroleuca* (Boll.) H.-Harrison f. DANDY 643/3/d.
 (c) subsp. *PULCHELLA* (H.-Harrison f.) Soó.
Dactylorchis incarnata (L.) Vermeul. subsp. *pulchella* (Druce) H.-Harrison f. DANDY 643/3/b.
Orchis strictifolia Opiz subsp. *strictifolia* var. *pulchella* (Druce) Clapham CTW.
 (d) subsp. *COCCINEA* (Pugsl.) Soó.
Orchis latifolia L. var. *coccinea* Pugsley. J. Linn. Soc. Bot. 49, 578 (1935).
Dactylorchis incarnata (L.) Vermeul. subsp. *coccinea* (Pugsl.) H.-Harrison f. DANDY 643/3/c.
Orchis strictifolia Opiz subsp. *coccinea* (Pugsl.) Clapham CTW.
5. **DACTYLORHIZA CRUENTA* (O.F. Muell.) Soó.
Dactylorchis incarnata (L.) Vermeul. subsp. *cruenta* (O.F. Muell.) Vermeul. DANDY 643/3/d.
Orchis cruenta O.F. Muell. CTW.
6. *DACTYLORHIZA PSEUDOCORDIGERA* (Neum.) Soó.
7. *DACTYLORHIZA SALINA* (Turcz.) Soó.
8. *DACTYLORHIZA SANASUNITENSIS* (Fleisch.) Soó.
9. *Dactylorhiza cilicica* (Klinge) P. F. Hunt & Summerh., **comb. nov.**
Orchis cilicica (Klinge) Schltr. Feddes Rep. Sonderbeih. A, **1**, 178 (1927).
Orchis orientalis Klinge subsp. *cilicica* Klinge in Acta Hort. Petrop. **17** (1) 36, (1898).
10. *Dactylorhiza kotschyi* (Rchb.f.) P. F. Hunt & Summerh., **comb. nov.**
Orchis kotschyi (Rchb.f.) Schltr. in Fedde Rep. **19**, 48 (1923).
Orchis incarnata L. var. *kotschyi* Rchb.f. in Orch. Fl. Germ. Recens. 53 (1851).
11. *Dactylorhiza osmanica* (Klinge) P. F. Hunt & Summerh., **comb. nov.**
Orchis osmanica (Klinge) G. Camus in Icon. Orch. Europ. 222 (1929).
Orchis orientalis Klinge subsp. *osmanica* Klinge in Acta Hort. Petrop. **17**(1), 188 (1898).
12. *DACTYLORHIZA UMBROSA* (Kar. & Kir.) Nevski.
13. *DACTYLORHIZA PERSICA* (Schltr.) Soó.
14. *DACTYLORHIZA GRAGGERIANA* (Soó) Soó.
15. *DACTYLORHIZA HATAGIREA* (Don) Soó.
16. *Dactylorhiza majalis* (Rchb.) P. F. Hunt & Summerh., **comb. nov.**
Orchis majalis Rchb. in Pl. Crit. **6**, 7 (1828).

Although there have been many papers dealing with the supposed identity of *Orchis latifolia* L., no universally accepted decisions have been reached. At some time or another the three entities we now call *D. incarnata*, *D. praetermissa* and *D. majalis* have been variously referred to *O. latifolia* L., together with less well known species. On careful

consideration of the evidence we agree with many taxonomists that *O. latifolia* L. is best looked upon as a *nomen confusum* and therefore to be disregarded (Art. 69). Soó, however, uses *Dactylorhiza latifolia* for what we here call *Dactylorhiza majalis*. Three other names published between *O. latifolia* L. (1753) and *O. majalis* Rchb. (1828) have been quoted in the major monographs as synonyms of *O. latifolia*. Vermeulen and others who have accepted *majalis* in preference to *latifolia* have not, however, stated why they did not use any of the above mentioned synonyms. We have therefore looked into these names with the following results:

(i) *Orchis comosa* Scop. Fl. Carn. ed. 2, 2, 198 (1772).

This is based on Bauhin's *Palmata vilissima* (Hist. Plant. Univ. 2, 776 (1651)). The identity of this plant is very doubtful but it may possibly be equal to *Dactylorhiza latifolia* (L.) Soó subsp. *alpestris* (Pugsl.) Soó, which, however, may prove to be distinct from *D. majalis* proper.

(ii) *Orchis palmata* Gilib. Exercit. Phytol. 2, 479 (1792).

This is not a binomial name, being given as *Orchis palmata rubra nectarii labio maculato*. The great majority of names in this book consist of two words but these are to be regarded as abbreviated phrase names and not Linnaean binomials.

(iii) *Orchis fistulosa* Moench, Meth. 713 (1794).

In this case *Orchis latifolia* L. is given as a synonym; *O. fistulosa* is therefore illegitimate.

From the above it is clear that no one of the above three names can be used and we are consequently adopting the epithet *majalis* since it is the earliest legitimate one which can be identified unequivocally.

17. **Dactylorhiza kerryensis* (Wilmott) P. F. Hunt & Summerh., **comb. nov.**

Orchis kerryensis Wilmott in Proc. Linn. Soc. Lond. Sess. 148, 126 (1936).

Dactylorhiza majalis (Rchb.) Vermeul. subsp. *occidentalis* (Pugsl.) H.-Harrison f. DANDY 643/6.

Orchis occidentalis Pugsl. subsp. *kerryensis* (Wilmott) Clapham CTW.

18. DACTYLORHIZA CORDIGERA (Fries) Soó.

19. DACTYLORHIZA CATAONICA (Fleisch.) Holub. Preslia 36, 252 (1964).

Orchis cataonica Fleisch. in Ann. Nat. Hofmus. Wien 28, 34 (1914).

Orchis caucasica (Klinge) Medvedev. Acta Hort. Tiflis 18, 271 (1926), non Regel (1809).

Orchis cordigera Kraenzl. Fedde Rep. Beih. 65, 39 (1931), non Fries (1842).

Orchis euxina Nevski in Komarov F. URSS 4, 709 (1935).

Dactylorhiza euxina (Nevski) Soó and *D. caucasica* (Medvedev) Soó were simultaneously published as alternative interchangeable names for this concept in 'Nomina nova generis *Dactylorhiza*'. According to Article 34 of the Code both must be regarded as not validly published. Soó, although including *Orchis cataonica* as a synonym of this concept and making it a variety, overlooked the fact that it is the earliest available specific epithet.

20. *DACTYLORHIZA PRAETERMISSA (Druce) Soó.

Dactylorhiza praetermissa (Druce) Vermeul. DANDY 634/4.

Orchis praetermissa Druce CTW.

21. *DACTYLORHIZA PURPURELLA (T. & T.A. Steph.) Soó.

Dactylorhiza purpurella (T. & T.A. Steph.) Vermeul. DANDY 643/5.

Orchis purpurella T. & T.A. Steph. CTW.

22. DACTYLORHIZA ARISTATA (Fischer ex Lindl.) Soó.

23. DACTYLORHIZA LAPPONICA (Laestad. ex Rchb. f.) Soó.

24. *DACTYLORHIZA TRAUNSTEINERI (Sauter) Soó.

Dactylorhiza traunsteineri (Sauter) Vermeul. DANDY 643/7.

Orchis traunsteinerioides (Pugsl.) Pugsl. CTW.

25. DACTYLORHIZA ELATA (Poir.) Soó.

26. DACTYLORHIZA FOLIOSA (Vermeul.) Soó.

27. **DACTYLORHIZA MACULATA* (L.) Soó.
Dactylorchis maculata (L.) Vermeul. DANDY 643/2.
 (a) subsp. *ericetorum* (Linton) P. F. Hunt & Summerh., **comb. nov.**
Orchis maculata L. subsp. *ericetorum* Linton in Fl. Bournemouth 208 (1900).
Dactylorchis maculata (L.) Vermeul. subsp. *ericetorum* (Linton) Vermeul.
 DANDY 643/2/b.
Orchis ericetorum Linton CTW.
 (b) subsp. *rhoemensis* (H.-Harrison f.) Soó.
Dactylorchis maculata (L.) Vermeul. subsp. *rhoemensis* (H.-Harrison f.)
 H.-Harrison f. DANDY 643/2/a.
Dactylorchis fuchsii (Druce) Vermeul. subsp. *rhoemensis* (H.-Harrison f.)
 Clapham CTW ed. 2.
Orchis fuchsii Druce subsp. *rhoemensis* H.-Harrison f. CTW ed. 1.
28. *DACTYLORHIZA SACCIFERA* (Brongn. ex Bory) Soó.
29. **DACTYLORHIZA FUCHSII* (Druce) Soó.
Dactylorchis fuchsii (Druce) Vermeul. DANDY 643/1.
 (a) subsp. *FUCHSII*.
Dactylorchis fuchsii (Druce) Vermeul. subsp. *fuchsii* DANDY 643/1/a.
Orchis fuchsii Druce CTW.
 (b) subsp. *OKELLYI* (Druce) Soó.
Dactylorchis fuchsii (Druce) Vermeul. subsp. *okellyi* (Druce) Vermeul. DANDY
 643/1/b.
Orchis okellyi Druce CTW in obs.
 (c) subsp. *HEBRIDENSIS* (Wilmott) Soó.
Dactylorchis fuchsii (Druce) Vermeul. subsp. *hebridensis* (Wilmott) H.-Harrison f.
 DANDY 643/1/c.
Orchis fuchsii Druce subsp. *hebridensis* (Wilmott) Clapham CTW.

BIGENERIC HYBRIDS

We are taking this opportunity of publishing some bigeneric hybrid names in which *Dactylorhiza* is one of the parent genera. In our opinion such hybrid names should be regarded as mere formulae and no descriptions should be needed for validation, which is effected solely by stating the parent genera concerned. Being formulae and therefore not tied to the rules of priority (except that when the same two generic names have been combined in various ways the earliest ought to be chosen), hybrid generic names should be altered whenever the generic position of one or other of the parent species alters. This should not, however, apply if the change is merely nomenclatural but this question does not arise here as we know of no bigeneric names formed with the name *Dactylorchis* used for one parent.

The necessary new formulae consequent upon accepting the genus *Dactylorhiza* are as follows:

1. $\times$ *Dactylocamptis* P. F. Hunt & Summerh. (*Dactylorhiza* $\times$ *Anacamptis* L. C. Rich.)
Orchis L. can also cross with *Anacamptis*; these are called $\times$ *Anacamptorchis* G. Camus 1892 (syn. $\times$ *Orchidanacamptis* Labrie 1927)
2. $\times$ *Dactyloglossum* P. F. Hunt & Summerh. (*Dactylorhiza* $\times$ *Coeloglossum* Hartm.)
Orchis L. is not known to cross with *Coeloglossum*; previous names applied to hybrids referable to $\times$ *Dactyloglossum* are $\times$ *Coeloglossorchis* Guétrot 1927, $\times$ *Orchi-coeloglossum* Aschers. et Graebn. 1907 and $\times$ *Habenariorchis* Rolfe 1892.
3. $\times$ *Dactylitella* P. F. Hunt & Summerh. (*Dactylorhiza* $\times$ *Nigritella* L. C. Rich.)
Orchis L. is not known to cross with *Nigritella*; a previous name for hybrids referable to $\times$ *Dactylitella* is $\times$ *Nigrorchis* Godfery 1925.

4. $\times$ **Rhizanthera** P. F. Hunt & Summerh. (*Dactylorhiza* $\times$ *Platanthera* L. C. Rich.)

Orchis L. is not known to cross with *Platanthera*; an earlier name for the hybrids referred to $\times$ *Rhizanthera* is $\times$ *Orchiplatanthera* G. Camus.

5. $\times$ **Orchidactyla** P. F. Hunt & Summerh. (*Dactylorhiza* $\times$ *Orchis* L.)

At the species level Soó has made all the necessary new combinations in *Dactylorhiza* for the various interspecific hybrids occurring in Britain. We do not propose to deal with these here as we are not certain that the correct epithet has been used in each case.

BOOK REVIEWS

CHROMOSOMES AND PLANTS

Chromosome Botany and the Origins of Cultivated Plants. By C. D. Darlington. Revised Second edition. Allen & Unwin. 1963. Price 36s. 0d.

This revised edition of *Chromosome Botany* differs from the first (apart from the startling increase in price) mainly in the addition of 20 new pages to the section on cultivated plants, though the remainder of the text has also been revised and a number of useful tables and figures based on the work of the past few years has been added. The new material on cultivated plants should be of interest to all botanists; but this part of the book, though very stimulating and well documented, is tantalizing in the incompleteness of its information, and still too compressed to be entirely intelligible to a reader who is not already familiar with the literature. Is it too much, for example, to ask that we should somewhere be told not merely the chromosome numbers and supposed countries of origin of emmer, *einkorn* and *durum* wheat, but also given some information on their appearance and economic status today? Nor is the author's style of exposition, which suggests that few problems remain, well suited to a field in which over every species there broods either a controversy or a mystery. Darlington purports to summarize Hutchinson's views on the evolution of the cottons, but he does not even mention what is for Hutchinson the most important problem outstanding—how to explain the apparent identity of one genome of the New World tetraploids with that of the Old World diploids. There is a real need for a comprehensive book on the origin and evolution of cultivated plants, and in many ways Darlington would be the ideal author, as there are few other men with a sound knowledge of genetics and cytology who share his interests in pre-history and archaeology and his courage in attempting to master such a complex field. But the ideal author needs also the power to sift evidence dispassionately and to present both sides of an argument fairly, and at this point some doubts must arise.

For the early part of the book remains, unfortunately, what it was in the first edition—an extraordinary mixture of judicious summary of well-chosen fact, cogent and often subtle argument, stimulating, if rash speculation, staggering *non sequitur*, and ill-mannered nonsense. The worst passages, in which the author presents a loaded caricature of orthodox taxonomy before it has been sanctified by chromosome studies, is reminiscent of nothing so much as Marxist journalism; a stereotype of the fascist hyenas of Kew is sketched and duly demolished. And even in the constructive passages (some of which are excellent) the tone is a curious one. Eventually one recognizes it: it is that of the hot-gospeller. For Darlington the study of plant chromosomes is not merely an interesting intellectual pursuit, not merely a means towards better vegetables and more luscious fruits; it is a way of life and a path to salvation. 'Have you studied the breeding system?' he asks, with a cold and accusing eye, much as a century ago he would have asked 'Are you saved?' It is no use for us to protest that we have studied the plant in the field and the herbarium, that we know all about its anatomy and its ecological tolerance, its biochemical constituents and the structure of its pollen grains. All this righteousness is as filthy rags; we cannot be justified by works. We are either for him or against him, and no compromise is possible; so, at least, he tells us on p. 37. 'Can we', he asks, 'add the chromosomes as an appendix to the otherwise sound work of museum classification? The answer is that we cannot. We must make it clear that the two systems are unavoidably in conflict. There can be no compromise between them. Either we follow a scholastic system . . . or we can follow an experimental system.'

C. D. Broad once remarked of behaviourism that it was such an exceedingly silly theory that only a very clever man could have thought of it. One is tempted to pay the same tribute to Darlington. The ostensible message of the book is that interesting information about plants can be obtained only by a study of their chromosomes, and that this study provides by itself a satisfactory basis for their classification, *all* traditional taxonomy being thrown aside as superficial and useless. What makes an acute intellect subscribe to a theory which is disproved by almost every other page of his book? When he writes, for example (p. 85) that '*Penthorum sedoides* has 16 chromosomes in . . . China. But the same species has 18 chromosomes when it reaches the eastern United States', what conceivable meaning can this statement have except in terms of the despised, classical morphological taxonomy? Darlington, of course, abuses the laws of nomenclature and their exponents, but if he were true to his principles he need not worry about them. For he would refer to plants not by Latin names but by cytological formulae. It would, of course, be a slight disadvantage that these formulae could be applied only to plants in the experimental garden—those that had been subjected to cytological analysis, or bred from such plants in one way or another. The fact that a wild cherry in the woods shared some morphological features with a labelled one in his garden would be irrelevant, for morphological comparisons are scholastic. In fact, of course, Latin names occur on almost every page of the book when they suit the author's purpose, and only on the occasions when they do not, as with *Brassica* and *Taraxacum*, does he sneer at them.

What has produced this extraordinary and deplorable situation? Darlington may have been bitten by a taxonomist in his youth, but the trouble lies deeper; this book is only an extreme example of a lack of

understanding of what should be the relation between taxonomy and cytogenetics. Löve & Löve, for example, are far more temperate than Darlington both in their claims and their controversial methods; but the dispute which continues over their attempt to impose a purely biological meaning on the species concept raises the same fundamental issues. Taxonomy and cytogenetics are too often quarrelling when they should be co-operating; and when they attempt to co-operate the results are often disappointing. I believe that the first is due to methodological misconceptions, and the second to factual ignorance.

The charge against the orthodox taxonomist who despises cytogenetics is so obvious that it needs no elaboration; such a man will be defended only by his like. But the cytogeneticist who goes out scalping taxonomists has beside him a crowd of physiologists, biochemists and scientific journalists yapping after the quarry. This is because of the fashionable misconception that in a scientific context the cause is more important than the effect. Some sciences seek out causes; they are therefore more fundamental; they are therefore more important. Those which chronicle events are trivial, old-fashioned and superficial. So the story goes. Now the cause is, of course, by definition more fundamental than the effect, but it is not for that reason more important. It is only because the effect exists that we look for the cause. Without the cause the effect is inexplicable; but without the effect the cause may be meaningless. Samuel Butler ingeniously argued that, from the point of view of an egg, a hen is merely a mechanism for producing another egg. But the hen will not see it like that, and neither will a man, except temporarily at breakfast. Nor can humanity at large be expected to regard plants primarily as boxes for chromosomes. Chromosomes are important, but they are important solely because they determine the characters of plants. If their genes never found expression they would simply be boring little blobs, and nobody would care twopence about the structure of DNA. But plants without chromosomes can be studied, granted with one hand tied behind your back, but not totally without profit as the history of botany up to 1880 shows.

I do not wish it to be thought that I am here censuring the enthusiastic cytogeneticist who lives, dreams, eats and drinks chromosomes and has thought for nothing else. Many people become obsessed by their specialities, and no great harm is done. But he should not try to impose his obsession on others. Morphology and taxonomy divorced from cytogenetics is incomplete and misleading. But cytogenetics divorced from morphology and taxonomy is tedious and meaningless.

The power-complex of the practitioners of the 'fundamental' sciences which make them so often announce an impending take-over of the derived and complex sciences (take-overs which always, for some mysterious reason, have to be postponed when the moment comes), and the consequent retreat of the practitioners of the older disciplines into an ignorant and obscurantist conservatism—this is one cause of the poor relations between taxonomy and cytogenetics. But another, I think, is the well-meaning efforts of those who would keep the two snarling dogs apart. I refer to the idea, tirelessly propagated by Gilmour for many years and now taken up by others in this country, that the categories of taxonomy and of bio-systematics belong to different universes of discourse, and that they should be used quite separately, according to one's mood and purpose, rather than fitted together. From the purely formal point of view there is much sense in this, but if adopted uncritically as a general philosophy of taxonomy it offers too ready a temptation to the taxonomist to turn his back on cytogenetics and vice versa. For all the battering it has received I am convinced that the synthesis elaborated in the second quarter of this century and best recognized under the title of 'The New Systematics' was an achievement of great and permanent value; and that the systematist, whether or not he wants at times to talk of gametopodemes, can now, if he takes the trouble, give to his categories of species, subspecies and even genus a richer, more precise and more public meaning than he could before he knew of ecads and ecotypes, autotetraploidy and introgression. Anything which tempts the taxonomist to regard *Taxon* as intrinsically more relevant to his studies than is *Evolution* or *Hereditas*, or which tempts the cytogeneticist to regard the museum taxonomist as damned beyond redemption and to include the *Index Kewensis* in his *Index Librorum Prohibitorum* is surely to be deplored. Darlington is right, in most of his book, in at least wishing to weld together our morphological and our cytological knowledge of plants, even if he substitutes for the federalism that is needed a chauvinistic imperialism.

But even if all these misunderstandings were cleared away, and if the relationship between taxonomy and cytogenetics were everywhere what it is here and there—a co-operation based on mutual respect—there are still some disturbing features about the situation. It is, of course, a large task to count, characterize and interpret the chromosome complement of every plant in which the results are likely to be of taxonomic value, and one should not complain that the task is only begun. What is disappointing is that the accumulation of data does not appear to be proceeding in the way that is likely to be most fruitful. Apart from detailed studies on cultivated plants, which have an interest all their own but are only marginal to the main field of taxonomy, most lists of chromosome numbers tend to fall under one of three heads. One may find *Chromosome numbers of some Ruritanian plants*, published, as often as not, by the local Academy of Sciences; or else *A study of the Stirps litigiosa complex in Ruritania*, which is usually the expansion of a doctoral thesis

and is published wherever the supervisor can most easily place it; or, finally, *Chromosome numbers in the Coccolaceae, with notes on the evolution and affinities of the family*, published in a journal of genetics or general botany, often in America. Each type has its merits, and each its drawbacks; they will be referred to as A, B and C respectively.

The interest aroused among botanists generally (and consequently the prestige value to the author) is certainly greatest for C and least for A. C, we say, has a plan; it is of worldwide sweep; it makes a synthesis. A is an accumulation of facts of mainly local interest. This is fair enough in one sense, but it omits an important consideration. The entire value of C is probably on the surface; nobody will go back to it to quarry in it for facts to correlate with others as yet unknown. This is because, in nine cases out of ten, the origin of its plants is unknown and their identification uncertain. Botanic garden material has been used, and scarcely ever have voucher specimens been kept. When, therefore, it is alleged that the diploid number for *Pseudococcoloba emetica* is 100, all that is really meant is that a plant in a pot in a (usually named) botanic garden had 100 chromosomes in one of its root-tips, and that in the same pot there was a label on which had been written, on an authority that is unspecified, the name *Pseudococcoloba emetica*. The identification may have been right; but if it was wrong there is no means of ascertaining, or even guessing, what the plant really was. In A and B, on the other hand, we are nearly always told the *provenance* of the plants; local knowledge in A and specialist knowledge in B makes misidentification very unlikely; and the author of B is likely to have deposited voucher specimens in a herbarium. The results are, therefore, of permanent comparative value.

Is it possible to combine the wide range of A, the meticulous detail of B and the adequate documentation of both with the broader speculative and synthetic sweep of C? Probably not in a paper by a single author. But surely this should be our aim in planning the progress of the science as a whole. And the sad truth is that the organization of research in most countries, and in Britain in particular, makes this almost impossible to achieve. No university botanist with his name to make is likely to submit to the tedium of counting innumerable accurately identified and localized specimens simply as a contribution to a synthesis in the future; and it is difficult to find the necessary taxonomic and cytological skills united in a single person. Nor is it reasonable to ask the author of B to substitute for the 'neat' problem that will get him his doctorate the more urgent task of investigating the cytology of intermediates in a group where somebody has already produced a 'neat' solution. To elevate subspecies into species because two or three counts reveal different chromosome numbers in plants 'typical' of the different taxa, while we remain ignorant of the cytology of those intermediates whose existence made the taxonomist originally decide on subspecific status—this is, even on the assumptions of Löve & Löve, a questionable procedure; only when we have far more complete information on the correlation (or lack of it) between morphology and chromosome number can the argument about biological species fairly begin. The number of groups for which we have this information is woefully small.

And what of C? Can this type of paper be made more useful? The growing tendency of botanic gardens to specify the source of their seeds and of authors to preserve voucher specimens are both hopeful signs, but it will be a long time before they have much effect on a typical study of a tropical family. And it is natural for the cytologist to resent having to turn round and dabble in the unfamiliar world of drying-paper. Only a team can achieve the discipline, the planning and the variety of expertise that is needed; and the team would need to be composed, in part at least, of civil servants who do not fret at routine, and whose promotion is not dependent mainly on output of published work. Such a team might also help to close the gap between the cytogenetics of wild and of cultivated plants. Editorial work on *Flora Europaea* has revealed how often an imposing superstructure of speculation on the origin and evolution of cultivated plants is built on a foundation of ignorance of the cytology of their wild ancestors; in *Prunus*, for example, one learns with astonishment that, despite the numerous papers on the cytology of cultivated cherries, not a single count has been made on a wild tree of *P. avium*. And the *Flora Europaea* rule that only counts made on wild material of known European origin are included means that for some families there must be almost complete silence: in the whole of the Malvaceae, for example, only one count is available, published in an obscure but very useful paper of type A in Hungary.

The organization of botanical research in the British Isles gives little hope of assembling a team of this kind. Some of the 'Botanical Institutes' of the Continent might offer more hope, but even in countries like the Soviet Union where the organization would permit such a scheme there is little evidence of any serious or well-thought-out attack on a broad front on the fundamental questions of cytotaxonomy. Meanwhile, if we can only potter, let us at least see to it that we potter in such a way as to give our results the greatest permanent value. Even a statement as to who identified a plant, or what flora was used in assigning it a name will clear away many ambiguities. For Darlington's book, in spite of its limitations, shows more vividly than any other I have seen how great are the taxonomic rewards to be gained from cytological study if it can be pursued free from impatience and free from obsessions.

D. A. WEBB

The Flowering Process. Frank B. Salisbury. Pp. xii + 234 (with 17 photographs and 60 figures in the text). International Series of Monographs on Pure and Applied Biology, Plant Physiology Division, Vol. 4. Pergamon Press, Oxford, 1963. Price 50s. 0d.

The flowering of particular plants at particular times of the year is perhaps one of the first biological facts to be brought to the notice of schoolchildren, although the explanation tends to be treated in a religious rather than a scientific manner. Only when a plant flowers at more than one time of year does the situation arouse comment; proverbial comment in the case of gorse. Both temperature and daylength vary with the time of year. Although daylength provides an accurate basis for a biological calendar, it was not until 1920 that the phenomenon of 'photoperiodism' was discovered.

In *The Flowering Process* Professor Salisbury gives an account of how the change from a vegetative to a reproductive phase is controlled by environmental factors and discusses the present state of knowledge regarding the underlying physiological mechanisms. The excitement of being involved in this rapidly expanding field of research is successfully communicated, many of the experiments with cocklebur (*Xanthium pennsylvanicum*) described in this book having been carried out by the author and his students at Colorado State University. Although the book is very much concerned with experimental studies of flowering and is directed at University students, the introductory chapters should prove of much wider interest. Chapter 3, for instance, deals with the ecological significance of the environmental control of flowering, a topic which one suspects has received too little consideration from those interested in field studies. *Oxyria digyna* has been shown to include a number of genotypes each accurately adapted with respect to the daylength requirement for flowering to the latitude in which it is found.

At the end of the book Professor Salisbury has provided a list of plant species classified into 48 groups according to the response to temperature and daylength. This list will prove useful to experimental botanists, but perhaps less useful to British ecologists, since many of the plants listed are inevitably cultivated species. The various 'response types' would appear to have little taxonomic significance, since varieties of the same species may show marked differences in their flowering response to daylength or temperature. Despite the differing requirements for flowering, present experimental evidence suggests that the basic mechanism is the same in all plants. The photoreceptor involved in photoperiodism, 'phytochrome', and the elusive flowering hormone, 'florigen', would appear to be of universal occurrence.

B. FRANKLAND

A New Illustrated British Flora. Roger W. Butcher. Vol. 1, Lycopodiaceae to Salicaceae, Pp. vi + 1016. Vol. 2, Ericaceae to Gramineae. Pp. vi + 1080. Leonard Hill (Books) Limited, London, 1961. Price £4 4s. 0d. each volume.

The publication of a uniform series of excellent illustrations covering some 1825 species of British flowering plants and ferns is a most welcome addition to botanical literature. These line drawings are accompanied by short but adequate descriptions, identification keys, and an introductory section including definitions of the terms used. Dr. Butcher's work is intended as the successor to a series which has provided the standard introduction to field botany in this country for several generations.

Bentham's *Handbook of the British Flora* of 1858 was rearranged as a delightful illustrated edition in two volumes in 1865, but this proved too expensive for the general public, and further editions, right up to the last of 1925, came out in one cheap volume without illustrations. To meet a widespread need the wood engravings by W. H. Fitch and W. G. Smith from the illustrated edition were issued separately in 1880 under the title *Illustrations of the British Flora*, and these have been reissued, with some revision and additions, at frequent intervals to 1954. 'Bentham' and the companion illustrations have been a boon to a vast number of people. Pictures and text together assisted them to identify their plants, while a great many adopted the practice of colouring in the line drawings as each species was found, and thus impressed the characters on their memory and preserved a record of what they had seen.

The over-cautious revisions of these two works failed to keep pace with the rapidly increasing knowledge of our flora and led to the production by Dr. Butcher of *Further Illustrations of British Plants* in 1930. The 485 line plates by the late Miss Florence E. Strudwick with which this book was illustrated were outstanding for the careful selection of material, the accuracy and delicacy of the drawings, and the high standard of reproduction. With the two earlier volumes, the new book formed a series, complete at the time, which was portable and convenient. The aim of *A New Illustrated British Flora* is to combine the scope of all three volumes into one work. Most of Miss Strudwick's fine drawings have been used as they are. The species depicted by Fitch & Smith have been redrawn from fresh material for larger plates with additional dissections, and further species have been added. Bentham's *Handbook* has been replaced by a shorter text, and brief descriptions arranged beneath, or opposite, the species to which they refer.

The first 35 pages are devoted to an 'Introduction to Descriptive Botany' with an index to the terms used. This is followed by 82 pages of an artificial key to the species, of which a further 89 pages appear

in the second volume. An immense amount of labour must have gone into the production of this key, and clearly considerable care has been taken over the selection of characters, but its very size seems to defeat its purpose. Experience shows that beginners are daunted by long keys, and easily discouraged when they find that a single false step amongst so many will give them a totally wrong answer. They learn more easily when taught to recognize families and genera, and to use the shorter keys to genera such as those in the old Bentham. Dr. Butcher has tried to give them the best of both worlds by including references to the key in the indices to the volumes, but they will not find it easy to pick out from the clavis the stages they need. There is no synopsis of families.

Descriptions of genera appear with those of species with the illustrations concerned. The scientific names are mainly based on Dandy's *List of British Vascular Plants*, and English names are included. These are usually descriptive, with references to features likely to be helpful to beginners, but the way in which they have been introduced into the text is unnecessarily ugly and irritating. 'This *Round Prickly-headed Poppy* is a slender, little-branched, hairy, erect annual . . .', 'This *Prickly Long-headed Poppy* is a rather slender, hairy, almost simple or bushy annual . . .', suddenly changing to 'The *Opium Poppy*', 'The *Welsh Poppy*,' and reverting a few pages later to 'This *Cornish Fumitory*', are representative examples of the style. The descriptions are based on well-chosen characters given in uniform sequence so that comparison between species is facilitated, but they would have been easier to use if important characters had been picked out in different type. Thus, for example, the beginner naming a poppy will need to go right through the descriptions to discover that the capsule should be looked at first. Alternatively he could refer to the key via the index, but comparing the steps in the key on page 50 for example with the illustrations on pages 246 and 247 is unnecessarily cumbrous.

The final choice of species for inclusion in a book of this kind is very much a matter of personal opinion. The author decided to exclude those which grow only in the Channel Isles and this is logical, although many users of the book will regret it. His selection of aliens is reasonable on the criteria he has adopted. For critical species his selection is less defensible. For the larger groups he has made a praiseworthy attempt to compromise by illustrating a selection but the result is unlikely to be very helpful. Of 25 species of *Euphrasia* there are illustrations and descriptions of six, and there is no warning, for example, under *E. gracilis* that there is an allied species *E. scottica*, or under *E. brevipila* that there is *E. borealis*. In the north the one not illustrated is sometimes more plentiful. In *Hieracium* at least five of the drawings are not representative, and one (no. 1356) belongs to a different section. In other genera, such as *Thalictrum*, *Ranunculus*, *Erodium*, *Viola*, and *Saxifraga*, 'species' are illustrated which are not accepted in leading recent works. A botanist of the experience of Dr. Butcher is perfectly entitled to his own opinion on the validity of such taxa, but, in view of all the evidence which has been accumulated, it is very difficult indeed to justify such conservative treatment. To the advanced worker these additional accounts of no longer accepted 'splits' do not detract from the value of the work, since the source of the material is given in all cases, and the illustrations can be cited under other names. The beginner, however, will find them a handicap. The time he will spend trying to separate *Thalictrum montanum* from *T. collinum*, *Erodium lebelii* from *E. neglectum*, etc., and trying to match them up with accounts in 'CTW' and other books, will give him little encouragement. If indeed there is a case for trying to maintain some of these old names it is not appropriate in a book intended for a wide public. Other examples of the author's reluctance to adopt current usage are in the rejection of use of the grade of subspecies (for which he gives his reasons on page 27), and in referring to families as 'Natural Orders', which they are not. Minor errors which should have been corrected in proof are far too numerous.

The artists are to be most warmly congratulated on their work. With few exceptions he plates are excellent representations of the plants depicted, executed with accuracy and at the same time conveying the general impression of the appearance which is so important for easy recognition. The co-ordination of the work of eleven artists to avoid major differences in style must have been a most difficult task and Dr. Butcher has succeeded admirably. Abundant dissections and enlargements are included and the work will be especially valuable in providing a full series of the fruits and seeds of British plants. It is unfortunate that such a fine series of drawings could not have been produced in a more convenient form, but it is appreciated that the publishers had to face an unusually difficult production problem. These two clumsy volumes are each three inches thick, and together weigh 6 lb. 10 oz. Whereas their predecessors Fitch and *Further Illustrations* were easily included in the luggage of travelling botanists, the new work is too cumbrous even for the dashboard of a car. The volumes are so thick that they fail to open flat, and if thick paper was chosen for the benefit of people who colour in the outlines, they will find it difficult to work on them. Finally the price, eight guineas, will place it out of reach of many marginal botanists who would otherwise like to buy it. In size and cost the *New Illustrated British Flora* has repeated the objections to the illustrated edition of Bentham of just a century ago. In spite of this it should be in the library of every enthusiastic botanist.

J. E. LOUSLEY

Huntia. A year book of botanical and horticultural bibliography. Editor G. H. M. Lawrence. Vol. I, 15 April 1964. Pp. vi+222, 9 $\frac{1}{8}$ × 7 $\frac{1}{8}$ in.; 27 figs. in stiff covers. The Hunt Botanical Library. Carnegie Institute of Technology. Pittsburgh, Pennsylvania. Subscription \$7.50 (U.S.) a volume.

Huntia is a year book devoted to studies of the literature on systematic botany and horticulture, botanical voyages and explorations, early agriculture, medical botany and related subjects of botanical biography, iconography, and bibliography. Primarily it is a record of investigations at the Hunt Botanic Library, but papers from workers in other institutions will appear.

The contents of this first volume are divided into ten articles on various subjects, departmental studies, autograph letters and manuscripts, botanical portraiture, bibliographical notes and Hunt Botanical Library activities 1963. These are followed by notes on the contributors and a very full index.

The first article by the editor gives a very clear account of the year book's aims and a description of the Hunt Library and its publications. Then follows an obituary of Rachel McMasters Miller Hunt, with a portrait. Her life and the ideals that prompted her in forming the library are vividly portrayed. This is followed by an announcement of *Bibliographia Huntiana*, a project to produce a guide to the world's botanical literature, 1730–1840, under the general supervision of an advisory editorial board. It is proposed to produce some sixteen volumes quarto in the next ten years. A sample is given of L'Héritier de Brutelle and his *Sertum Anglicum*. A facsimile of this book was produced in the Hunt facsimile series in 1963.

Another article, by J. L. Heller, is on the early history of binomial nomenclature, some 37 pages long, with reproductions of pages from various authors. In footnotes may be found works consulted by the author. The presentation of facts brought together in one article will be found to be most useful to workers studying this subject.

Two other items are on David Fairchild, his life and a bibliography of his works. Two papers by I. MacPhail, an introduction to bibliography for botanists, and on Titford's *Hortus*, are most useful as showing how full bibliographical details may assist in discovering the date of publication of works.

The production is remarkable for its very high standard of typography and reproduction of the illustrations.

N. DOUGLAS SIMPSON

Wild Flowers of Southern Africa—Natal. Dr Winifred Wright (assisted by Penny Miller and a foreword by Professor R. H. Compton). Pp. xvi+168, with eight colour plates and over 200 line drawings. Nelson & Sons Ltd., Edinburgh, 1963 (28 January 1965). Price 25s.

The advertising 'blurb' on the dust jacket begins 'This is a real Rambler's pocket book of the wild flowers . . .'. It must be admitted that such a book is needed for Natal and other areas of the Republic of South Africa. This one, however, is disappointing in both its text and illustrations. The colour plates are fairly good, but the line drawings which form its main part lack artistic merit and botanical accuracy. The article on 'Fertilization' (pp. 9–11) is chiefly remarkable for its inaccuracies, but this may be the result of a somewhat slipshod English style. On p. 13 we learn that 'Hybridization of the *Haemanthus* and *Watsonia* genera is very rewarding, *Watsonia densiflora* producing exceptionally lovely colours'.

A real Rambler's guide to local South African wild flowers is still required.

A. A. BULLOCK

A BIBLIOGRAPHICAL INDEX OF THE BRITISH FLORA

COMPILED BY

N. DOUGLAS SIMPSON, M.A., F.L.S.

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LIST OF BRITISH VASCULAR PLANTS

prepared by J. E. DANDY for the British Museum (Natural History) and the Botanical Society of the British Isles.

Many botanists have assisted in the preparation of this work, which incorporates the *London Catalogue of British Plants* and was undertaken by Mr. Dandy on behalf of a sub-committee of the Society appointed for this purpose.

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STUDIES ON BRITISH PANSIES

III. A FACTORIAL ANALYSIS OF MORPHOLOGICAL VARIATION

By A. PETTET

*Department of Botany, University of Southampton**

ABSTRACT

A factorial analysis was made of the variation in a representative selection of British pansies. Two parallel analyses involving the R-technique were made on 'qualitative' and 'quantitative' data and both factor and component solutions obtained for each.

The results from the factor analyses of the two types of data were more instructive than the corresponding component analyses.

Three factors were extracted in the factor analyses of the qualitative data and the attributes separated into two groups with respect to the first two factors, i.e. attributes associated mostly with reproduction, and attributes involving shapes of leaf and stipule end-lobe. The factor specifications of plants for these factors showed a well-defined division between outbreeding and inbreeding pansies with the cream-flowered *Tricolores* lying close to the inbreeding ones.

Four factors were extracted in the factor analysis of the quantitative data which separated the attributes into 3 groups, i.e. petaline, sepaline and foliar—stipular attributes. The factor specifications of plants for these factors showed no distinct discontinuities although there was a marked stratification along the axis of the second factor for which the petaline attributes had high loadings.

The results of the two types of data demonstrate the importance of reproductive features in separating the recognized taxa and provide evidence for probable evolutionary trends within the pansies.

1. INTRODUCTION

Following Clausen's cytogenetical study of the *Melanium* subgenus of *Viola* (Clausen 1926, 1927, 1931) and Fothergill's cytological examination of British representatives (Fothergill 1944), it has been customary to consider British pansies as belonging to a few rather variable, taxa (e.g. Dandy 1958, Warburg 1952, 1962). Like other 'critical groups', however, the morphological variation is such that clear-cut differences are not always present, and taxonomic discrimination often involves one or a few characters. At times these characters break down and misclassification can occur, e.g. a number of cream-flowered pansies, referable to *V. tricolor* on the basis of the key character of the upper petal/upper sepal ratio, have been shown to be more closely allied to *V. arvensis* (Pettet 1964b).

Since simultaneous examination of a larger number of characters, including those which appear too variable to be valuable, might reduce this chance of misclassification, a factorial analysis of a representative collection of British pansies has been carried out. Factorial analysis, frequently referred to as 'factor analysis', is a general method for classifying data and examining the number of possible factors contributing to the variation within them and as such it is a more efficient way of analysing variation than a piecemeal comparison of 2 or 3 characters at a time. The method was originally developed in the field of psychological research and detailed treatments of the theory with examples of computation can be found in Cattell (1952), Thurstone (1947), Harman (1960) and Thomson (1951). In recent years the increasing availability of electronic computers has removed the tedium of computation associated with this method and has allowed its general application to ecological and taxonomic problems. A discussion of some of the principles involved in this kind of application will be found in Sokal & Sneath (1963).

* Now at Department of Botany, University of Khartoum.

2. MATERIALS AND MODE OF ANALYSIS

The plants examined for analysis were chosen as being representative of the range of variation found in British pansies. Some belonged to populations grown for an experimental study; others were selected from the herbarium of the British Museum (Nat. Hist.) (BM).

For any particular 'population' a single plant was taken unless the population was particularly variable, in which case two examples were taken. Details of all plants used are given in Table 1.

Much of the herbarium material in the British Museum had been named by Drabble and other authorities so, partly as a matter of convenience and partly to avoid ambiguity, the plants are referred to in the text under the names of Drabble's series, i.e. *Arvenses*, *Tricolores*, *Curtisieae*, *Saxatiles*, *Luteae* and *Nanae* (Drabble 1909). For practical reasons it has been found advisable to divide the *Tricolores* into two groups on the basis of flower colour, i.e. cream-flowered *Tricolores* and blue-flowered *Tricolores*. These series correspond in most cases with the taxa recognized in the *Flora of the British Isles* (Warburg 1962) as shown below:

Series	Taxa recognized by Warburg (1962)
Arvenses	.. <i>V. arvensis</i> Murr.
Cream-flowered Tricolores ..	.. <i>V. arvensis</i> Murr. (and AT-intermediates, Pettet 1964b)
Blue-flowered Tricolores ..	.. <i>V. tricolor</i> L. subsp. <i>tricolor</i>
Curtisieae	.. <i>V. tricolor</i> L. subsp. <i>curtisii</i> (E. Forst.) Syme
Saxatiles	.. <i>V. tricolor</i> L. subsp. <i>tricolor</i>
Luteae	.. <i>V. lutea</i> Huds.
Nanae	.. <i>V. kitaiabeliana</i> Schult. (<i>V. nana</i> auct.)

The correspondence cannot be considered complete for all examples, e.g. '*V. carpatica* Borbás', classified as belonging to the *Saxatiles*, might be a hybrid between *V. tricolor* and *V. arvensis*, or might be an unusual form of *V. tricolor*; the two examples of *V. lepida* Jord. may not be identical with *V. tricolor* subsp. *tricolor* (British examples still require study); lastly, not all the cream-flowered *Tricolores* listed may be identical with the AT-intermediates discussed by Pettet (1964b).

Using these plants two parallel sets of analyses were made involving 'qualitative' attributes (Table 2) and 'quantitative' attributes (Table 3, Fig. 1). Each plant was examined for both and to avoid undue bias, the two types of data were taken from the same organs in each case (Appendices 1 and 2).

The 'qualitative' attributes and the method of scoring were based on these characters used to delimit the various taxa of pansies; these are for the most part the 'traditional' characters and some, of course, are quantitative. Because the herbarium specimens were sometimes incomplete or were too distorted for some attributes to be assessed, the number of characters which could be used was not as great as wished. Similarly, a lack of data or incomplete characterization prevented ecological features from being incorporated into the analysis even though these have important implications in the interpretation of the pattern of variation. A few attributes presented their own peculiar difficulties. Scoring for flower colour had to be done on fully open flowers which showed no obvious signs of undue fading and, for a convenient representation of overall flower colour, assessed on the lateral petals. The degree of development of stylar-flap could only be determined after the style had been soaked in water to regain something of its former shape and had to be assessed under a binocular microscope against a group of standard styles.

The 'quantitative' attributes were measurements taken to express variation in the sizes and shapes of flowers, leaves and stipules which contribute to the majority of taxonomic characters used in delimiting the various taxa. To reduce experimental error all measurements were made on water-softened herbarium material, the fresh material being pressed before use.

TABLE 1. List of plants used.

No.	Name	Locality	V.C.	Habitat	Date of collection	Det.	Series
1	<i>agrestis</i>	Beggary Shot, Hitchin, Herts.	20	—	4.10.30	E.D.	Arrvenses
2	<i>agrestis</i>	Stourport, Worcs.	37	—	9.27	E.D.	"
3	<i>segetalis</i>	Dolgelley, Merioneth, Wales	48	—	18. 8.23	E.D.	"
4	<i>segetalis</i> f. <i>obtusifolia</i>	Hallthwaites, S. Cumberland	70	With <i>segetalis</i> among turnips	10. 9.26	E.D.	"
5	<i>segetalis</i> f. <i>obtusifolia</i>	Dedham, N. Essex	19	Gravel pit	11. 6.39	E.D.	"
6	<i>obtusifolia</i>	Hitchin, Herts.	20	Potato ground	17.10.30	E.D.	"
62	<i>curtisii</i>	Caner River, Co. Clare, Ireland	H9	Sand mfls	18. 5.55	H.W.P.	Curtisaeae
63	<i>curtisii</i>	Aberffraw, Anglesey	52	—	12. 9.02	H.W.P.	"
64	<i>curtisii</i>	Braunton Burrows, N. Devon	4	Sand hills	9. 9.03	H.W.P.	"
65	<i>curtisii</i>	Woolacombe, N. Devon	4	Sand hills	6. 6.01	H.W.P.	"
66	<i>curtisii</i> <i>pesneui</i>	Thetford Heath, nr. Barnham, Suffolk	26	—	4. 5.35	H.W.P.	"
67	<i>curtisii</i> <i>pesneui</i>	S. of Southport, Lancs.	59	Sand dunes	22. 8.34	H.W.P.	"
68	<i>curtisii</i> <i>pesneui</i>	S. of Golspie, Sutherland	107	Sand dunes	29. 7.29	H.W.P.	"
69	<i>curtisii</i> <i>symei</i>	Benbecula, O. Hebrides	110	Sand banks near coast	28. 7.1894	H.J.W.	"
70	<i>curtisii</i> (? <i>symei</i>)	Lahinch, Co. Clare, Ireland	H9	Sand hills	8.59	A.P.	"
71	<i>lutea</i>	Widdiwbank Fell, Teesdale	65/66	Pasture	6.57	A.P.	Luteae
72	<i>lutea</i>	Widdiwbank Fell, Teesdale	65/66	Pasture	6.57	A.P.	"
73	<i>lutea</i>	Wardlow Hay Cop, Derbyshire	57	Pasture	7.57	A.P.	"
74	<i>curtisii</i>	Broughton Burrows, Gower, Glam.	41	Sand dunes	5.58	A.P.	Curtisaeae
75	<i>curtisii</i>	Kenfig Burrows, Glam.	41	Sand dunes	5.58	A.P.	"
76	<i>curtisii</i>	Kenfig Burrows, Glam.	41	Sand dunes	5.58	A.P.	"
77	<i>nana</i>	Appletree Banks, Tresco, Scilly	1	Sand dunes	4.58	A.P.	Nanae
78	<i>nana</i>	St. Brelade's Bay, Jersey	—	Sand dunes	16. 5.57	A.P.	"

TABLE 1. List of plants used.

No.	Name	Locality	V.C.	Habitat	Date of collection	Det.	Series
1	<i>agrestis</i>	Beggarly Shot, Hitchin, Herts.	20	—	4.10.30	E.D.	Arvenses
2	<i>agrestis</i>	Stourport, Worcs.	37	—	9.27	E.D.	"
3	<i>segetalis</i>	Dolgelley, Merioneth, Wales	48	—	18. 8.23	E.D.	"
4	<i>segetalis</i> f. <i>obtusifolia</i>	Hallthwaites, S. Cumberland	70	With <i>segetalis</i> among turnips	10. 9.26	E.D.	"
5	<i>segetalis</i> f. <i>obtusifolia</i>	Dedham, N. Essex	19	Gravel pit	11. 6.39	E.D.	"
6	<i>obtusifolia</i>	Hitchin, Herts.	20	Potato ground	17.10.30	E.D.	"
7	<i>ruralis</i>	Odham, N. Hants	12	—	5. 5.00	E.D.	"
8	<i>ruralis</i>	Linton, Cambs.	29	Hedgebank	29. 5.39	E.D.	"
9	<i>ruralis</i>	Nr. Ashbrook, St. Ippolyts, Herts.	20	Market garden	21. 5.30	E.D.	"
10	<i>deseglisei</i>	Sowerby, nr. Thirsk, Yorks.	62	Stubble field	6. 5.36	E.D.	"
11	<i>deseglisei</i>	Sandyland, N.E. Rowney, Warren, Beds.	30	—	26. 6.28	E.D.	"
12	<i>anglica</i>	'Lurgashall', W. Sussex	13	—	8.32	E.D.	"
13	<i>arvensis</i>	Nr. Chipstable, Somerset	5	Oat field	29. 8.18	E.D.	"
14	<i>derelicta</i>	Wilsbury Hill, Herts.	20	—	5.30 9.30	E.D.	"
15	' <i>arvensis</i> '	Knowle Hill, nr. Eastleigh, Hants	11	Wheat field on clay	3. 6.58	A.P.	"
16	' <i>arvensis</i> '	Nr. Kings Somborne, Hants	11	Wheat field on chalky soil	5. 6.58	A.P.	"
17	' <i>arvensis</i> '	Nr. Winchester, Hants	11	Wheat field on chalky soil	5. 6.58	A.P.	"
18	' <i>arvensis</i> '	Nr. Winchester, Hants	11	Wheat field on clay with flints	14. 6.58	A.P.	"
19	' <i>arvensis</i> '	W. of Corhampton, Hants	11	Wheat field	18. 6.58	A.P.	"
20	' <i>arvensis</i> '	Wheatfen, Norfolk	27	Barley field	7.58	A.P.	"
21	' <i>arvensis</i> '	Kingsdown, E. Kent	15	Barley field	7.56	A.P.	"
22	' <i>arvensis</i> '	Nr. Aberystwyth, Cards.	46	Disturbed bank	7.56	A.P.	"
23	' <i>arvensis</i> '	Porton, Salisbury, Wilts.	8	Derelict corn field	9.11.56	A.P.	"
24	' <i>arvensis</i> '	Twyford, nr. Winchester, Hants	11	Barley stubble	25. 8.57	A.P.	"
25	' <i>arvensis</i> '	Nr. Southampton, Hants	11	Building site	26. 8.56	A.P.	"
26	' <i>arvensis</i> '	Sholden Downs, nr. Deal, Kent	15	Lucerne field	7.56	A.P.	"
27	' <i>arvensis</i> '	Southampton Common, Hants	11	Disturbed ground	6.56	A.P.	"
28	' <i>arvensis</i> '	University Grounds, Southampton, Hants	11	Disturbed ground	6.56	A.P.	"
29	' <i>arvensis</i> '	Wareham, Dorset	9	Wheat field	30. 6.57	A.P.	"
30	' <i>arvensis</i> '	Aberystwyth, Cards.	46	Kale field	7.56	A.P.	"
31	AT-intermediate	Durham, Durham	66	Allotments	7.56	A.P.	Cream-flowered Tricolores
32	AT-intermediate	Kilmuir, Black Isle, Cromarty	106	Root field	9.11.56	A.P.	"
33	AT-intermediate	Ruislip Common, Middx.	21	Corn field	21. 9.56	A.P.	"
34	Exp. hybrid (T10 × A10)	—	—	—	1957	A.P.	—
35	<i>contempta</i> var. <i>patula</i>	Beggarly, Shot, Hitchin, Herts.	20	—	20. 9.30	E.D.	Cream-flowered Tricolores
36	<i>lloydii</i>	Salop, Shropshire	40	—	1886	E.D.	Blue-flowered Tricolores
37	<i>lloydii</i>	Fleet, Hants	12	—	30.10.31	E.D.	Cream-flowered Tricolores
38	<i>lloydii</i> var. <i>insignis</i>	Melvic, N. Sutherland	108	—	15. 7.15	E.D.	Blue-flowered Tricolores
39	<i>lejeunei</i>	Fleet, Hants	12	—	10.32	E.D.	Cream-flowered Tricolores
40	<i>vectensis</i>	White Hill, Hitchin, Herts.	20	Allotments	15. 5.31	E.D.	"
41	<i>variata</i>	Westerham, Kent	16	—	9. 4.32	E.D.	Blue-flowered Tricolores
42	<i>variata</i>	Tresta, Shetland	112	Hay field	22. 6.27	E.D.	"
43	<i>variata</i>	Stribers' Moss, N. Lancs.	69	—	23. 6.23	E.D.	"
44	<i>variata</i> var. <i>sulphurea</i>	White Hill, Hitchin, Herts.	20	Allotments	15. 5.31	E.D.	Cream-flowered Tricolores
45	<i>variata</i> var. <i>sulphurea</i>	Nr. Blandford, Dorset	9	—	10. 4.1894	E.D.	"
46	<i>variata</i> var. <i>sulphurea</i>	Locality unknown	—	—	—	E.D.	"
47	<i>variata</i> var. <i>sulphurea</i>	Old Byfleet Rectory, Surrey	17	Sandy field	—	E.D.	"
48	<i>variata</i> var. <i>sulphurea</i>	Old Down, Jockington, W. Gloucs.	34	—	12. 5.25	E.D.	"
49	<i>monticola</i>	Nr. Nine Springs, St. Ippolyts, Herts.	20	—	6.10.31	E.D.	"
50	<i>tricolor</i> ssp. <i>genuina</i> var. <i>faerensis</i>	Mainland, Stromness, Orkney	111	—	14. 8.25	Osten- field	Blue-flowered Tricolores
51	' <i>tricolor</i> '	Nr. Aberystwyth, Cards.	46	Kale field	7.56	A.P.	"
52	' <i>tricolor</i> '	Nr. Aberystwyth, Cards.	46	Kale field	7.56	A.P.	"
53	' <i>tricolor</i> '	Nr. Durham	66	Stubble field	7.56	A.P.	"
54	' <i>tricolor</i> '	Nr. Aberfeldy, Perthshire	88	—	8.56	A.P.	"
55	<i>lepidia</i>	Killeen, Argylshire	101	Sandy fields	7.31	E.D.	Saxatiles
56	<i>lepidia</i>	Killeen, Argylshire	101	Sandy fields	7.31	E.D.	"
57	<i>carpatia</i>	Cockerham Peat Moss, W. Lancs.	60	Freshly reclaimed ground	6.00	Borbás	"
58	<i>lutea</i>	Loch Rannoch, Perthshire	88/89	Field	17. 7.15	H.W.P.	Lutecae
59	<i>lutea</i>	Nr. Corriemulgie, Braemar, Aberdeen	92	—	8. 7.10	H.W.P.	"
60	<i>lutea</i>	Latrigg, nr. Keswick	70	—	2. 7.03	H.W.P.	"
61	<i>lutea</i>	Dochart, nr. Killin, Perthshire	88	Meadow	20. 7.35	H.W.P.	"
62	<i>curtisii</i>	Caher River, Co. Clare, Ireland	H9	Sand hills	18. 5.35	H.W.P.	Curtisiae
63	<i>curtisii</i>	Aberffraw, Anglesey	52	—	12. 9.02	H.W.P.	"
64	<i>curtisii</i>	Braunton Burrows, N. Devon	4	Sand hills	9. 9.03	H.W.P.	"
65	<i>curtisii</i>	Woolacombe, N. Devon	4	Sand hills	6. 6.01	H.W.P.	"
66	<i>curtisii pesneani</i>	Theiford Heath, nr. Barnham, Suffolk	26	—	4. 5.35	H.W.P.	"
67	<i>curtisii pesneani</i>	S. of Southport, Lancs.	59	Sand dunes	22. 8.34	H.W.P.	"
68	<i>curtisii pesneani</i>	S. of Golspe, Sutherland	107	Sand dunes	29. 7.29	H.W.P.	"
69	<i>curtisii symei</i>	Benbecula, O. Hebrides	110	Sand banks near coast	28. 7.1894	H.J.W.	"
70	<i>curtisii (symei)</i>	Lahinch, Co. Clare, Ireland	H9	Sand hills	8.59	A.P.	"
71	<i>lutea</i>	Widdybank Fell, Teesdale	65/66	Pasture	6.57	A.P.	Lutecae
72	<i>lutea</i>	Widdybank Fell, Teesdale	65/66	Pasture	6.57	A.P.	"
73	<i>lutea</i>	Wardlow Hay Cop, Derbyshire	57	Pasture	7.57	A.P.	"
74	<i>curtisii</i>	Broughton Burrows, Gower, Glam.	41	Sand dunes	5.58	A.P.	Curtisiae
75	<i>curtisii</i>	Kenfig Burrows, Glam.	41	Sand dunes	5.58	A.P.	"
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77	<i>nana</i>	Appletree Banks, Tresco, Scilly	1	Sand dunes	4.58	A.P.	Nanae
78	<i>nana</i>	St. Brelade's Bay, Jersey	—	Sand dunes	16. 5.57	A.P.	"

TABLE 2. Qualitative attributes and method of scoring.

No.	Attribute	Method of scoring	
1	Annual/perennial	Annual	1
		Perennial	2
2	Shape of leaf	Ovate (width/length > 0.5)	1
		Ovate-lanceolate (width/length $0.3-0.5$)	2
		Lanceolate (width/length < 0.3)	3
3	Shape of stipule	Pinnate	1
		Pinnate—palmate	2
		Palmate	3
4	Shape of stipule mid-lobe	Leafy, ovate (width/length > 0.5)	1
		Ovate—lanceolate (width/length $0.3-0.5$)	2
		Not leafy, lanceolate (width/length < 0.3)	3
5	Colour of lateral petals	Cream	1
		Pale blue or blotched	2
		Deep blue	3
6	Upper petal/upper sepal	Petals shorter than sepal	1
		Petals as long as sepal	2
		Petals longer than sepal	3
7	Spur/sepaline appendage	Spur shorter than sepaline appendage	1
		Spur as long as sepaline appendage	2
		Spur longer than sepaline appendage	3
8	Honey streak	Absent	1
		Present, unbranched	2
		Present, branched	3
9	Stylar streak	Absent	1
		Intermediate	2
		Distinct	3
10	Stylar flap	Absent	1
		Intermediate	2
		Distinct	3
11	Pollen assemblage	More than 60% of grains 5-colpate	1
		40–60% of grains 5-colpate	2
		Less than 40% of grains 5-colpate	3

The computational stages in the analysis of the two sets of data (R-technique) are shown in the flow-diagram (Fig. 2). As will be seen a component analysis as well as a factor analysis (*sensu* Kendall 1950, Rao 1955) was carried out for each set of data. Most of the computation involved was carried out by the Ferranti 'Pegasus' electronic computer of Southampton University, although, at the start of the study in 1959, the standardization of data and calculation of correlation matrices had to be undertaken with a hand-operated calculating machine as these were not yet programmed for. This was practical for the qualitative data where relatively few attributes were involved but the quantitative data had to wait until the whole analysis had been fully programmed. Rotation of axes for 'simple structure', *sensu* Thurstone (1947), was not attempted.

3. RESULTS

(a) Qualitative data

Inspection of the residual matrices during a centroid analysis of the correlation matrix of the qualitative attributes showed that at least 2, and probably 3, factors were significant. The factor-loadings of the attributes for these three factors are given in Table 4 and their configuration in the three dimensional common factor space shown graphically in Fig. 3. These show that the factor-loadings are orthogonal to the axes and that they fall into two

TABLE 3. Measurements used as quantitative attributes.

Attribute No.	Type	Measurement
1	Foliar attributes	Length of flower stalk (measured when fruit mature)
2		Width of leaf
3		Length of leaf
4		Length of leaf stalk
5		Number of notches on leaf (left side)
6	Stipular attributes	Length of stipule base
7		Width of stipule base
8		Length of stipule mid-lobe
9		Width of stipule mid-lobe
10		Length of stipule mid-lobe stalk
11		Number of teeth on stipule mid-lobe (left)
12		Number of lobes on left side of stipule
13		Number of lobes on right side of stipule
14		Length of upper left lobe of stipule
15		Width of upper left lobe of stipule
16	Petaline attributes	Width of lower petal
17		Length of lower petal (including length of pollen chamber)
18		Length of spur
19		Width of lateral petal
20		Length of lateral petal
21		Length of limb of lateral petal
22		Width of upper petal
23		Length of upper petal
24	Sepaline attributes	Length of lower sepal
25		Width of lower sepal
26		Length of appendage of lower sepal
27		Length of lateral sepal
28		Width of lateral sepal
29		Length of appendage of lateral sepal
30		Length of upper sepal
31		Width of upper sepal
32		Length of appendage of upper sepal

groups. The majority of the attributes have high positive loadings for Factor I, low loadings for Factor II, and variable loadings for Factor III. Two attributes, i.e. the shape of the leaf and the shape of the stipule mid-lobe, form the second group with relatively low negative loadings for Factor I, high positive loadings for Factor II, and negligible loadings for Factor III.

The configuration of the factor specifications of plants in the common factor space is also shown graphically in Figs. 4(a)-(c). The distribution of plants within this space suggests the presence of 2, perhaps 3, groups of plants largely through the effect of Factor I. The upper group consists of the *Luteae*, *Curtisieae*, *Saxatiles* and the blue-flowered *Tricolores*, while the lower group consists of the *Arvenses* and *Nanae* with the cream-flowered *Tricolores* somewhat separated from them and perhaps composing a third group. Factor I, therefore, serves to separate the outbreeding from the inbreeding pansies—not unexpectedly in view of the high loadings that the attributes concerned with reproductive organs received from this factor. Factor II does not resolve the plants into any of the major categories so far recognized. Factor III, on the other hand, tends to separate the blue-flowered *Tricolores* from the *Curtisieae* in the upper group and the cream-flowered

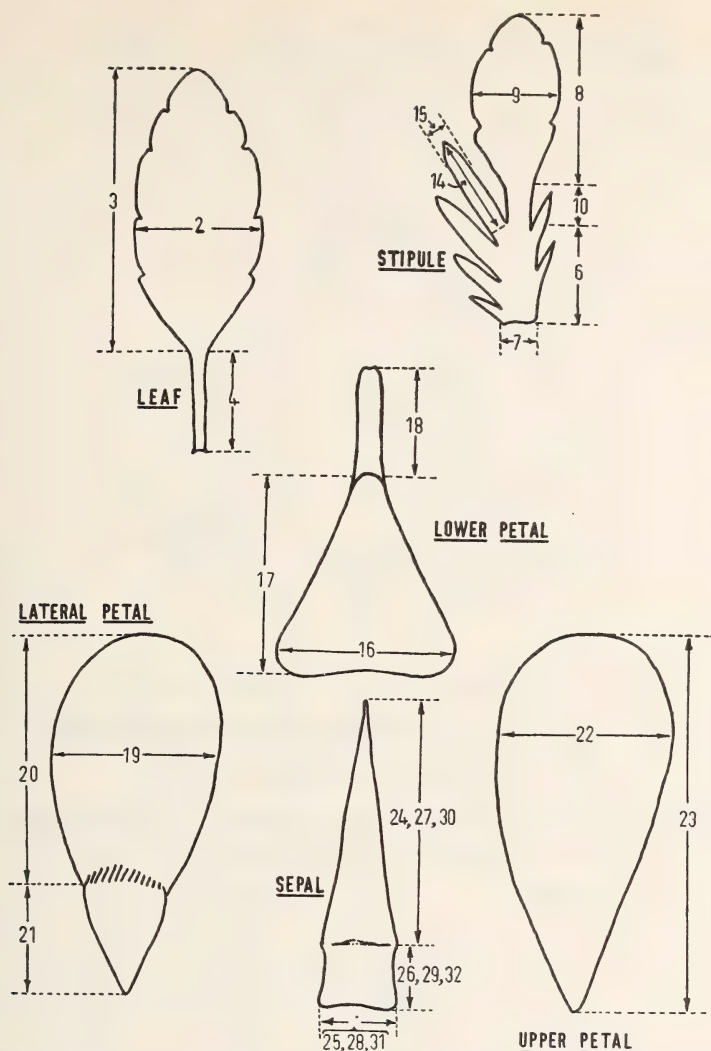


Fig. 1. Measurements used in analysis of quantitative data. The numbers refer to attributes listed in Table 3.

Tricolores from the *Nanae* and, to a lesser extent, the *Arvenses* in the lower group. The tilt of the cream-flowered *Tricolores* and *Arvenses* suggests that within these the Factors I and III are not acting completely independently of each other.

These factors are algebraic abstractions necessary for the solution of various matrix equations. This is not normally a unique solution and in consequence, the factors cannot strictly represent the operation of biological factors (in the broadest sense). None the less their effects may have a parallel to those of biological factors and from an examination of the configurations of factor loadings and factor specifications it is possible to suggest a biological interpretation of the variation.

In the present case Factor I has the overriding effect and most attributes have high loadings for it, in particular, the presence/absence of stylar-flap, the type of pollen assemblage and upper petal/upper sepal ratio. Since it brings about the separation of groups on the basis of reproductive behaviour, Factor I can be compared with the genetic complex responsible for the evolution of the inbreeding pansies from the outbreeding ones. It may also be considered the 'general taxonomic factor', since the attributes affected by it are important taxonomically.

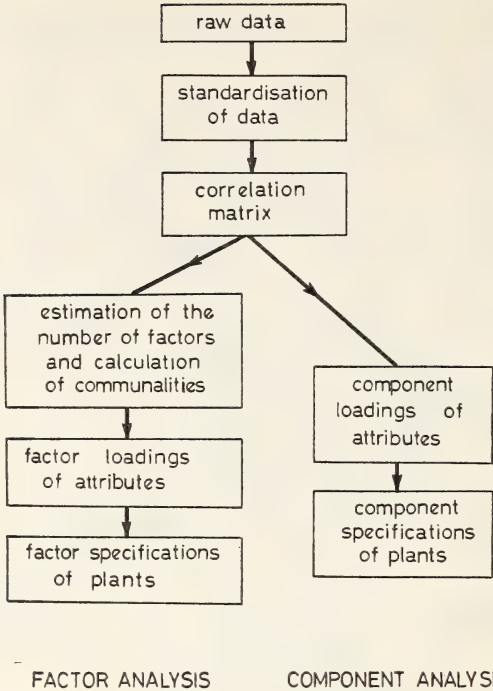


FIG. 2. Flow-diagram of computational stages in factorial analysis.

TABLE 4. Factor-loadings for qualitative attributes for 3 common factors.

<i>Attributes</i>	<i>Factors</i>		
	I	II	III
1	+0.70	+0.12	+0.32
2	-0.28	+0.75	+0.02
3	+0.60	-0.07	+0.49
4	-0.02	+0.74	-0.02
5	+0.63	+0.09	-0.14
6	+0.80	-0.02	-0.22
7	+0.61	-0.03	+0.23
8	+0.57	-0.06	-0.42
9	+0.55	+0.03	-0.08
10	+0.96	+0.10	-0.13
11	+0.94	+0.09	+0.02

The second factor which affects virtually only the shape of the leaf and the stipule mid-lobe is a 'leaf-shape factor' acting $\pm$ independently of Factor I. Previously this was identified as a morphogenetic factor associated with the position on the axis of the node scored for the analysis (Pettet, in Williams & Lambert 1961). In all taxa the shape of the leaf and the stipule mid-lobe varies from the base of the plant to the apex and, to avoid unnecessary complications, the node taken for scoring was always taken near the top of the plant. Those chosen in plants with few nodes per branch would, of course, not be at the strictly comparable stage as those chosen in plants with many nodes per branch. It was originally thought that the analysis was revealing this difference as Factor II, but now this

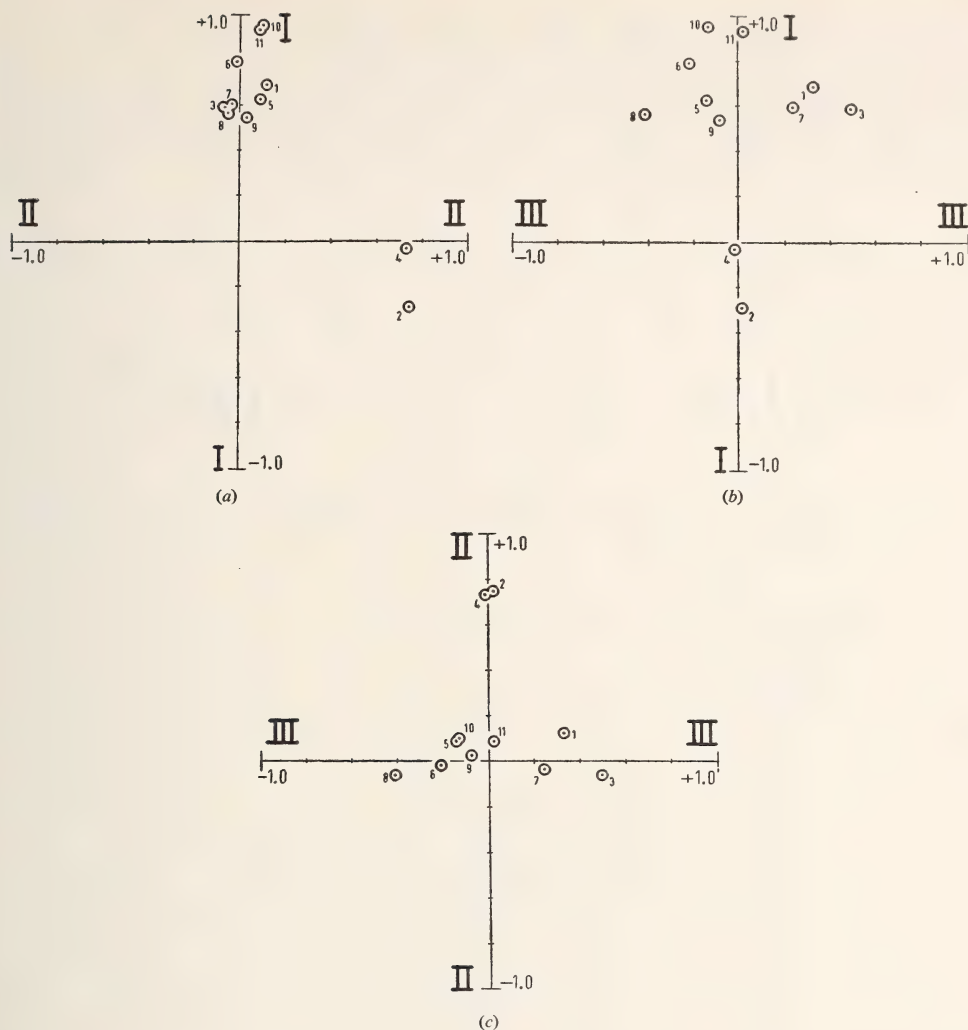


Fig. 3. Factor-loadings of qualitative attributes in common factor space. 1 = annual/perennial; 2 = shape of leaf; 3 = shape of stipule; 4 = shape of stipule mid-lobe; 5 = colour of lateral petals; 6 = upper petal/upper sepal; 7 = spur/sepaline appendage; 8 = honey streak; 9 = stylar streak; 10 = stylar flap; 11 = pollen assemblage.

is considered not to be the case. The difference in leaf and stipule mid-lobe shape is not very great after a few nodes from the base and would be too small to account for the effect of Factor II which, on closer study, appears independent of the number of nodes on the plant axis. The inbreeding forms, which are generally many-noded, have as wide a range with respect to this factor as the outbreeders which include plants with a varying number of nodes, while the factor does not separate the blue-flowered *Tricolores* with many nodes from the *Luteae* and *Curtisieae* with a smaller number of nodes. The existence of this 'leaf-shape factor' and its independence of the first factor have been largely responsible for the recognition of many of the microspecies by Drabble (1909, 1926, 1927), particularly within the inbreeding or partially inbreeding taxa where emphasis has been laid on leaf and stipule mid-lobe shape.

Factor III is of low order and it is rather difficult to suggest its biological parallel. It affects most of the attributes showing high loadings in Factor I while the factor specifications

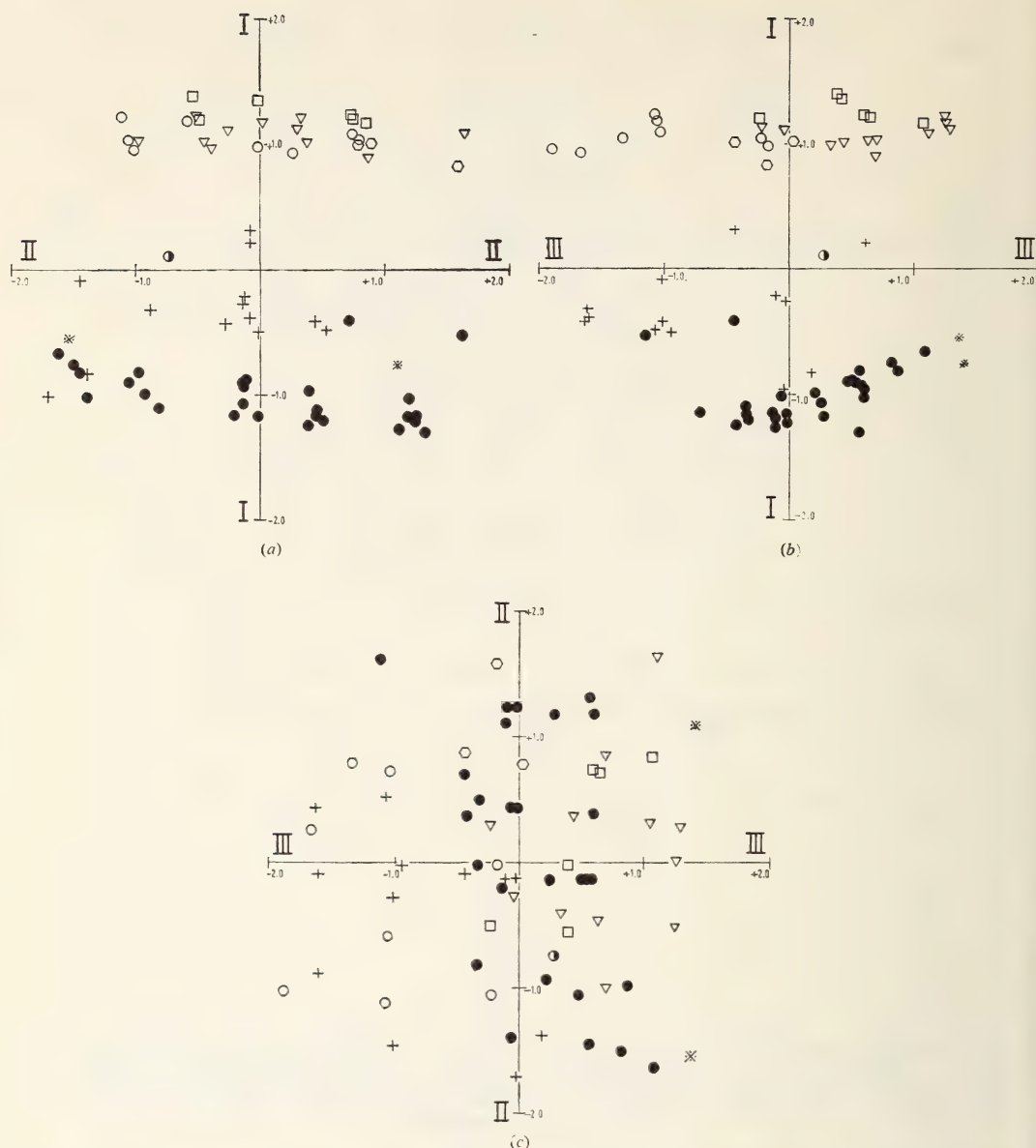


Fig. 4. Factor specifications of plants for common factor space. (a) Factor I/Factor II; (b) Factor I/Factor III; (c) Factor II/Factor III. □ = Luteae; ◊ = Saxatiles; ▽ = Curtisieae; ○ = blue-flowered *Tricolores*; ⊕ = cream-flowered *Tricolores*; ◐ = F₁ hybrid, *V. tricolor* (blue-flowered) × *V. arvensis*; ● = *Arvenses*; * = *Nanae*.

show some separation of the blue-flowered *Tricolores* from the *Luteae*, *Curtisieae*, *Arvenses* and *Nanae*, paralleling the edaphic ranges of these plants. The latter groups which are affected by Factor III in a similar manner, are plants of neutral to basic soils whereas the blue-flowered *Tricolores* are plants of acidic to neutral soils and the cream-flowered *Tricolores* probably occur mainly in neutral soils (although information on the edaphic ranges of these plants is scanty). This suggests a connection between certain combinations of attributes and habitat preferences and one which might have been demonstrated more convincingly by the inclusion of ecological data had these been available for all plants.

The component analysis of the complete correlation matrix gave much the same configuration of component specifications as factor specifications (Figs. 5(a)–(c)). The major groups are, however, much less distinct because of the increased range along the axis of the first component and a corresponding contraction along the axes of the second and third components. This difference reflects the greater part of the total variance accounted for by the first component and the smaller parts by the second and third components.

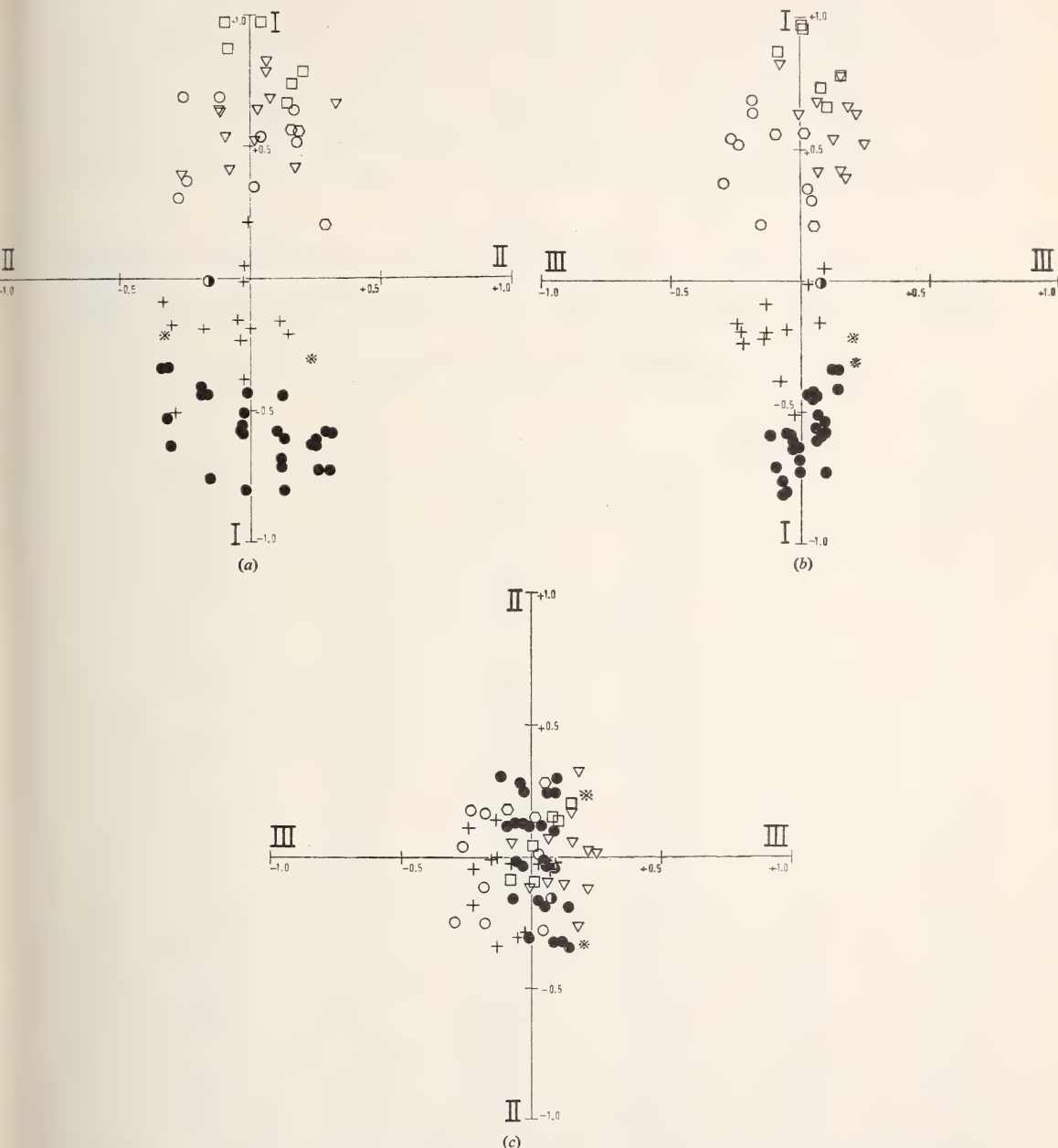


Fig. 5. Component specifications of plants for first three components. (a) Component I/Component II; (b) Component I/Component III; (c) Component II/Component III. □ = Luteae; ◻ = Saxatiles; △ = Curtisiae; ○ = blue-flowered Tricolores; ⊕ = cream-flowered Tricolores; ● = F₁ hybrid, *V. tricolor* (blue-flowered) × *V. arvensis*; ● = Arvenses; * = Nanae.

The difference in the effect between the first component and the first factor can be seen in Fig. 6 where the specifications for these alone have been plotted. The factor specifications show a complete break about the middle, separating the two main groups, and show, what is perhaps more obvious here than before, that the first factor alone is insufficient to show any definite break between the cream-flowered *Tricolores* and the *Arvenses* although a short steepening in the lower group can be seen about a third of the way from the left. In the component specifications there is no similar break in the slope although there is some steepening in the position corresponding to the break in the factor specifications. The two types of specifications can be compared with the upper line which represents the distribution of total attribute scores of each plant. As was first pointed out by Valentine (personal communication) this distribution resembles that of the first component specifications except for some minor changes of position. This is in some ways fortuitous—the resemblance arising because most attributes had high positive loadings for the first component. Had there been fewer of these high loadings for the first component there would have been little resemblance between the two.

(b) *Quantitative data*

In the factor analysis of quantitative data four common factors were extracted. The factor loadings of the attributes for these four factors are given in Table 5 and shown graphically in Fig. 7. The only clear-cut separation of attributes occurs for Factor II where

TABLE 5. Factor-loadings for quantitative attributes for 4 common factors.

Attributes	Factors			
	I	II	III	IV
1	+0.502	-0.076	-0.381	-0.250
2	+0.652	+0.168	-0.535	-0.212
3	+0.704	+0.282	+0.073	-0.371
4	+0.451	+0.448	-0.444	-0.368
5	+0.510	+0.161	-0.187	+0.278
6	+0.640	+0.186	+0.460	-0.147
7	+0.781	+0.143	+0.058	+0.276
8	+0.702	+0.439	-0.397	-0.215
9	+0.659	+0.376	-0.483	+0.209
10	+0.196	+0.372	-0.633	+0.013
11	+0.386	+0.400	-0.372	+0.565
12	+0.513	+0.219	+0.078	+0.579
13	+0.372	+0.102	+0.333	+0.556
14	+0.584	+0.282	-0.414	-0.047
15	+0.592	+0.018	-0.272	+0.231
16	+0.313	-0.876	-0.193	+0.078
17	+0.257	-0.790	-0.264	-0.035
18	+0.158	-0.730	-0.160	-0.175
19	+0.358	-0.862	-0.154	+0.182
20	+0.186	-0.938	-0.199	+0.004
21	+0.299	-0.628	+0.152	-0.047
22	+0.337	-0.864	-0.182	+0.179
23	+0.149	-0.957	-0.168	+0.001
24	+0.846	-0.092	+0.215	-0.175
25	+0.715	-0.107	+0.283	-0.060
26	+0.816	-0.075	+0.205	-0.052
27	+0.854	-0.146	+0.233	-0.098
28	+0.743	+0.049	+0.319	-0.022
29	+0.813	-0.023	+0.300	+0.008
30	+0.861	-0.007	+0.274	-0.160
31	+0.673	+0.040	+0.221	-0.082
32	+0.834	+0.128	+0.263	+0.031

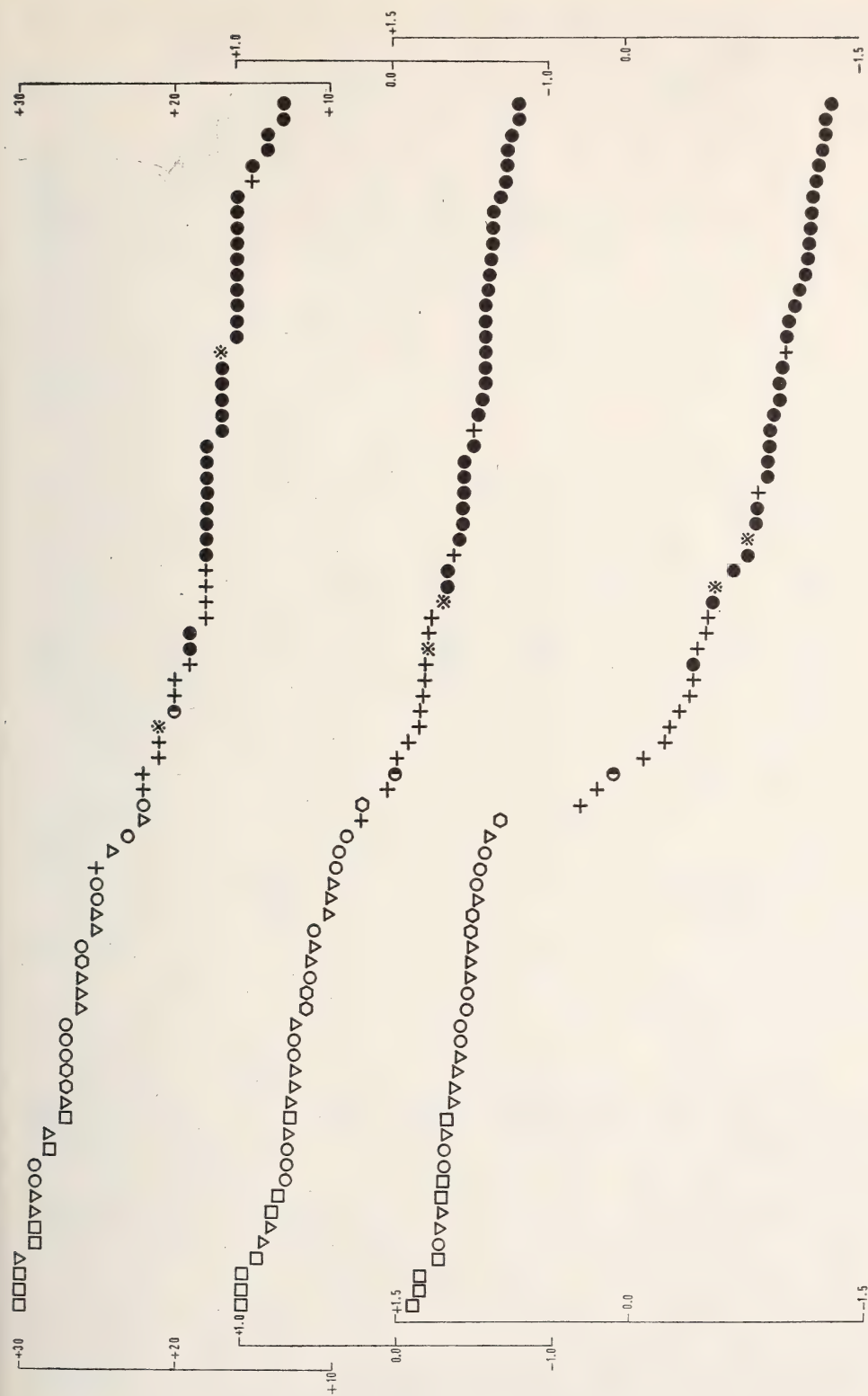


Fig. 6. Comparison of sums of attribute scores with first component and first factor specifications. Upper row represent sums of attribute scores; the middle row, the first component specifications; and the lower row, the first factor specifications. The plants are spaced horizontally for convenience. $\square$ = Luteae; ∇ = Saxatiles; $\circ$ = Tricolores; $+$ = cream-flowered Tricolores; $\bullet$ = *F*₁ hybrid, *V. tricolor* (blue-flowered) $\times$ *V. arvensis*; $\circ$ = Arvenses; $*$ = Nanac.

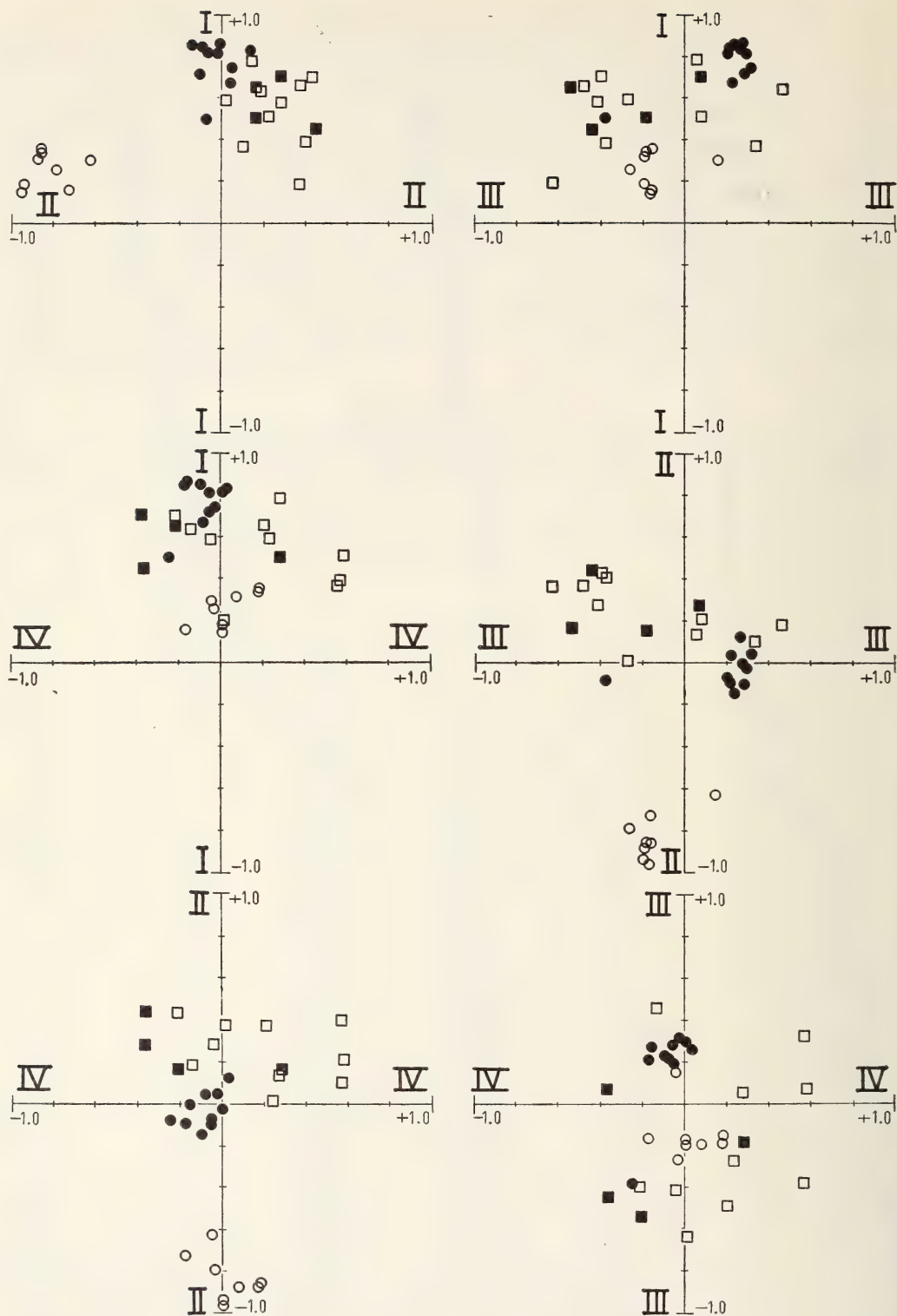


Fig. 7. Factor-loadings of quantitative attributes in common factor space. ■ = foliar attributes; □ = stipular attributes; ○ = petaline attributes; ● = pedicel and sepaline attributes.

the petaline attributes (high negative values) are separated from the sepaline attributes (low negative and positive values) and the stipular and foliar attributes (moderately low positive values). The second cluster of attributes is partially resolved by Factor III which partly separates the stipular and foliar attributes from the sepaline attributes.

The configuration of these attributes in the four dimensional common factor hyper-space can be examined in successive permutations of three dimensional space. The effect of Factor II can be seen in I/II/III, I/II/IV and II/III/IV common factor spaces. In I/II/III and I/II/IV the attribute loadings separate into two groups, viz, a separate cluster of petaline attributes orthogonal to the three axes and a cluster of sepaline, stipular and foliar attributes forming a group oblique to all 3 axes. In II/III/IV space, the cluster of petaline attributes forms a group orthogonal to the axes very close to the positive end of the axis of Factor II, while the sepaline attributes form a small cluster near the centre of the three axes and the stipular and foliar attributes are spread out into a relatively flat disc roughly in the plane of the Factor II axis. The I/III/IV space has but a single cluster of attribute loadings oblique to all three axes with the sepaline attributes forming a relatively denser node towards the positive end of the axis of Factor I and the petaline attributes forming a similar node at the base of the cluster.

The configuration in the common factor space would seem to indicate, then, that there are three groups of attributes, i.e. sepaline, petaline and foliar-stipular attributes—the last mentioned not being resolvable on the basis of the four factors extracted. The biological factors affecting these groups of attributes will clearly be of a morphogenetic nature since the analysis was based on measurements alone. Factor I affects all attributes positively, the attributes of the green organs having middling to high loadings and the attributes of the non-green, petaline organs having generally low loadings. The factor could be called a 'general growth factor' but, since the sepaline characters show the highest loadings for this factor and the foliar-stipular attributes have lower loadings with indications of interdependence between this factor and Factor II, it is possible to envisage this factor as the 'sepal-growth factor'. Factor II, on the other hand, could be considered the 'petal-suppression factor' since the petaline attributes have high negative loadings for it whereas the other attributes have generally low loadings, except for some stipular and foliar attributes with positive loadings of middling magnitude. The effects of Factors I and II emphasize the difference between the sepaline and petaline attributes. The former have the highest loadings for Factor I and the lowest loadings for Factor II; the latter have the lowest loadings for Factor I and the highest for Factor II. This demonstrates that variation in these two parts of the flower is produced by two different, independent factors and confirms the value attached by taxonomists to general flower size and the petal-sepal ratio. Factor III would appear to be a foliar-stipular factor affecting mainly stipule shape and leaf size. Its highest loadings are on the length of the stipule base (positive), width of leaf (negative), and length of the stalk of the stipule mid-lobe (negative). Similarly, Factor IV seems to be a foliar-stipular factor affecting mainly the relationship between leaf size and degree of dentation, stipule size and amount of lobing.

The factor specifications of the plants for the four factors show a somewhat different pattern from that of the previous analysis of 'qualitative data' and clearly demonstrate the overlapping variation of related taxa when morphometric data alone are considered (Figs. 8(a)–(f)). The different factors only partially resolve the recognized taxa. As might be expected the best resolution occurs with Factor II, the 'petal-suppression factor', which partially 'stratifies' the taxa into relatively narrow segments, going from positive to negative in the following order, *Nanae*, *Arvenses*, cream-flowered *Tricolores* with the *Curtisieae*, *Saxatiles* with the blue-flowered *Tricolores*, *Luteae*. Factor I, the 'sepal-growth factor', does not appear particularly important but partly separates the smaller *Curtisieae* from the blue- and cream-flowered *Tricolores* which are themselves partially resolved by Factor IV. The *Nanae* are almost separated from the *Arvenses* by Factor I, as well as Factor II, confirming the idea that the small size of the plant and the very small petals are almost adequate features for separating the group from the *Arvenses*.



Fig. 8. Factor specifications of plants for common factor space. (a) Factor I/Factor II; (b) Factor I/Factor III; (c) Factor I/Factor IV; (d) Factor II/Factor III; (e) Factor II/Factor IV; (f) Factor III/Factor IV. □ = Luteae; ▽ = Saxatiles; ○ = Curtisieae; + = cream-flowered Tricolores; ● = Arvenses; * = Nanae.

Inspection of the configuration of the factor specifications in the four dimensional hyperspace by means of different permutations of three dimensional spaces shows roughly tetrahedral or spherical clusters of plants. In the I/II/III space, perhaps the most important 3-factor space, the roughly tetrahedral cluster shows very clearly the stratification along the II axis mentioned above, as well as the partial separation of the *Curtisieae* (negative) from both cream- and blue-flowered *Tricolores* (positive) and the *Saxatiles* (positive), and the *Nanae* (negative) from the *Arvenses* (negative and positive). The *Arvenses* group forms a fairly distinct segment with the approximate boundary between it and the other groups lying in the $+0.5$ plane of the II axis. The tetrahedral cluster appears slightly tilted with respect to all axes, suggesting some interdependence of all three factors within the plants. The stratification along the II axis is also to be seen in the roughly spherical clusters of the I/II/IV and II/III/IV spaces although the change of factors occasions some small alterations of relative positions of the various groups. Within the I/III/IV space there is a less obvious sorting within the cluster. The cream-flowered *Tricolores*, blue-flowered *Tricolores*, *Curtisieae* and *Luteae* tend to occupy different positions towards the periphery of the spherical cluster but there is a great volume of overlap at the centre and the *Arvenses* are distributed more or less throughout. In the configurations involving Factor IV there is a fairly sharp truncation of the cluster in the plane of the IV axis at about -1.5 , beyond which there are no other plants except for a single extreme example of the *Arvenses*. This exceptional plant, No. 19 of Table 1, is one with exceptionally large vegetative parts. The leaves and stipule mid-lobes were unusually long and wide and their petioles, like the flower-stalk, were also unusually long. Since all these attributes received moderately high negative loadings for Factor IV, the plant is situated towards the negative end of the IV axis. The abrupt termination of the main cluster suggests that a segment of the variation in leaf and stipule characters is missing. Plants with large leaves and stipules like No. 19 have not been included in the analysis, presumably because for some reason they are rare in Britain and consequently were not available in any numbers when plants were selected for the analysis.

The corresponding component specifications of plants are illustrated in Figs. 9(a)–(f). Since most of the total variance has been extracted by the first component, and a smaller amount by the second, and little by the succeeding components, the distribution of these specifications is less revealing of the variation than that of the factor specifications. The configuration in the I/II/III component space is rather similar to that of the I/II/III factor space and shows a similar distribution of taxa with the stratification along the II axis emphasized in II/III by the relatively low values for component III. The generally low values for components III and IV obscure the distribution of taxa in the other three dimensional spaces.

DISCUSSION

There were two aims in carrying out this factorial analysis of British pansies: firstly, to determine the probable factors (in the broadest sense) producing the variation, and secondly, to see if the plants separated into discrete clusters corresponding to taxa already recognized. The first has been largely realized; the second has been less conclusive—clear-cut clustering of specifications within the common factor space was not obtained in every case. The condensing of the variability by component analysis was also far less successful than expected. There are reasons, of course, for not expecting a complete resolution of the variation into groups corresponding to the recognized taxa. To call the group a ‘critical’ one is tantamount to saying there are no obvious discontinuities in the pattern of morphological variation. In the particular case of the pansies this has been overcome by attaching considerable weight to cytological and ecological features, and as criteria these admit overlap in morphological features.

Before discussing the main aspects of the analyses the limitations involved in the method should be stressed. The results apply to particular sets of attributes for a particular selection of plants. The latter feature—the selection of plants—seems to be a limitation of minor

importance. Initially the number of plants was limited by having to carry out the first phases of the computation using a hand-operated calculating machine. To overcome this a careful selection of plants was made to represent, as far as possible, the full range of variation present in the British Isles. It should also be remembered there is a 'diminishing returns' relationship to be considered and beyond a certain stage extra plants do not materially affect the picture revealed by the analysis. It is believed that the number of plants used here represents approximately the optimum number for what was expected of the analysis.

The results of the two parallel analyses (of 'qualitative' and 'quantitative' characters) show that the content of attribute sets is of importance in affecting the picture obtained. At first glance the results derived from the two analyses are quite different, but closer examination shows underlying similarities. In the factor analysis of the qualitative data many of the attributes used were associated with reproduction and it is, therefore, not surprising that the analysis gave a clear-cut division between outbreeders and inbreeders in the first factor specifications. There was no marked resolution with respect to Factors II and III but this might have occurred had more attributes been used. The component analysis produced a similar distinction but the retention of specific variances obscured the difference.

This primary division on reproductive behaviour reflects the probable recent evolutionary trends in pansies, some details of which have already been discussed (Pettet 1964b). It is apparent that ecological adaptation and subsequent isolation has been accompanied by a certain amount of morphological differentiation which has, in some cases, been associated with cytological changes. These ancestral types were entirely outbreeders and one recent, but important, change has been the development of an inbreeding system associated with the exploitation of transitorily favourable habitats, e.g. arable farmland and dry sand dunes. This change from one system to the other has been picked out by the analysis. In addition, an incidental feature of Factor I has been the demonstration of the high degree of correlation between most of the attributes. Of particular interest is the correlation of stylar-flap and pollen assemblage with the upper petal-upper sepal, confirming the value of these features in distinguishing between *V. tricolor* and *V. arvensis* (Pettet 1964a).

The division of outbreeders from inbreeders obtained in the first analysis is not so clear cut in the case of the quantitative data. These attributes are, of course, of a different nature, expressing differences in the dimensions of floral, foliar and stipular parts. Factor analysis produces no clear breaks in the configuration of plant specifications, instead it produces a large indistinct cluster. This corresponds with the general impression of the group where variability is so great in such attributes that most taxonomic characters involve comparisons between different parts of the same plant such as was analysed in the first analysis. It also serves to demonstrate the small degree of morphological divergence between the various taxa—perhaps not remarkable in itself since all taxa are exploiting approximately similar niches in the communities to which they belong. Had there been marked divergence this analysis would not, of course, have been undertaken!

The stratification along Factor II in the I/II dimensions is roughly comparable to the arrangement along Factor I of the factor analysis of qualitative data. Since Factor I is the 'sepal-growth' factor and Factor II is the 'petal-suppression' factor, this confirms the emphasis of reproductive characters as important and consistent features of the variation pattern. The foliar-stipular factors of III and IV show even greater overlap and less discrete grouping of the taxa which partly confirms the idea that foliar and stipular characters have limited taxonomic value because of their wide and intricate variability.

An interesting point shown by the analysis of quantitative attributes is that the *Arvenses* exhibit the greatest range within the common factor space. This no doubt arises because the *Arvenses* represent many relatively homozygous, inbreeding lines developed from heterozygous, outbreeding ancestors and which, in consequence, show a greater range of variation than in the related outbreeding pansies. The related AT-intermediates, here classified under the cream-flowered *Tricolores*, have already been indicated as representing

the remnants of these ancestral outbreeding *arvensis* pansies (Pettet 1964b). This would explain their position in the factor spaces of the two analyses, i.e. lying between the in-breeding *Arvenses* and the remaining outbreeding pansies in both cases. The morphological similarity between cream-flowered *Tricolores* and the hybrid, *V. tricolor* × *V. arvensis*, is shown by their similar positions in the common factor space of the qualitative attributes. In the case of the quantitative attributes the hybrid shows a close affinity to the *Arvenses*, especially in the case of the second factor.

Factorial analysis should not be considered an end in itself. If done at the beginning of a study into the variation of a group it should suggest immediately the more important aspects to be concentrated on. In the present case the analyses were carried out towards the end of an experimental study on pansies in which the problem of the AT-intermediates had arisen incidentally during a general survey of the group. Had the analyses been done earlier the problem posed by these plants would have been pin-pointed immediately. One gratifying feature of the analysis has also been the way in which the various aspects of the variation pattern were thrown into emphasis at one and the same time—aspects which had been laboriously formulated by other methods.

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APPENDIX 1. Scores of qualitative attributes.

Plant No.	Attribute No.											Sums of scores
	1	2	3	4	5	6	7	8	9	10	11	
1	1	3	1	3	1	1	2	2	1	1	1	17
2	1	2	1	3	1	1	2	2	2	1	1	17
3	1	3	1	3	1	2	2	2	1	1	1	18
4	1	3	1	3	1	1	2	2	3	1	1	19
5	1	2	2	2	1	1	2	2	3	1	1	18
6	1	2	1	3	1	1	1	2	1	1	1	15
7	1	1	1	1	1	1	2	2	1	1	1	13
8	1	2	1	2	1	1	1	2	1	1	1	14
9	1	2	2	2	1	1	2	2	1	1	1	16
10	1	1	3	1	1	2	2	2	1	1	1	16
11	1	1	2	2	1	2	2	2	1	1	1	16
12	1	2	2	3	1	1	2	2	1	1	1	17
13	1	2	1	2	1	2	2	2	1	1	1	16
14	1	1	1	2	1	1	3	2	2	1	1	16
15	1	2	2	2	1	1	2	2	3	1	1	18
16	1	1	2	1	1	1	3	2	2	1	1	16
17	1	1	2	1	1	1	2	2	1	1	1	14
18	1	2	2	2	1	1	2	2	2	1	1	17
19	1	1	2	2	1	1	3	2	1	1	1	16
20	1	1	1	2	1	1	1	2	1	1	1	13
21	1	2	1	3	1	1	3	2	1	2	1	18
22	1	3	1	3	1	1	2	1	3	1	1	18
23	1	3	1	3	1	1	3	2	1	1	1	18
24	1	2	1	3	1	2	1	2	1	1	1	16
25	1	3	1	3	1	2	2	2	1	1	1	18
26	1	2	1	2	1	1	3	2	1	1	1	16
27	1	2	2	3	1	1	2	2	1	1	1	17
28	1	2	1	3	1	1	2	2	1	1	1	16
29	1	3	2	3	1	1	2	2	1	1	1	18
30	1	3	1	3	1	1	1	2	3	2	1	19
31	1	2	2	2	1	3	3	2	1	2	3	22
32	1	2	2	2	1	3	3	2	3	2	1	22
33	1	2	1	3	2	3	2	2	2	2	1	21
34	1	1	2	2	2	2	3	2	1	2	2	20
35	1	2	2	2	1	3	3	2	1	2	1	20
36	1	2	2	3	3	3	2	3	3	3	3	28
37	1	1	2	1	1	3	2	3	1	2	1	18
38	1	1	2	2	3	3	3	3	3	3	3	27
39	1	2	1	3	1	3	2	3	2	2	1	21
*40	1	1	2	1	1	1	1	2	3	1	1	15
41	1	1	1	1	2	3	2	3	3	3	3	23
42	1	1	2	2	3	3	3	3	3	3	3	27
43	1	1	2	1	3	3	3	3	3	3	3	26
44	1	2	2	2	1	3	2	3	3	2	3	24
45	1	1	1	1	1	3	3	2	3	1	1	18
46	1	1	1	2	1	3	2	3	1	2	1	18
47	1	2	1	2	1	3	2	3	1	2	1	19
48	1	1	1	3	1	3	2	2	3	2	1	20
49	1	2	1	2	1	3	2	2	1	2	1	18
50	1	2	1	2	3	3	3	3	3	3	3	27
51	1	2	2	3	3	3	3	3	3	3	3	29
52	1	2	2	3	3	3	3	3	3	3	3	29

APPENDIX 1—cont.

Plant No.		Attribute No.										Sums of scores
53	1	1	2	1	2	3	3	2	1	3	3	22
54	1	1	2	3	1	3	3	2	3	3	3	25
55	2	2	2	3	3	3	2	3	1	3	3	27
56	2	2	2	3	1	3	3	3	2	3	3	27
†57	1	3	2	3	2	3	3	2	1	3	3	26
58	2	2	3	3	3	3	3	2	3	3	3	30
59	2	1	3	3	3	3	3	3	3	3	3	30
60	2	1	3	3	3	3	3	3	3	3	3	30
61	2	1	2	2	3	3	3	3	3	3	3	28
62	2	1	2	1	1	3	3	2	1	3	3	22
63	2	2	3	2	1	3	3	2	2	3	3	26
64	2	2	2	3	1	3	3	2	2	3	3	26
65	2	1	3	3	1	3	3	2	3	3	3	27
66	2	2	3	2	3	3	3	2	3	3	3	29
67	2	3	3	3	3	3	3	2	2	3	3	30
68	2	2	2	2	3	3	3	2	3	3	3	28
69	2	1	3	2	1	3	3	2	3	3	3	26
70	2	1	2	2	1	3	2	2	3	3	3	24
71	2	2	3	3	1	3	3	3	3	3	3	29
72	2	1	3	2	3	3	3	3	3	3	3	29
73	2	2	3	3	1	3	3	3	2	3	3	28
74	2	1	2	2	1	3	3	2	3	3	3	25
75	2	2	2	2	3	3	3	3	3	3	3	29
76	2	2	2	1	1	3	3	3	3	3	3	26
77	1	3	3	3	2	1	3	2	1	1	1	21
78	1	1	3	1	2	1	3	2	1	1	1	17

* Although Drabble named No. 40 as *V. vectensis* it does not in fact agree with the description of the species.

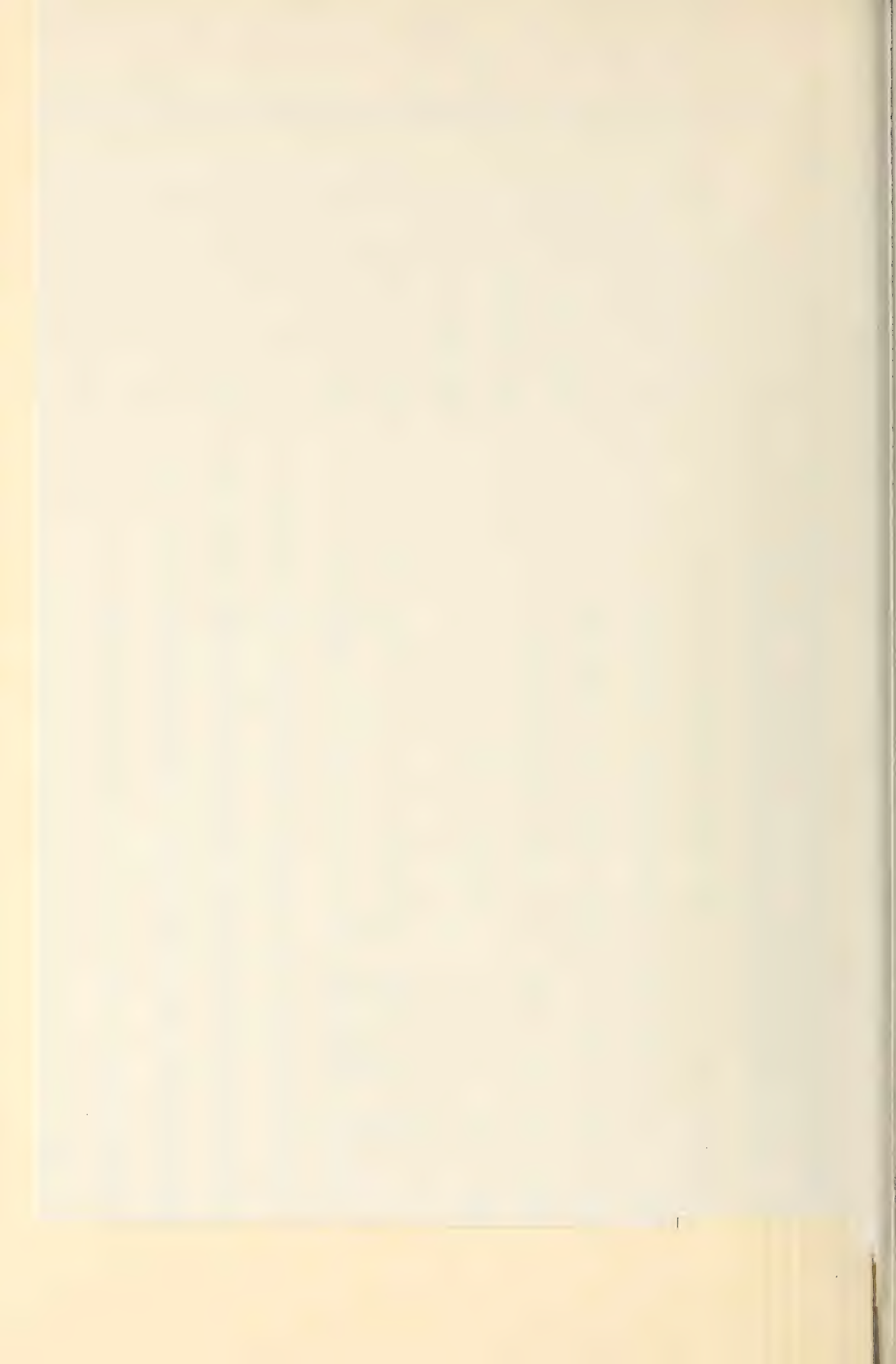
† The herbarium specimen of No. 57 is an annual notwithstanding the published accounts of this plant.

*Plant
No.*

		1	2	25	26	27	28	29	30	31	32
1	49.00	6.									
2	63.00	13.		2.00	2.50	6.75	2.00	2.00	6.50	1.75	1.75
3	67.00	9.		1.75	4.50	9.00	1.75	3.00	8.75	2.00	4.00
4	38.00	7.		2.75	4.00	10.00	2.50	3.50	9.00	2.75	2.50
5	49.00	9.		2.75	3.50	8.50	2.75	3.50	8.50	3.50	4.00
6	58.00	13.		2.00	3.50	8.00	2.25	2.50	8.00	2.00	2.75
7	47.00	10.		3.75	4.75	10.75	3.25	3.50	10.75	3.75	4.75
8	52.00	6.		2.00	3.50	7.50	1.75	3.00	8.00	1.50	3.25
9	63.00	9.		3.00	4.00	8.50	2.50	4.00	9.50	2.50	3.50

APPENDIX 2. Measurements of quantitative attributes (in mm).

Plant No.	Attribute No.																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	49.00	6.00	21.50	10.00	4.00	6.00	2.00	13.00	2.75	0.00	0.00	3.00	2.00	6.50	1.00	5.50	7.75	2.50	2.50	3.75	2.75	2.75	4.50	7.50	2.00	2.50	6.75	2.00	2.00	6.50	1.75	1.75
2	63.00	13.00	34.00	15.00	4.00	5.00	3.00	29.00	7.00	5.00	2.00	5.00	2.00	12.00	1.50	4.50	7.50	3.75	2.75	2.75	3.00	3.00	4.50	10.00	1.75	4.50	9.00	1.75	3.00	8.75	2.00	4.00
3	67.00	9.50	33.00	8.00	4.00	9.00	2.50	18.00	4.50	0.00	1.00	4.00	2.00	6.50	1.00	7.25	9.50	3.50	4.75	5.50	3.75	5.25	9.00	11.50	2.75	4.00	10.00	2.50	3.50	9.00	2.75	2.50
4	38.00	7.50	38.00	6.00	5.00	11.50	2.50	20.50	4.50	0.00	1.00	5.00	2.00	5.50	1.25	7.50	8.0	2.75	4.50	4.50	3.00	5.00	5.75	10.00	2.75	3.50	8.00	2.75	3.50	8.50	3.50	4.00
5	49.00	9.50	21.00	8.00	5.00	6.00	3.50	15.00	6.00	2.50	3.00	5.00	2.00	9.00	1.50	5.50	7.75	3.75	3.25	4.50	3.00	4.00	6.25	8.75	2.00	3.50	8.00	2.25	3.00	8.00	2.00	2.75
6	58.00	13.00	46.00	14.00	5.00	16.00	4.50	23.00	5.00	0.00	0.00	6.00	3.00	7.00	1.50	8.00	10.50	3.25	4.50	4.50	3.50	4.50	7.25	12.00	3.75	4.75	10.75	3.25	3.50	10.75	3.75	4.75
7	47.00	10.00	16.00	10.00	4.00	6.50	3.00	14.50	6.00	3.00	2.00	5.00	2.00	8.00	1.75	5.75	7.00	3.50	3.25	2.75	3.50	3.25	5.00	8.75	2.00	3.50	7.50	1.75	3.00	8.00	1.50	3.25
8	62.00	6.50	18.00	8.00	4.00	7.00	2.50	14.50	4.50	0.00	2.00	5.00	2.00	7.00	1.00	7.00	9.25	4.00	4.25	4.50	3.50	4.75	8.00	9.50	3.00	4.00	8.50	2.50	4.00	9.50	2.50	3.50
9	63.00	9.50	27.00	12.00	4.00	11.00	4.00	19.00	6.50	0.00	1.00	6.00	3.00	10.50	2.00	7.00	10.00	3.50	4.75	4.50	3.50	5.00	7.50	11.50	3.50	4.00	10.00	2.50	4.00	9.50	3.00	4.00
10	30.00	8.00	8.50	6.00	4.00	2.00	2.00	10.50	4.75	2.00	2.00	6.00	2.00	6.75	1.25	6.00	8.50	3.00	3.50	4.50	3.00	3.25	6.50	7.50	1.75	2.25	6.00	1.75	1.75	5.00	1.75	2.00
11	39.00	6.00	10.50	7.00	4.00	3.00	2.00	13.00	4.50	2.00	2.00	5.00	2.00	6.50	0.75	5.50	8.00	3.00	2.75	3.00	3.00	2.75	5.25	7.50	1.50	2.50	6.25	1.50	1.75	6.00	1.25	1.75
12	29.00	4.75	13.00	6.00	3.00	4.00	1.25	8.50	1.75	1.00	0.00	2.00	1.00	3.50	0.50	4.50	7.50	3.00	2.50	2.50	2.50	2.00	4.75	6.75	2.00	2.50	5.50	1.75	2.00	5.00	1.75	1.75
13	34.00	5.00	14.00	8.00	5.00	4.50	1.50	10.00	2.50	2.00	1.00	5.00	2.00	4.00	0.50	5.00	6.50	3.50	3.00	2.50	3.50	2.75	5.00	7.50	2.00	2.50	6.00	1.75	2.50	5.00	1.50	1.50
14	63.00	5.50	10.50	7.00	4.00	2.50	1.50	11.00	3.50	3.00	1.00	4.00	2.00	5.00	0.75	4.75	7.50	3.50	2.75	2.50	3.00	2.50	4.00	6.75	1.75	2.50	5.50	1.50	1.50	5.00	1.25	1.50
15	72.00	6.50	13.50	6.00	4.00	5.50	2.50	13.50	6.00	6.00	2.00	5.00	2.00	7.00	1.50	7.50	9.50	3.75	3.75	4.50	2.75	3.75	5.57	9.00	2.00	3.00	8.50	1.75	2.50	7.50	2.25	2.50
16	80.00	9.50	16.00	8.00	5.00	5.50	2.50	13.50	6.00	6.00	2.00	5.00	2.00	7.00	1.50	7.50	9.50	3.75	3.75	4.50	2.75	3.75	5.57	9.00	2.00	3.00	8.50	1.75	2.50	7.50	2.25	2.50
17	73.00	15.00	18.00	20.00	4.00	1.00	2.50	25.00	9.00	10.00	2.00	5.00	1.00	10.00	1.00	6.00	8.00	3.00	3.50	4.00	2.75	3.00	5.50	6.25	1.50	3.50	4.50	1.25	2.50	5.25	1.50	2.50
18	75.00	8.00	20.00	12.00	5.00	9.00	3.00	16.00	5.00	3.00	2.00	6.00	3.00	7.00	1.50	6.75	9.00	3.25	3.50	4.50	3.00	3.50	6.50	9.00	2.00	3.00	7.25	1.75	2.75	7.00	2.00	3.25
19	114.00	18.00	24.00	32.00	5.00	3.00	1.50	27.00	5.00	12.00	1.00	3.00	0.00	8.00	1.00	6.25	9.25	3.50	3.25	4.00	2.75	3.00	5.25	9.75	2.00	2.75	7.75	2.00	2.50	7.75	2.50	2.25
20	82.00	13.50	23.00	13.00	4.00	6.00	2.00	15.00	5.00	1.00	1.00	4.00	1.00	7.50	1.50	5.50	9.00	3.00	3.50	4.50	3.00	4.50	7.00	9.25	2.50	2.00	8.00	2.00	2.75	7.50	1.50	2.00
21	63.00	6.50	21.00	6.00	4.00	7.50	2.00	8.50	2.00	0.00	0.00	4.00	2.00	4.00	0.75	6.25	7.75	3.25	3.25	4.00	2.75	3.75	5.75	7.75	2.50	2.00	6.00	1.75	2.25	6.50	2.00	2.50
22	43.00	4.50	24.50	9.00	3.00	8.75	1.75	12.75	3.00	0.00	1.00	5.00	2.00	5.00	0.75	5.00	7.25	3.00	2.75	3.00	3.00	3.00	5.00	9.00	2.25	2.50	7.50	1.75	2.25	7.25	1.25	2.75
23	36.00	10.00	34.00	15.00	4.00	5.00	2.25	27.50	5.75	4.00	1.00	4.00	1.00	12.00	1.75	7.00	8.75	4.25	3.50	3.25	3.00	3.25	5.50	9.25	1.75	2.50	7.50	2.00	2.50	6.00	1.50	2.50
24	62.00	8.50	22.50	11.00	4.00	6.00	2.00	13.00	3.25	0.00	0.00	3.00	1.00	6.25	0.50	6.00	7.50	3.25	2.75	3.00	3.50	2.75	5.75	7.25	1.75	3.50	6.25	1.50	2.50	6.25	1.50	2.50
25	38.00	7.00	31.00	10.00	5.00	7.00	2.50	13.00	2.50	0.00	0.00	4.00	2.00	6.50	0.75	8.00	10.00	3.75	3.75	5.00	2.75	4.75	7.00	9.50	1.75	2.75	8.00	1.25	2.50	7.50	1.50	2.50
26	51.00	9.00	24.00	8.00	3.00	12.50	1.50	9.50	4.00	0.00	0.00	4.00	1.00	4.25	0.75	6.00	7.75	3.50	3.75	4.00	3.50	3.50	6.00	9.50	2.00	3.00	7.50	2.00	3.00	7.50	2.00	2.50
27	46.00	7.00	18.50	8.00	4.00	2.50	2.50	14.00	3.00	0.00	1.00	4.00	2.00	6.50	0.75	7.25	9.00	3.50	4.50	4.25	3.00	4.50	6.25	9.25	2.50	3.50	8.00	2.00	3.25	8.00	2.25	3.00
28	58.00	6.00	19.00	7.00	3.00	6.50	2.00	13.00	3.00	0.00	0.00	5.00	1.00	7.50	1.00	5.75	7.50	3.50	2.75	2.75	3.00	2.50	4.25	8.00	1.50	2.75	7.25	1.75	2.50	7.50	2.50	2.50
29	46.00	5.25	18.00	8.00	4.00	5.00	2.00	11.50	2.25	0.00	1.00	4.00	2.00	5.50	0.50	6.00	8.50	3.50	3.50	4.50	3.00	3.75	5.75	9.75	2.25	2.75	7.50	1.50	2.50	7.50	1.50	2.50
30	52.00	6.00	30.00	10.00	4.00	15.00	3.00	13.00	2.75	0.00	0.00	5.00	2.00	5.00	1.00	8.75	9.75	4.50	5.00	5.00	4.25	5.75	9.00	12.25	3.75	5.50	10.50	3.00	4.00	11.50	3.25	4.00
31	56.00	6.75	17.50	4.00	3.00	6.00	2.75	11.50	4.25	0.00	1.00	4.00	2.00	4.50	1.25	10.50	11.50	3.50	7.00	7.50	4.00	11.50	10.75	2.50	3.25	8.50	2.00	2.50	6.50	2.25	2.25	
32	81.00	18.50	43.50	7.00	5.00	10.00	4.50	19.50	8.50	0.00	2.00	4.00	2.00	9.50	2.00	10.50	11.50	4.50	6.25	6.50	3.00	8.50	9.25	8.75	3.00	3.75	8.00	2.50	3.00	6.50	2.25	2.75
33	99.00	13.00	33.00	12.00	5.00	5.50	4.00	27.50	5.50	5.00	2.00	5.00	2.00	10.00	1.50	13.00	14.25	5.00	7.25	9.00	3.50	9.00	13.00	12.50	3.00	4.00	10.25	2.50	3.00	10.50	2.75	4.25
34	79.00	17.50	29.00	15.00	5.00	8.00	2.00	21.50	8.50	1.00	2.00	4.00	1.00	8.00	1.25	7.50	10.00	4.00	3.50	4.50	3.00	3.75	7.25	8.50	2.25	2.75	6.00	1.50	1.75	6.50	2.00	2.00
35	38.00	5.50	14.00	7.00	3.00	5.50	2.25	9.00	3.3																							



THE STATUS OF THE PEDUNCULATE AND SESSILE OAKS IN BRITAIN

By J. E. COUSENS

Department of Forestry and Natural Resources, University of Edinburgh

ABSTRACT

Introgression in the pedunculate oak (*Quercus robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.) in Scotland was known to be so extensive that neither could be defined satisfactorily. Population studies were therefore carried out in Eire to clarify the status of the sessile oak and in south-east England and in the flood-plain oak forests of Yugoslavia in an attempt to find good pedunculate oak. Each of these collections revealed some evidence for introgression. A method of analysis has been devised to distinguish between currently active introgression and a condition due either to incomplete evolutionary divergence or to old introgression now largely assimilated into the gene pool. *Q. petraea* is a relatively good species in Eire and possibly in southern England too. *Q. robur* is diagnosed as a species, possibly as homogeneous as *Q. petraea* at one time, but, if so, introgressed by a number of related species during the last glaciations or earlier; it arrived in post-glacial Britain already a very variable species and was subjected to a little secondary introgression by *Q. petraea*. Introgression of both species increases northwards into Scotland. The much greater introgression of *Q. petraea* in Scotland has been made possible by the practice of planting *Q. robur* to maintain the stocking of *petraea* coppice woods. The observed variation in the selected diagnostic characters in the Yugoslavian and Irish collections is outlined to provide a provisional definition of *Q. robur* and *Q. petraea* in Britain.

INTRODUCTION

A study of the partially interfertile *Quercus robur* and *Q. petraea* in Scotland revealed considerable reciprocal introgression (Cousens 1963). In a few populations of *Q. petraea* the selected diagnostic characters were reasonably homogeneous; but even these populations were a little suspect since characters such as 'veins to sinus of leaf' occurred among them. In the absence of satisfactory definitions of either species it was not possible to estimate the extent of introgression. This paper describes subsequent studies to clarify the status of these two species by comparison with populations elsewhere. The methods of sampling and specimen collection have already been described (Cousens 1963).

QUERCUS PETRAEA IN EIRE

The forests of Ireland have been more completely destroyed than those of Scotland or England. By A.D. 1600 about one-eighth of the country still carried forest but during the next two centuries their destruction was greatly accelerated when iron-smelting with charcoal was developed on a large scale (McCracken 1963). Labour costs were relatively low and it became profitable to import iron ore from Wales or Spain and smelt it in or near the woods; when an area of forest was exhausted the smelters moved on to another centre. The only reports of attempts at forestry management come from Co. Wicklow which had exported oak billets to Wales prior to this period. In spite of the acknowledged fact that coppice-oak billets gave best results in smelting, the short-term approach, exploitation of existing woodland, seems to have prevailed. The situation in Ireland was thus very different from that in Scotland or England where there had been a long history of intensive coppice management and by implication a great deal of planting of oak to replace standards and old coppice stools.

Tree planting on any scale is not recorded in Ireland till the sixteenth century and even then was mostly within the Pale (around Dublin). The Williamite wars discouraged planting through much of the seventeenth century and by the eighteenth century planting was mainly of exotic species, largely larch and pine (McEvoy 1943). All these plantations

were included in the 2 per cent. of Ireland that carried woodland in 1840 (McCracken 1963). At the end of the Napoleonic wars (about 1820) charcoal smelting became unprofitable with the advent of coal smelting and a majority of the stands of oak to be found in Eire today are derived from woodland last felled about that time.

Both *Q. petraea* and *Q. robur* occur in Eire today but varying opinions have been expressed about the status of *Q. robur*. According to McEvoy (1943) it is native and was the main oak of the central limestone area which was not overlain by bog. The only extensive remnants of oak woodland are all peripheral to the central area, mainly on siliceous rocks and of undoubted *Q. petraea* affinity. The populations sampled include well documented localities for *Q. petraea* in the Wicklow mountains, in the south-west near Glengariff and Killarney and in the west near Pontoon and Sligo (Praeger 1934). Fig. 1 shows the location of all the major samples.



Fig. 1. EIRE—location of populations sampled.

ANALYSIS OF THE IRISH DATA

The main analysis was confined to six diagnostic characters; contrary to opinions expressed on p. 283 of the previous paper (Cousens 1963) it will be argued later that all are probably under polygene control. Two of these characters, Petiole per cent. of leaf length and Peduncle length to first flower bract, are readily recorded as continuous variables and have been called the Primary Characters. The other four, Auricle type, Abaxial leaf pubescence, Peduncle diameter and Peduncle pubescence, are each classified as nominal *Q. robur*, indeterminate or nominal *Q. petraea* on the basis of multiple correlation within the Scottish material: these are the Secondary Characters. The presence of such a correlation in the Scottish material (which exhibited complete intergradation between the species) confirms the diagnostic value of these characters. Specimens in which all four characters were within the nominal *Q. robur* or *Q. petraea* range were called the Theoretical Species Types (or TSTs). By definition then the TSTs show less than the normal species variation for the four characters from which they were derived. It follows that specimens differing from the TSTs to a certain degree may still represent only the normal variability of the species. To test this the range of variation of the Primary Characters for TST and non-TST specimens may be compared. The ranges should be similar if both are part of a non-introgressed population. It has been shown for the Scottish collections that if specimens are classified according to the degree of their difference from the TSTs, then the plotted

mean values of the Primary variables for each class fall on a curve linking the two TSTs. This curve has been called the Introgression Path and is shown in Fig. 2. The degrees of difference from the TST can be compiled as in Hybrid Index scoring but the resultant index indicates only the degree of heterogeneity. Determination of the level at which such an Heterogeneity Index is indicative of hybrid origin requires a knowledge of the normal

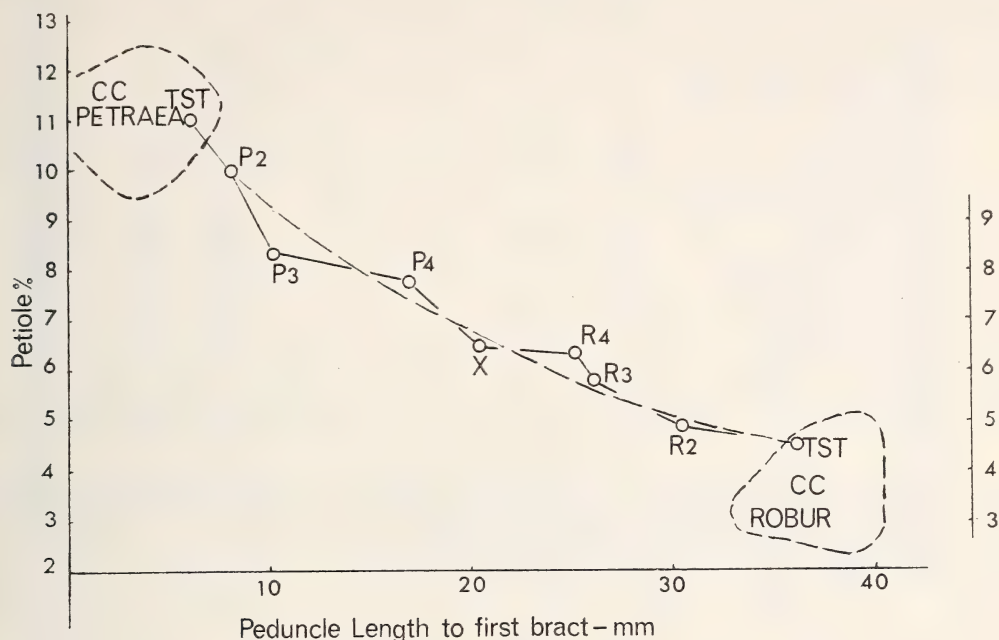


Fig. 2. The INTROGRESSION PATH constructed from the mean peduncle and petiole values for the nine combination classes P(TST), P2, P3, P4, X, R4, R3, R2, R(TST) (Scottish data).

species variability. The Eire data are first presented in this way (Table 1). Note that the percentage of TSTs is uniformly high while, with one exception, the Heterogeneity Indices are uniformly low. The 'B' collection from Croniebyrn in the Wicklow mountains is the exception and it happens to be the only sample from an area known to have been under long-standing coppice management. The proportion of truly intermediate specimens (i.e. classes P4, X and R4) is less than 2 per cent.

Fig. 3 shows the distribution of the values for the Primary Characters. Note that the index is largely determined by values for TSTs and that there is no obvious trend in the direction of the Introgression Path. The greatest concentration of non-TST values does lie on the Introgression Path, however, indicating the possibility of slight introgression.

DISCUSSION OF THE IRISH RESULTS

It may be objected that the Irish samples, being selective for good *Q. petraea*, cannot be validly compared with those from Scotland. Table 2 lists the equivalent Scottish aff. *Q. petraea* samples, i.e. those with no specimens showing more than four degrees of difference from the *Q. petraea* TST. Note that the proportion of truly intermediate class specimens is higher at 7 per cent. and that the overall Heterogeneity Index is nearly twice that for the Eire collections. That these differences are likely to be very significant can be seen more clearly when the Primary variables are compared in Secondary Character combination classes. Fig. 4 is an enlargement of the *Q. petraea* end of the Introgression Path (Fig. 2) with the values for the Eire collections and the Scottish equivalents superimposed on it. When individual values are plotted there is extremely wide scatter; means

TABLE 1. Range and frequency of secondary character combinations in the major Eire population samples.

No.	Locality	Degrees of difference from <i>petraea</i> TST								Total	HI†	Height above sea-level feet
		0 P	1 P2	2 P3	3 P4	4 X	5 R4	6 R3				
1.	Ballycoyl	15	3	2		1			21	0.52	500	
2.	Powerscourt, Deer Park ..	16	6	1					23	0.35	500	
3.	Glendalough, Lugduff Wood	13	7						20	0.35	950	
4.	Vale of Clara:											
	Croniebyrn A	11	2	2					15	0.40	450	
	Croniebyrn B	4	4	3	1				12	1.08	450	
5.	Shillelagh, Culliton Estate ..	13	1	1				1*	16	0.20	400	
6.	Portlaw, Curraghmore Estate	23	4	3	1		1*	1*	33	0.42	150	
7.	Glengariff Estate	25	5	2		1			33	0.39	50	
8.	Killarney, Tomies Wood ..	37	9	6	1			2*	55	0.45	250	
9.	Connemara, Ballynahinch ..	12	4	1					17	0.35	100	
10.	Lough Conn, Pontoon ..	20	4	1					25	0.25	150	
11.	Lough Gill, Cullendra ..	23	6		1				30	0.30	200	
12.	Lough Eske, Ardnamona Estate	17	7	5					29	0.59	200	
Totals		229	62	27	4	2	1*	4*	329	0.42		
Per cent.		71	19	8	1.2	0.6						

* Specimens taken on the margin of the wood in each case; they do not form a continuous series with those in the wood and have been treated as extraneous to the populations sampled.

† Heterogeneity Index.

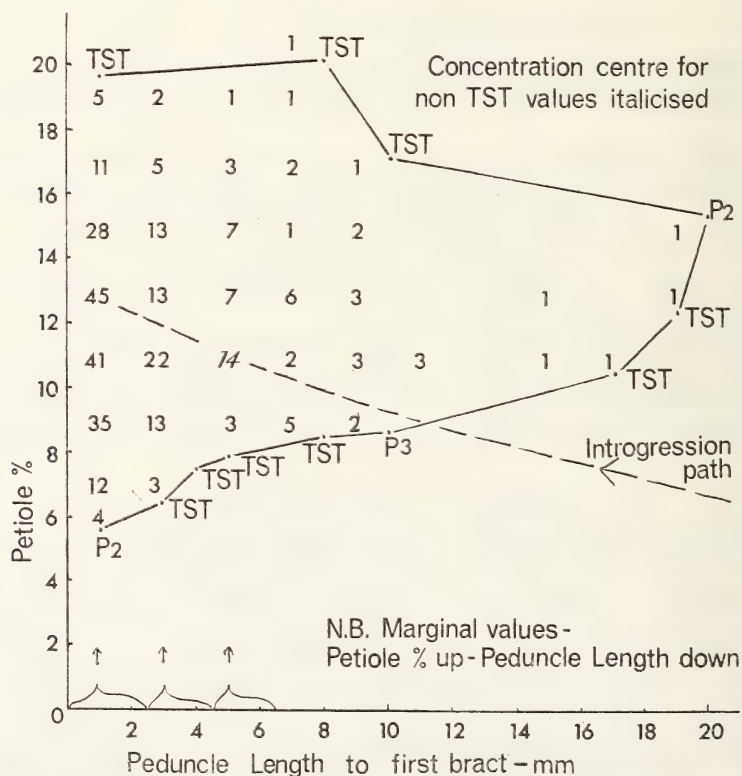
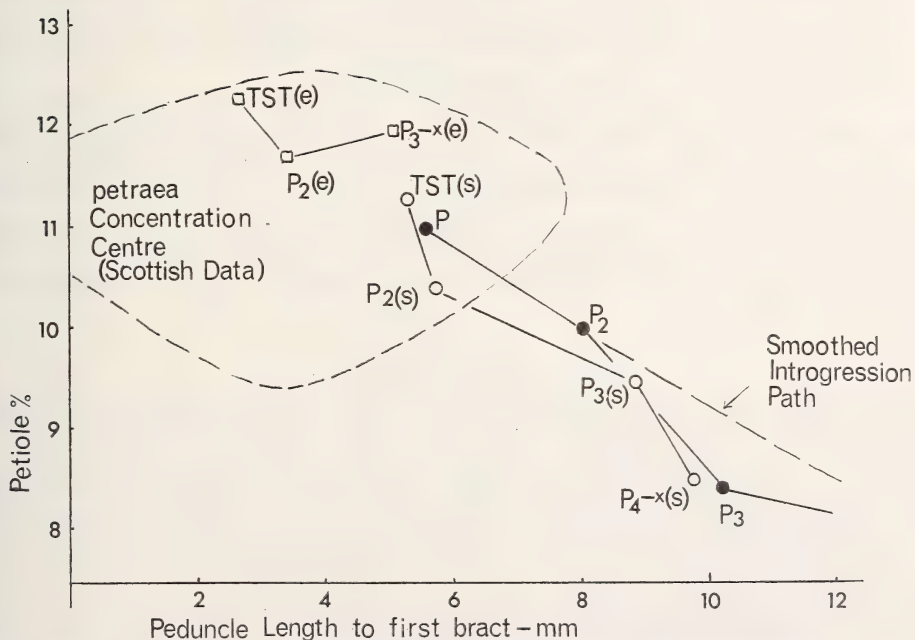


Fig. 3. Distribution of the combined Petiole % and Peduncle Length values for the Eire collections.

TABLE 2. Range and frequency of secondary character combinations in Scottish samples within an equivalent range.

O.S. Grid	Serial No.	Locality			Degrees of difference from <i>petraea</i> TST					Total	HI
					0	1	2	3	4		
					P	P2	P3	P4	X		
NJ	3	Elgin Town Wood	..	..	4	3	2			9	0.78
NH	3	Locan a' Chuillin	..	..	2		2	2		6	1.67
NM	4-5	Loch Sunart	..	..	4	3	3	2	1	13	1.46
NN	5	Loch Arkaig	..	..	12	10		1		23	0.56
NN	7	Spean Bridge	..	..	5	6	4	3		18	1.28
NN	9	Glen Falloch	..	..	1	2	2	1		6	1.50
NN	23	Glen Goil	..	..	3	5	4		1	13	1.31
NR	1	Claonig	..	..	4	3			1	8	0.88
NS	1	Menstrie Burn	..	..	3	3				6	0.50
NS	7	Ross Wood	..	..	3	3	3	1		10	1.20
NT	8	Cheviot	..	..	4	2				6	0.33
NT	15	Aikieside Wood	..	..	9	2				11	0.18
NT	18	Jedforest remnant	..	..	18	8	2	2	1	31	0.71
NT	21	Ettrick remnant	..	..	5	2	3	1		11	1.00
NX	1	Burnfoot Wood	..	..	8	1	1	1		11	0.55
NX	2	Curraie Glen	..	..	11	6				17	0.35
NX	3	Cairnryan	..	..	6	2				8	0.25
NX	4	Penkiln Burn	..	..	6	2				8	0.25
NX	7, 8, 11	Glentrool	..	..	20	6				26	0.23
Totals ..					128	69	26	14	4	241	0.74
Per cent. ..					53	29	11	6	2	100	

Fig. 4. The *petraea* end of the Introgression Path enlarged for comparison of (1) Eire values (e); (2) Values for equivalent Scottish populations (s); (3) Values for all Scottish populations (Fig. 2).

for the combination classes therefore tend to be erratic unless based on a sufficiently large number of specimens; for this reason classes P3 to X in the Eire data and P4 to X in the Scottish equivalents have been grouped together. Note that all the means for the Irish data lie above and to the left of those for the TST in both sets of Scottish data, i.e. on an extension of the Introgression Path. The Irish means do not give a very clear indication of the Introgression Path while the Scottish means do. Theoretical consideration of the effect of introgression on population statistics of this kind suggest that the following stages might be recognizable:

Stage I—a few hybrids are established and back-crossing has begun—the proportion of TSTs will be high; their mean values will lie at the very end of the Introgression Path but there will be a distinct ‘tail’ stretching out into the intermediate zone between the two species concentration centres.

Stage II—hybridization is continuing and introgression is well advanced—the TST Primary Character means will have moved down the Introgression Path and there will be a substantial proportion of the specimens contributing to the ‘tail’ which will also reach into the intermediate zone.

Stage III—hybridization has ceased (between the species) and continuing back-crosses are resulting in a gradual assimilation of the ‘alien’ genes—the TST Primary Character means will have moved a little further down the Introgression Path and the ‘tail’ will have contracted.

Stage IV—the process of assimilation is complete—there will be no obvious introgressive trend and its origin will only be apparent if there are data from non-introgressed populations for comparison.

Stage III, if seen in isolation, would not be distinguishable from a similar stage in evolutionary divergence.

Applying this theoretical picture to the Irish and Scottish collections compared above, it is clear that the Irish *Q. petraea* population is in a late phase of Stage III, while the equivalent Scottish woods are clearly in Stage II (as is confirmed by the full Scottish data).

Analysis of the Irish data therefore indicates either a situation in which a past introgression has been almost entirely assimilated into the *Q. petraea* gene pool, or, alternatively, one in which evolutionary divergence is not quite complete.

If it be assumed that Scottish and Irish *Q. petraea* both arrived by migration from southern Britain, then their rather different status today must be due to significant differences in the conditions they encountered in the two countries. Several possibilities suggest themselves: *Q. robur* may not have been indigenous in Ireland; or many fewer interspecific hybrids may have arisen in Ireland; or the virtual absence of oak planting on any scale in Ireland may be the key factor. These results therefore provide some support for the writer's contention that planting was a major factor in determining the extent of introgression of *Q. petraea* in Scotland.

QUERCUS ROBUR IN ENGLAND

In 1960 some oakwoods around Doncaster were examined. The data from these collections (Table 3) suggested that sampling in England would give similar results to Scotland. This conclusion conflicted with that of Jones (1959). He had observed great variability in *Q. robur* populations in situations where the historical and ecological evidence argued strongly against introgression by *Q. petraea* (Dr. E. W. Jones, personal communication, 1962). Reputed *Q. robur* woods were therefore sampled in the most ‘continental’ part of England and on some of the heavy wet clays around Oxford. Fig. 5 shows the location of the population samples which are also listed in Table 4. The intermediate classes, R4, X and P4, include 26 per cent. of the specimens and there appears to be a very considerable hybrid element. Fig. 6 shows the distribution of values of the Primary Characters. The concentration centre for all values lies below the Introgression Path and

TABLE 3. Range and frequency of secondary character combinations in the 1960 population samples.

Locality	Degrees of difference from robur or petraea TST										Total	HI
	0	1	2	3	4	3	2	1	0			
	P	P2	P3	P4	X	R4	R3	R2	R			

<i>Peak District:</i>													
Castleton	..	..	14	6								20	0.30(P)
Bamford Edge	..	..	5	4		1						10	0.70(P)
<i>Sherwood Forest:</i>													
Major Oak area	..	..	7	3	1	1	2		2	1		17	mixed*
<i>N. Lincolnshire:</i>													
Scrawby Estate	..	..		1	2	2	3	6	6	4	1	25	3.00(R)
<i>S. Lincolnshire:</i>													
Tumby Estate	..	..					3	4	5	13	2	27	1.74(R)
Woodhall Spa	..	..					1	1	4	2	1	9	1.89(R)

* Heterogeneity Indices have only been calculated when the data were unimodal in their frequency distribution.



Fig. 5. ENGLAND—location of populations sampled.

TABLE 4. Range and frequency of secondary character combinations in samples of *robur* affinity from southern England.

No.	Locality	Degrees of difference from the robur TST								Total	HI		
		0	1	2	3	4	5	6					
		R	R2	R3	R4	X	P4	P3					
<i>British Nature Reserves:</i>													
1.	Castor Hanglands	..	..	4	10	8	6	2			30	1.73	
2.	Monks Wood	..	..	4	5	9	4	1			23	1.70	
3.	Hales Wood	..	..	9	9	5	1				24	0.92	
<i>Oxford Area:</i>													
4.	Wytham Wood	..	..	6	14	5	4	4	1		34	1.68	
5.	Blenheim Palace	..	..	8	12	11	8	3	1	1	44	1.82	
6.	Weston Wood	..	..	3	10	3	7	3	1		27	2.00	
7.	Waterperry	..	..	3	4	7	6	3	1		24	2.21	
<i>Windsor Park:</i>													
8.	Highstanding Hill	..	..	3	4	3	2	2			14	1.71	
<i>Ashford, Kent:</i>													
9.	Hoad's Wood	..	..	..	4	6					10	1.60	
<i>Weald:</i>													
10.	Oakwood Hill	..	..	..	2	4	3				9	1.11	
11.	Hurtwood	..	..	..	3	4		1	2		10	1.50	
Totals		..	..	..	45	80	60	39	20	4	1	249	1.70
Per cent.		..	..	..	18	32	24	16	8	1.6	0.4	100	

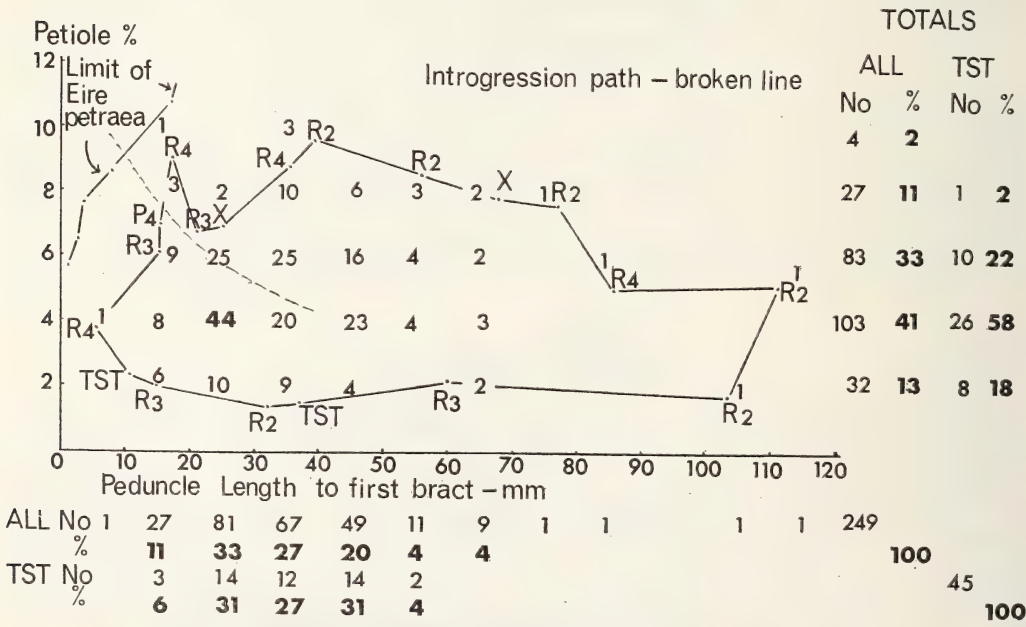


Fig. 6. Distribution of combined Petiole % and Peduncle Length values for collections of *robur* affinity in south-east and central England.

well to the left of the main concentration centre for *Q. robur* TSTs. Few of the peripheral values are TSTs and as in the Scottish data all the very high peduncle values are from non-TST specimens. These abnormally high values have a marked effect on the means of the combination classes to which they belong. In Fig. 7 their trend, with and without these high values, is shown and related to the Introgression Path. The introgressive trend is condensed but this might be expected in a series of collections from populations selected as most likely to be good *Q. robur*. It seemed that it should be possible to find better *Q. robur* than this somewhere in Europe.

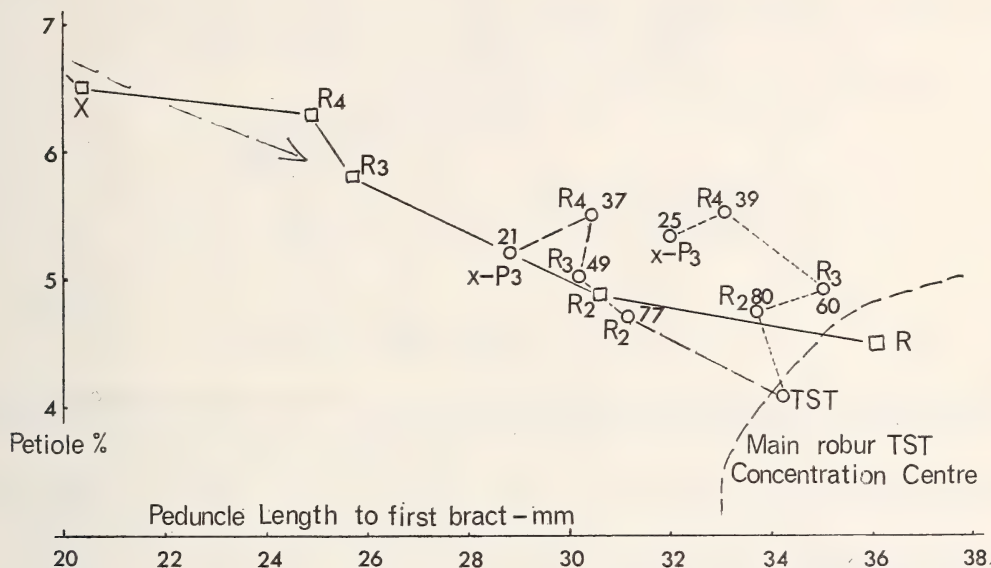


Fig. 7. Mean values for Petiole % and Peduncle Length by combination classes for (1) the Scottish data (squares); (2) English collections in Table 4 (circles right); (3) the latter with omission of abnormally high values (circles left).

QUERCUS ROBUR IN YUGOSLAVIA

Enough had been seen of *Q. robur* on the Continent to know that it could be as variable there as it was in Britain. *Q. robur* and *Q. petraea* are almost sympatric in Europe and are thought to have maintained their identity for two reasons (a) partial intersterility and (b) fairly distinct ecological requirements. In particular *Q. robur* tolerates a considerable degree of waterlogging and even flooding, while *Q. petraea* is oxyphilic and is excluded from such sites (Jones 1959). Of the flood-plain oak forests of the Danube and its tributaries the ancient Slavonian Forest is possibly the most famous; in it *Q. robur* is reputed to reach its finest development (see, for example, Silvy-Leligois quoted by Jones on p. 172). Glavac (1961) and Dekanic (1962) provide excellent accounts of the phytosociology and ecology of typical flood-plain *Q. robur* forest near Lipovljani on the River Sava (a remnant of the once more extensive Slavonian Oak Forest). The oak-dominated areas belong to the Association *Querceto-Genistetum elatae* Horv. and the only other oak in the vicinity is *Q. cerris* L. which belongs to a different Section of the genus *Quercus* and is not recorded as hybridizing with members of Section *Robur*. This therefore seemed a promising region in which to look for good *robur* populations and a visit was arranged in 1963. Fig. 8 shows the location of the population samples which are also listed in Table 5. Vratina Stara is an oak stand over 300 years old, now very open. Požeravač is park-like, reputedly remains of the original forest of that part of the River Morava flood-plain, and consists of trees over 250 years old. Of the second-growth stands sampled the youngest was 90 years old



Fig. 8. YUGOSLAVIA—location of populations sampled.

TABLE 5. Range and frequency of secondary character combinations in the Yugoslav flood-plain samples.

No.	Locality	Degrees of difference from the robur TST										Total	HI						
		0				1				2				3					
		R	R2	R3	R4	R	R2	R3	R4	R	R2			R3	R4	R	R2	R3	R4
1.	Strupnički Lug	..	..	..	..	..	4	6	7	3					20		1.45		
2.	Turopolški Lug	..	..	..	..	..	6	3	6	4					19		1.42		
3.	Lipovljani	..	..	..	..	..	6	5	5	2					18		1.16		
4.	Domoskela	..	..	..	..	..	3	4	2	1					10		0.90		
5.	Vratična Stara	..	..	..	..	..	10	10	2						22		0.64		
6.	Klještavića	..	..	..	..	..	7	10	2						19		0.74		
7.	Cret	..	..	..	..	..	8	5	5	3					21		1.14		
8.	Požeravać	..	..	..	..	..	18	21	9	6					54		1.06		
Totals		..	..	..	..	..	62	64	38	19					183		1.08		
Per cent.		..	..	..	..	..	34	35	21	10									

(Turopolški Lug) and all were reputed to have been obtained from natural regeneration alone. If the flood-plain is defined as the area regularly inundated each spring then Nos. 1, 2 and 8 were near its margin. Strupnički Lug was the only site where *Q. petraea* occurred nearby—less than a mile away on a low ridge—and Klještavića was the only alkaline site—a pH of about 8 as compared with pH 5–6 in the other areas.

Fig. 9 shows the distribution of the Primary Character values. Note that the concentration centre for all values is here the same as that for the *Q. robur* TSTs only and that it lies at the end of the Introgression Path.

DISCUSSION OF THE YUGOSLAVIAN RESULTS

The Heterogeneity Indices are high, not because there is a wide range of combination classes (R to R4 only) but because of the small proportion of TSTs (34 per cent.): nevertheless the English indices, ranging from 0.92 to 2.21, were considerably higher on the

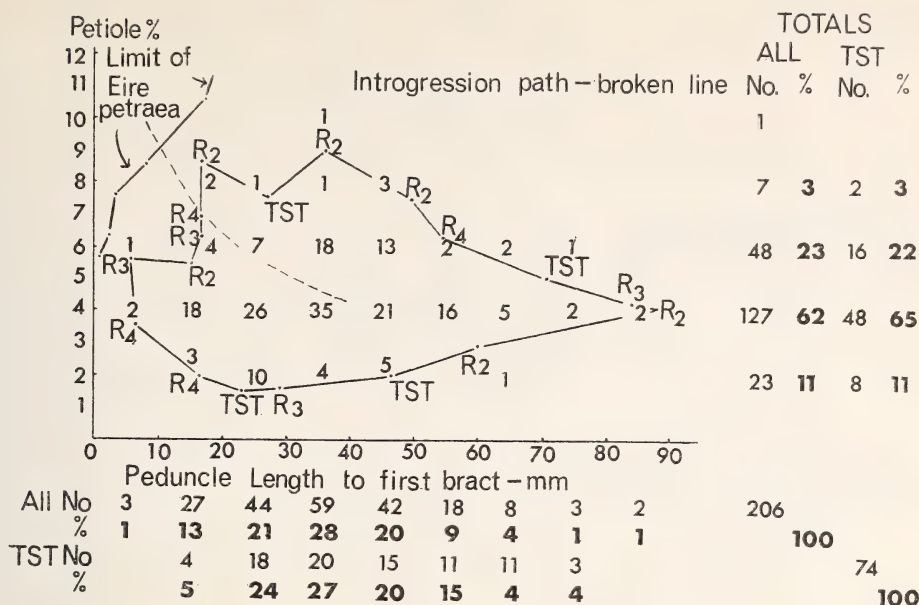


Fig. 9. Distribution of combined Petiole % and Peduncle Length values for all Yugoslav *robur* collections.

average (Table 5). Fig. 9 shows a very wide scatter of values but no obvious concentration of values along the *robur-petraea* introgression line.

In Fig. 10 the distribution patterns for various components are shown as simplified scatter diagrams. The first four diagrams show that divergence from the *Q. robur* TST is associated with a reduction in peduncle length but there is no tendency for the petiole per cent. to rise at the same time. The variability cannot therefore be ascribed to introgression by a species like *Q. petraea* which has high petiole per cent. and low peduncle length values. In the TST diagram there is a suggestion of a lower concentration centre (peduncles 20–25 mm to first bract). A lower concentration centre appears more markedly in the diagram for specimens with pubescent peduncles; but it is now in the 15–20 mm range. Such a pattern could have arisen through introgression by a species with short petioles like *Q. robur* but with short pubescent peduncles. In the TST diagram there is also the suggestion of an upper concentration centre in the range 55–60 mm for peduncle length to first bract. This could indicate introgression by a species with short petioles like *Q. robur* but longer peduncles. There are, in fact, two species of oak in this region which conform to these specifications, namely, *Q. conferta* Kit. and *Q. pedunculiflora* K. Koch; both belong to Section *Robur* of the genus and presumptive hybrids of both with *Q. robur* have been found in Bulgaria (K. Kostov, personal communication, 1964). One explanation of the great variability of *Q. robur* in Yugoslavia and elsewhere may lie in its introgression by a number of related species. There is no evidence of currently active introgression. If it occurred, the most likely period would be during the enforced migrations caused by the Pleistocene glaciations of northern Europe. The theory is an attractive one in that it could be held to account for several characters which appear occasionally in *Q. robur* but more consistently in related species—for example, forms with (a) very long peduncles or secondary leaf lobing (*Q. pedunculiflora*), (b) very deep regular lobing (*Q. conferta*), (c) abaxial stellate pubescence (most members of Section *Robur*).

For the present the Yugoslavian collections merely indicate that *Q. robur* is, or has become, an exceedingly variable species.

	Petiole %													Totals
R — <i>Robur</i> TST	8				1					1				2
	6				2	1	3	4	4	1			1	16
	4		1	2	6	5	5	8	2	4	4	6	2	48
	2			1	2	1				1	3			8
														74
R2—specimens showing one difference	10								1					1
	8		1						1	2				4
	6		1		4	2	5	3	2			1	1	19
	4		1	5	5	2	6	8	6	2	3	2	1	42
	2				1	3	1	1				1		7
														73
R3—specimens showing two differences	6		1	3					3	1				8
	4			3	2	1	4	3	4	3			1	24
	2			1		2		2		1				6
														38
R4—specimens showing three differences	8				1									1
	6							1	1	2			1	5
	4		2		4	1	2		1	1			1	12
	2				1		1							2
														20
All specimens with pubescent peduncles	8				1					1				2
	6		1	2		1	1	5	3	2		1		16
	4		2	3	8	4	5	5	8	6	4	2	1	50
	2				2	1	5		3	1				12
														80
	0 10 20 30 40 50 60 70 80 90													
	Peduncle to first bract—mm.													

FIG. 10. Simplified scatter-diagrams for various components of the complete Yugoslav data.

GENERAL DISCUSSION AND CONCLUSIONS

The pattern of distribution of petiole-peduncle values is very similar in outline in the Yugoslav and English *Q. robur* collections (cf. Figs. 6 and 9); equally the pattern for the TSTs only in Yugoslavia, England and Scotland is very similar (Fig. 11). All show a modal value for Petiole per cent. of between 4 and 5 and all are bi-modal for peduncle length, with peaks at 20–30 mm and around 40 mm; the Yugoslavian and English diagrams also have suggestions of a third peak in the upper fifties. In addition each collection is characterized by a few non-TST specimens with abnormally long peduncles. If Yugoslavian populations were transferred to south-east England and subjected to a little secondary introgression from *Q. petraea*, they would probably be indistinguishable from present populations in that part of England. The scale of introgression by *Q. petraea* would be roughly that

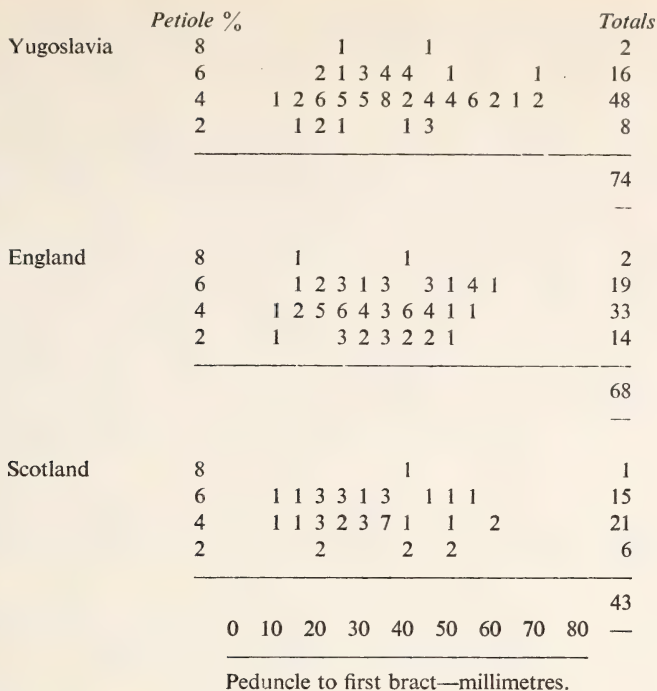


Fig. 11. Scatter diagrams for the *robur* TST in various collections.

suggested by Jones (1959, p. 198) in southern England, with a slight increase northwards into Scotland. It seems reasonable to conclude that the *Q. robur* that arrived in post-glacial Britain was very like present-day *Q. robur* in Yugoslavia; that it was even then a very variable species; and that it must be accepted now as a species very difficult to define.

In the previous paper the prevalence of *Q. petraea* forms of pubescence on the leaves and peduncles of Scottish hybrid specimens was tentatively ascribed to partial dominance by *Q. petraea*. It is now apparent that *Q. robur* already has some genes for such pubescence and there is no reason to believe that these characters are other than under polygene control.

It should be emphasized that none of these major collections were planned as representative samples of oakwoods in the regions concerned. Generally the aim was either to determine the range of variation in what were thought to be the most 'natural' woodlands (Irish and earlier Scottish collections) or to sample woodland reputed to consist of good *Q. robur* or *Q. petraea* (Eire, Yugoslavia, southern England and the later Scottish collections). Infertile specimens, which were ignored in the general analyses, are more likely to be hybrids than fertile specimens in areas where current introgression has been demonstrated (Cousens 1963, Table 6). Mixed populations have also been ignored. Overall there has been a bias against demonstrating the full extent of any introgression.

There seems to be a cline of increasing introgression northwards in England and Scotland. Planting of *Q. robur* in Scotland may explain the difference between Irish and Scottish *Q. petraea* populations but planting has been equally prevalent in England and another explanation is required for the increasing introgression northwards. Fig. 12 contrasts the extremes as exemplified by samples from Kent and the Central Highlands of Scotland; both have a long history of intensive forest management.

In Ham Street Nature Reserve *Q. robur* and *Q. petraea* are both reasonably good as now redefined (Table 6), while in the Loch Katrine sample a majority of the forms were intermediate and there were no TSTs. It has been suggested, but not demonstrated, that cross-pollination should occur more frequently in Scotland because the growing season is

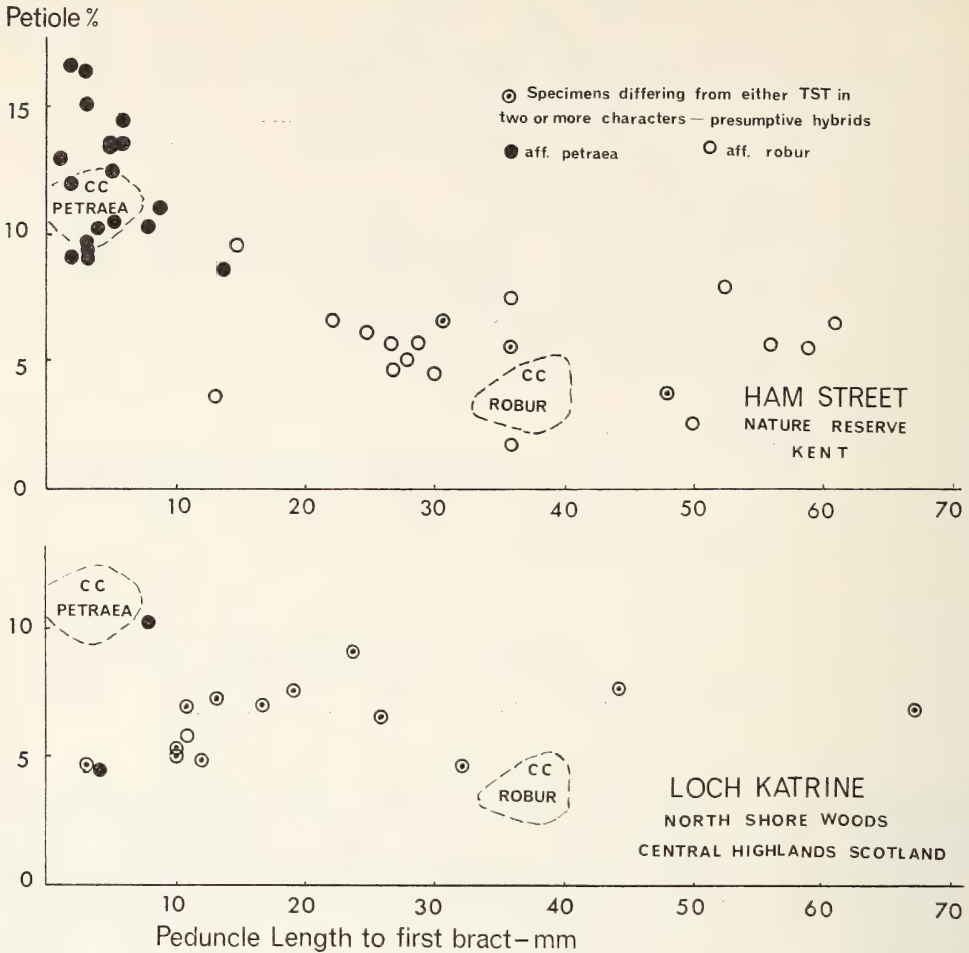


Fig. 12. Scatter Diagrams for samples from two woods with a long history of intensive forestry management, one from south-east England, the other from Scotland.

shorter and there is greater overlap in the flowering times of *Q. robur* and *Q. petraea*. Such an hypothesis is an essential part of any explanation of the increased introgression northwards. By itself it cannot explain the striking increase in the introgression of *Q. petraea*, considering the low level of interfertility found by Pyatnitski and Dengler under the optimal conditions of artificial cross-pollination. However, their crossing experiments are not necessarily conclusive; a few selected individuals of each species only were concerned and in one year the *robur* ♀ × *petraea* ♂ cross reached a level of 15 per cent. interfertility. If *Q. robur* is such a variable species, the degree of interfertility with *Q. petraea* may be very variable too. Crossing trials with a much wider range of parental genotypes would clear up this point. Some indirect evidence might be obtained by comparing the degree of introgression of *Q. petraea* in Devon and Wales with that in Scotland.

Assuming, then, that rather more first generation hybrids are likely to appear in the north wherever *Q. robur* and *Q. petraea* occur together, it is obvious that the extensive planting of *Q. robur* in *Q. petraea* areas (bringing the species together) and intensive coppice management (shortening the generation time) could have greatly accelerated the introgression of *Q. petraea* by *Q. robur*. *Q. petraea* was seldom used for planting and this factor alone is sufficient to account for the great difference in degree of introgression of

Q. robur and *Q. petraea* in Scotland. The very considerable introgression of *Q. robur* by *Q. petraea* in Scotland previously postulated (Cousens 1963) must now be considered illusory; most of the heterogeneity in *Q. robur* forms was probably there before the species arrived in Scotland.

The validity of most of these conclusions could be checked by crossing experiments but as the generation time would be of the order of 10 to 20 years at least, it would be a very long time before the genetic basis of variability could be established.

Table 6 shows the range of variation observed in the Yugoslavian *Q. robur* and Irish *Q. petraea* populations sampled. Ranges overlap for all the selected diagnostic characters but the species are separate entities in terms of petiole per cent. and peduncle length combined (see Fig. 9). Using these definitions it should be possible to diagnose good populations of either species. Individual trees, however, can only be identified as good *Q. robur* or *Q. petraea* when all four secondary characters are typical and petiole and peduncle values lie within the ranges shown in Fig. 9; this means, for example, that only about 25 per cent. of Scotland's oaks can be positively identified.

ACKNOWLEDGMENTS

I am indebted to all those who assisted me in planning or making the collections; to many members of the Forestry Division of the Department of Lands in the Republic of

TABLE 6. The observed range of variation of selected diagnostic characters for *Q. robur* (Yugoslavian collections) and *Q. petraea* (Irish collections).

<i>Diagnostic character</i>	<i>Q. robur</i>	<i>Q. petraea</i>
<i>Peduncle length to first bract—</i> mm.	(6)—15—22—38—60—(88)	0—1—4—(20)
Total Peduncle Length	14—35—55—80—(123)	1—10—26—(63)
<i>Petiole % of leaf length</i>	(1)—2—4—6—(9)	(5½)—9—12—15—(20)
<i>Auricle Type*</i>	Medium— <i>Strong</i>	Nil— <i>Weak</i> —(Medium)
<i>Stellate Pubescence</i> abaxially on lamina (small, prostrate) or along midrib (large, erect)	<i>Both types absent</i> 8%—one or both types represented by a few stellate hairs 1%—small but obvious amount of both types	<i>Both types well developed</i> 8%—one or both types deficient 1%—both absent
<i>Peduncle Pubescence</i> below first bract—in vicinity of first bract if peduncle very short (recorded from July onwards)	<i>Glabrous or with a few scattered hairs</i> (equally common) Forms with general pubescence may reach 30% in some populations	<i>At least patches of dense pubescence</i> 4%—only a trace of pubescence Less than 1% glabrous
<i>Peduncle Diameter</i> at narrowest point below first bract—if elliptical, mean of two diameters	<i>1 mm or less</i> 11%—c. 1.5 mm Less than 2% reaching 2 mm	<i>2 mm or more</i> 20%—c. 1.5 mm Less than 7% as little as 1 mm

Notes. Modal values and commonest forms in italics

Parentheses indicate fairly isolated extreme values.

Peduncle characters from longest peduncle on specimen.

Leaf characters from two mid-shoot leaves on a representative sun-shoot taken from the lower crown on the south or south-east side of the tree.

* For a description of auricle types see Cousens (1962).

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THE DISTINGUISHING CHARACTERS AND GEOGRAPHICAL DISTRIBUTIONS OF *ULEX MINOR* AND *ULEX GALLII*

By M. C. F. PROCTOR

Department of Botany, University of Exeter

ABSTRACT

The lengths of the petals and calyx provide the most satisfactory characters by which *Ulex minor* and *U. gallii* may be separated. Standard-length rarely exceeds 12 mm. in *U. minor*, and is rarely less than 12 mm. in *U. gallii*; population means for calyx-length are less than 9.5 mm. in *minor* and greater than 9.5 mm. in *gallii*. Calyx-length remains virtually unchanged from flowering time to the dehiscence of the fruits, and is the most generally useful diagnostic character. All other characters examined show greater overlap between the species. Both species are genetically variable and very plastic in vegetative characters, which are consequently of little use for identification.

The two species are almost perfectly vicarious in their distribution within the British Isles; their main areas are separated by a line running roughly through Weymouth, Salisbury, Marlborough, Oxford and Sheffield—*U. gallii* to the west of the line, *U. minor* to the east.

Ulex minor and *U. gallii* are not generally regarded as critical species. Nevertheless, they are widely misunderstood. Most Floras agree that *U. gallii* is a larger plant than *U. minor*, and quote a number of supposedly qualitative characters separating the two species. But there is little agreement beyond this, and different floras emphasize different diagnostic characters and give widely differing figures for such characters as plant size, spine length and seed number. The problem arises because most of the distinguishing characters are quantitative, while the species are highly plastic.

There is rarely serious difficulty in distinguishing either species from *U. europaeus*. That species has very much hairier calyces, so that the young buds have a conspicuous brown furry covering, bracteoles considerably wider than the pedicel, and primary spines which often bear branches (and flowers) a considerable distance from their bases. *U. europaeus* usually starts to flower in early autumn, bearing flowers sporadically throughout the winter whenever the weather is mild, and has its main flowering season from March to May. The other two species, by contrast, flower in late summer and early autumn, and are past their best by the end of October, though the odd flower may straggle on until New Year. Ecologically, too, *U. europaeus* is quite distinct. It is a plant of poor pastures, roadsides, scrub, wood margins, sea cliffs, etc., on poor soils, often where there has been some disturbance of the habitat. It is commonest on more or less acid soils, though it occurs even on thin rendzina soils over chalk and limestone. It is seldom found in quantity, or growing with any degree of luxuriance, in the extensive areas of undisturbed heath which are the most characteristic habitat of *U. minor* and *U. gallii*.

My own difficulties in placing many plants of *U. minor* and *U. gallii* convincingly in one species or the other prompted the investigation of which the results are set out in this paper. In the late summer and early autumn of 1958 I collected samples of the two species from a number of localities scattered over the south of England: usually single flowering shoots from ten individual plants in each population. With some additional samples collected since, these have provided the data on flower dimensions given below. The samples are small, and I emphasize that in collecting them I was on the look-out for intermediate and 'difficult' plants and populations. In the event, they proved more than adequate to show that the two species are quite clearly distinct. This provided a basis on which to evaluate the other characters of the species, both in the field and in the herbarium, and to re-examine their geographical distribution in the British Isles.

THE CHARACTERS

(a) Flower size

One representative flower from each of the flowering shoots collected was dissected, and the petals and calyx mounted under cellulose tape on 3 × 1 in. glass slides. The histograms (Fig. 1) show that, if the data are considered as a whole, the measurements for

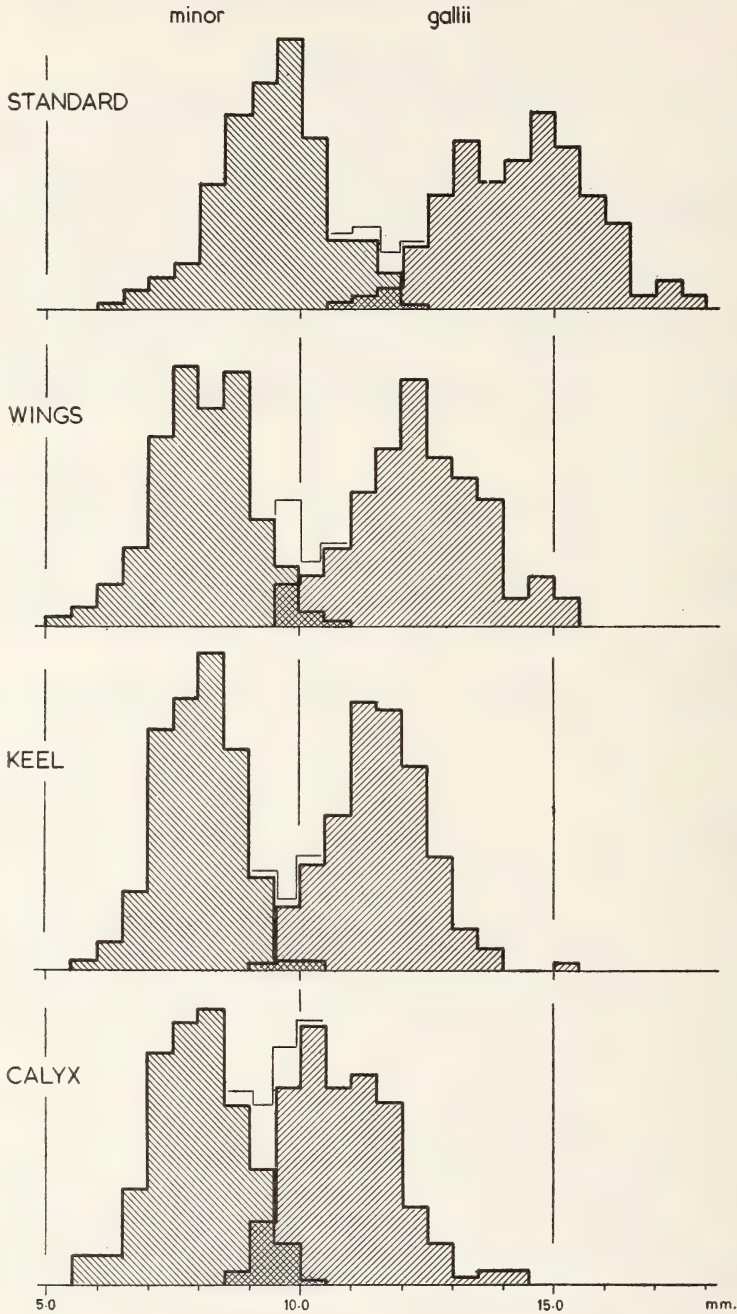


Fig. 1. Frequency histograms of petal and calyx lengths of *Ulex minor* and *U. gallii*; 1958 and later material. The thin line above the overlapping portions of the histograms indicates the total frequency for the two species combined.

any of these flower parts show a clearly bimodal distribution. The two peaks for standard-length are almost completely separated; intermediate values occur with greater or less frequency in the other three cases. However, if population means are considered rather than measurements of individual flowers, the populations fall quite sharply into two groups, whichever flower part is measured (e.g. calyx, Fig. 2). Mean standard-lengths for the populations are plotted on a map of the south of England in Fig. 7. Populations with a mean standard-length less than 12 mm are confined to an area from Dorset eastwards; to

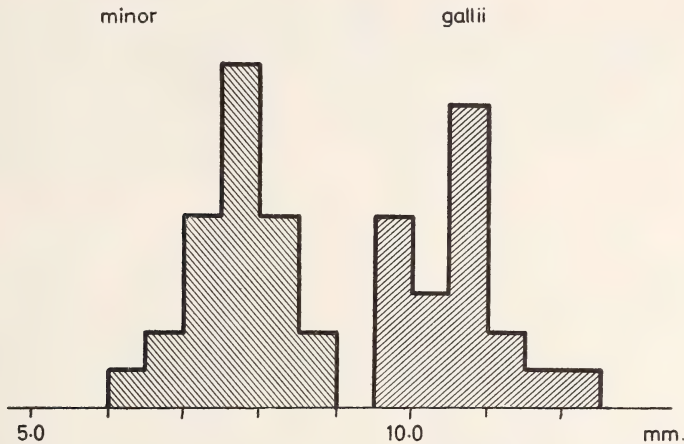


Fig. 2. Frequency histograms of mean calyx length in populations of *Ulex minor* and *U. gallii*; same material as Fig. 1 (usually 10 measurements per population).

the west all populations have a standard-length of 12 mm. or more. The large-flowered western plant is *U. gallii*, while the small-flowered eastern plant is *U. minor* (Fig. 3).

U. gallii usually has the wings rather strongly curved, and longer than the keel, though occasional plants are found with them shorter. In the collected samples the mean length of the wings is nearly 1 mm. longer than the keel. *U. minor* is more variable in these characters. In some populations the wings are nearly straight, and regularly shorter than the keel. On the other hand, there are many populations of undoubted *minor* which have the wings strongly curved and regularly longer than the keel. Taking the collected samples of *minor* as a whole, the mean lengths of wings and keel scarcely differ.

(b) Flower colour

The population samples collected in 1958 were scored for flower colour by matching the flowers with the standard tints in the R.H.S. *Horticultural Colour Chart* (British Colour Council 1938). Although there is considerable overlap the two species are fairly sharply separated (Fig. 4), with aureolin and lemon yellow the most frequent colours for *U. minor*, and buttercup yellow and indian yellow the most frequent colours for *U. gallii*.

(c) Bracteole size

Rothmaler (1951) considered the size of the small bracteoles just below the calyx to be the best critical character separating the two species. In the material I have examined the bracteoles are usually about 0.6–0.8 mm. long $\times$ 0.4–0.6 mm. wide in *minor*, and 0.5–0.8 mm long $\times$ 0.6–0.8 mm. wide in *gallii*. They seem to provide a fairly satisfactory separation between the two species, but not easy characters to work with, as they are small and often thickly covered with hairs which make accurate measurement difficult.



Fig. 3. Flowers of *Ulex minor* (left) and *U. gallii* (right), $\times 2.5$. Flowers of *U. minor* often have considerably longer wings than the specimen drawn.

(d) Fruiting characters

Pod measurements and seed counts from a number of localities are summarized in Fig. 6. Calyx length still remains a reasonably satisfactory distinguishing character, with the population means for the two species falling into two quite clear groups, though individual calyx measurements show considerable overlap. Pod length and breadth give a less satisfactory separation, and seed and ovule number none at all. There are indications that *gallii* averages slightly more seeds per pod than *minor*, but seed number is very variable in both species. It is interesting that ovule number shows even less difference between the species, and no less variation.

It is often said that the pods of *U. gallii* dehisce in spring while those of *U. minor* persist for almost a year. The seeds ripen at much the same time in both species (May), and the time of dehiscence probably varies a good deal with weather conditions in different years. Undoubtedly the pods of *U. gallii* do tend to dehisce somewhat earlier, probably because of their rather larger and firmer valves, but there is not a clear-cut difference between the species in this respect.

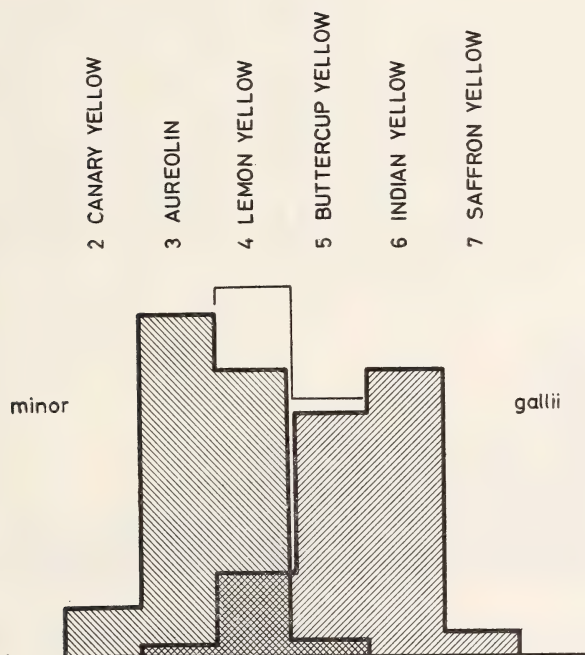


Fig. 4. Frequency histograms of flower colour, scored on RHS chart, of *Ulex minor* and *U. gallii*. In most cases the flower colours were close to the saturated hues; for convenience of representation in the few instances in which the flowers departed markedly from saturation 6/1 has been regarded as 6, and so on. 1958 material.

(e) Size of vegetative parts

Both species are extremely variable in size. In areas of poor short heath *U. minor* may grow as procumbent mats barely 5 cm. high; in roadside scrub and around wood margins in the New Forest and the Isle of Wight I have seen it as high as 1.5 m. *U. gallii* is a larger plant. Under poor conditions it may be only 10 cm. high, while bushes on neighbouring roadsides grow to 1–1.5 m.; old plants in scrub or open woodland may reach 2 m. The variation is partly genetic and partly due to plasticity. Plants of *U. gallii* from an exposed hillside at Mynytho in the Llyn peninsula grown for five years in Exeter reached only

25 cm., while plants from a heath near Woodbury, Devon, reached 100 cm.; *U. minor* from near Wareham formed a sprawling mat no more than 10 cm. from the ground while material of the same species from the New Forest reached 95 cm. The primary spines are also very variable in length, with a large overlap between the two species; Fig. 5 shows the distribution of spine length in the material used for the flower samples. The two species show widely differing means, but a histogram of the combined data is not convincingly bimodal.

Curved primary spines are often given as a character for *U. gallii*. It is true that *U. gallii* usually has rather strongly curved spines, especially in well-grown material, while the most poorly-grown (and to most people most typical) *minor* usually has straight spines. But *gallii* often has straight spines, and well-grown *minor* often has them strongly curved. The character is least helpful in those plants which are most likely to be difficult to determine. Much the same applies, *mutatis mutandis*, to the rigidity of the spines of *gallii*, which Tutin (1962) uses as a key character.

(f) Other characters

A number of other qualitative characters have been suggested. *Red veining* of the standard has been said to be characteristic of *gallii*. I have never observed this in any of the populations of *gallii* I have examined in the field. The veins of the petals do tend to go brown in badly dried specimens, and this affects the larger flowers of *gallii* more than the small flowers of *minor*. I assume that the character was drawn from herbarium material in which some specimens were affected in this way. The calyx teeth are sometimes described as 'connivent' in *minor* and 'spreading' in *gallii*. I am not clear what is meant by this. The calyx is deeply divided into an upper and a lower lobe. The flower as a whole opens more widely in *gallii* than in *minor*, especially after pollination. The individual calyx teeth at the ends of the lobes seem to offer no taxonomically useful characters.

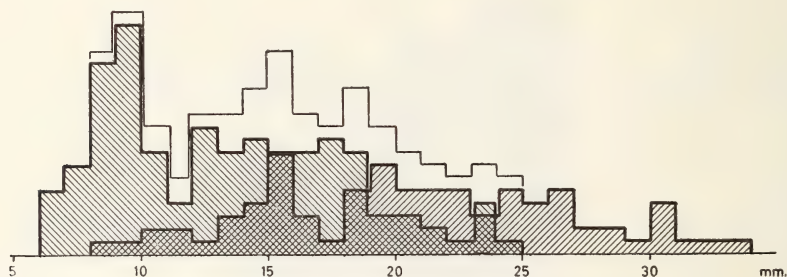


Fig. 5. Frequency histograms of the length of the longest primary spine on the flowering shoot of *Ulex minor* and *U. gallii*; 1958 material. Conventions as in Fig. 1.

DISCUSSION OF THE CHARACTERS

The characters considered above are all correlated, as might be expected if we are dealing with two distinct species. The best diagnostic characters are those that divide the populations most clearly into two groups, in this case the measurements of the flower parts. Standard-length is the easiest and most effective; measurement of the standard of a single flower will almost always place a plant correctly. Unfortunately its use is confined to the relatively short flowering season. Calyx-length shows more overlap, and it may be necessary to measure a number of calyces to arrive at a certain identification, but it has the great advantage of being a character which is available at almost any time of year. Mean calyx-length of 9 mm. or less indicates *minor*; a length of 10 mm. or more indicates *gallii*. There is virtually no change in calyx-length from flowering time to the dehiscence of the pods nine or ten months later, and calyces often persist even longer than that.

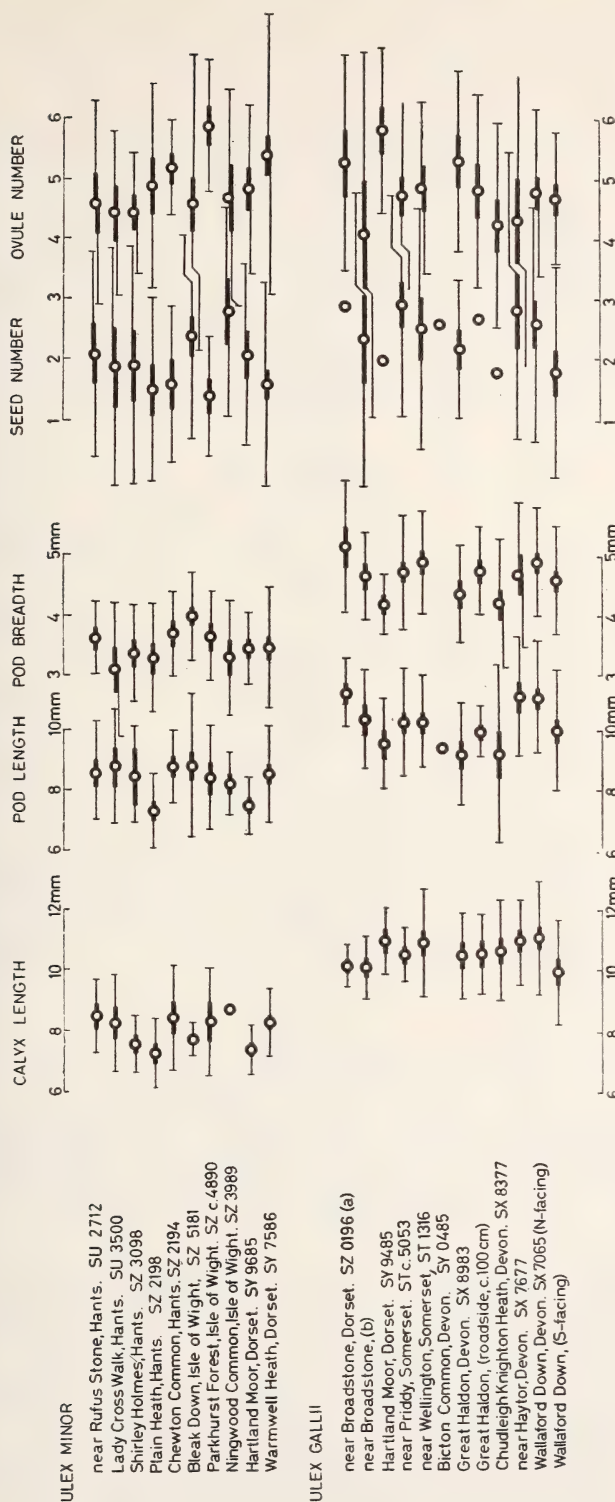


Fig. 6. Calyx and fruiting characters of *Ulex minor* and *U. gallii* in early summer. Circles indicate population means; thick bars are drawn a distance equal to twice the standard error of the mean, and thin lines a distance equal to twice the standard deviation on either side of the mean value.

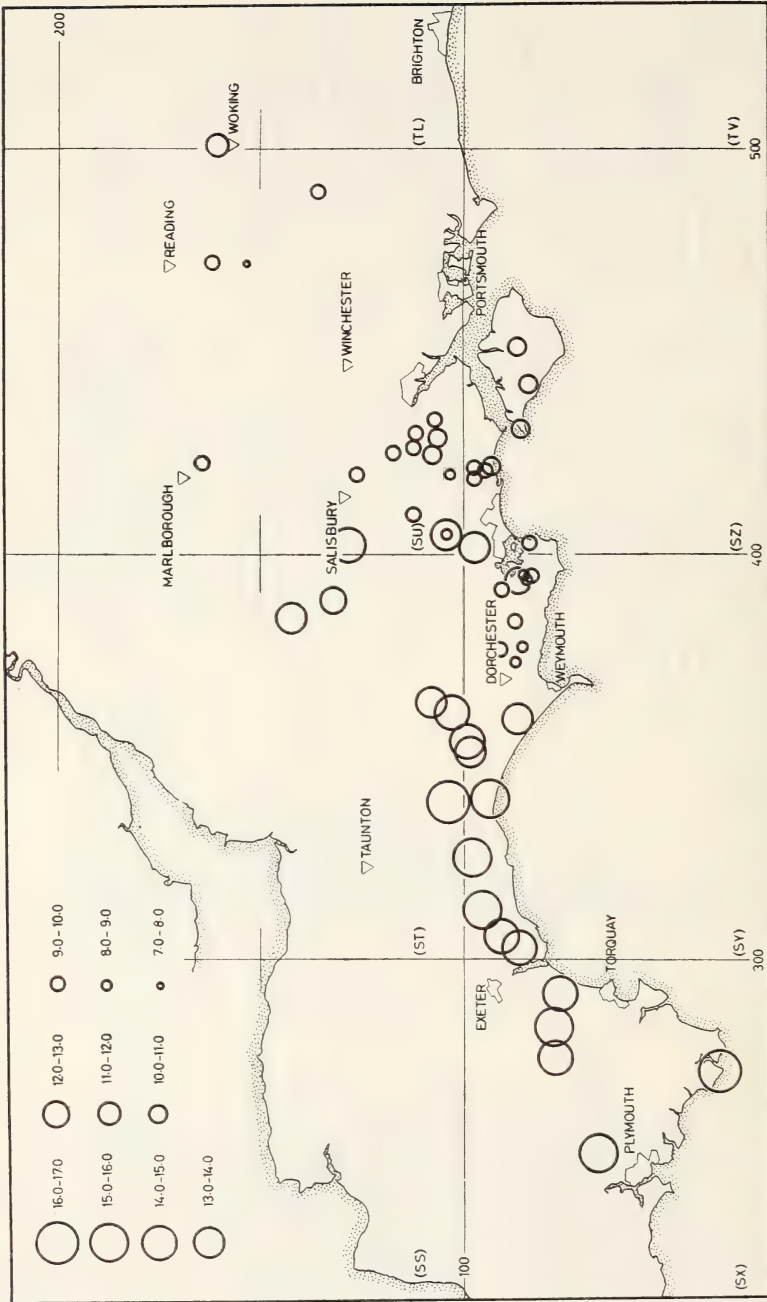


Fig. 7. Distribution of mean standard-length in populations of *Ulex minor* and *U. gallii* in southern England. Populations with mean of 12.0 mm. or more are *U. gallii*, those with means less than this are *U. minor*. Same material as Fig. 1.

GEOGRAPHICAL DISTRIBUTION

There has never been any question that *U. gallii* is a western species by contrast with *U. minor* which has its headquarters in south-east England. The striking fact that emerged in the course of the present work was the remarkable clarity of this pattern; in Britain the two species are almost perfectly vicarious. In the course of my field work this became very obvious in Dorset, where the areas of the two species are in contact. *U. minor* is abundant in the heaths on Eocene sands and gravels in the Poole basin, where *U. gallii* is very local and sporadic, and—apart from a substantial outlying area north-west of Bournemouth—almost always on roadsides. But farther west, on clay-with-flints over the chalk and on Cretaceous and Jurassic sands, *U. minor* is apparently completely absent, and every population I examined was *U. gallii*. In Hampshire and Wiltshire too, apart from one or two isolated localities west of Salisbury, *U. minor* seems to extend westwards only as far as the western limit of the Tertiary beds. Field records and herbarium material show that the main areas of the two species are separated by a line running roughly through Weymouth, Salisbury, Marlborough, Oxford and Sheffield (Fig. 8).

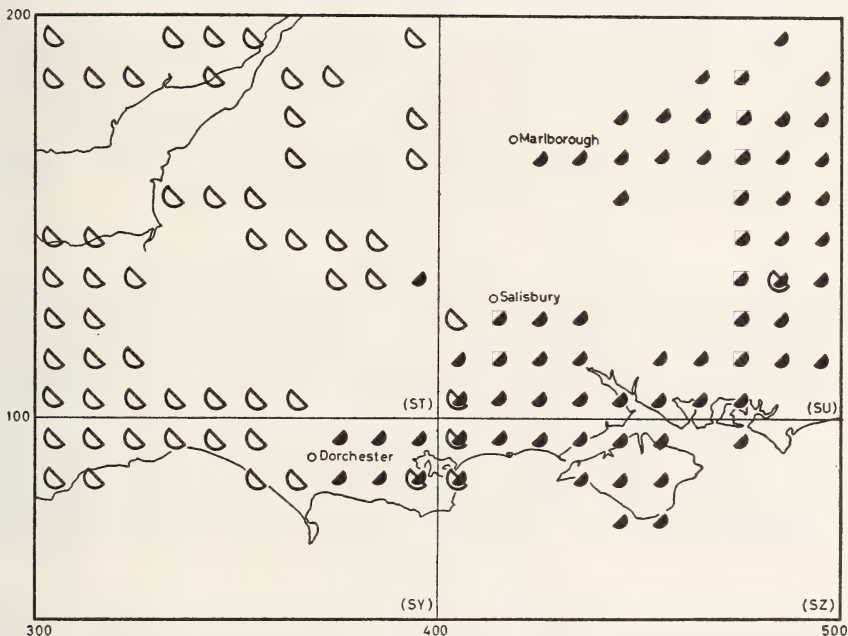


Fig. 8. 10 km. distribution of *Ulex minor* and *U. gallii* in the area of contact of the two species in southern England. All marginal and outlying records for both species are based on herbarium specimens or field records which I have been able to verify personally. Records of the two species within their main areas have in general been accepted without question.

Most of the apparent anomalies to this pattern that I encountered turned out to be due to errors in identification. Thus all the specimens I have seen labelled *U. minor* from Wales and Cornwall have been dwarf forms of *U. gallii*, usually from exposed places near the sea. Large bushes of *U. minor* have often been mistakenly named *U. gallii*; with good *gallii* for comparison there is seldom any difficulty in naming them correctly.

However, both species have outliers within the area of the other. *U. gallii* has a substantial detached area in a narrow strip along the coast of Norfolk and Suffolk; farther inland *U. minor* is apparently the predominant species in the heaths. *U. gallii* appears to have a further small outlier in Kent. Apart from these outliers, small colonies of *U. gallii* occur in a good many other localities, usually along roadsides and in other disturbed

habitats where it is probably a relatively recent arrival. *U. minor* has several stations near Carlisle. At the two I have visited, Sowerby Wood (NY c.365523) and Hosket Hill near Kirkcandrews-upon-Eden (NY c.347575), *U. minor* is growing in relic areas of sandy heath very reminiscent of south-east England, and *U. gallii* is not present in the immediate vicinity. Good specimens of *U. minor* also exist from Slieve Donard, Co. Down (S. A. Stewart, 22 July 1879, DBN) and from between Holy Loch and L. Eck, Argyll (Wm. Neathead (?), 1 September 1884, BM). I have not visited either locality and both need confirmation; a note on the Argyll sheet suggests that the plant—which was apparently present in quantity—may possibly have been introduced from the south of England with rhododendrons and rare conifers.*

The clear geographical separation of *U. minor* and *U. gallii* in England parallels strikingly the situation demonstrated in north-west France by Des Abbayes & Corillion (1949) and Corillion (1950a, 1959). There, *U. gallii* is abundant to the exclusion of *U. minor* in Brittany west of a line roughly from Dinard to Vannes, and in a small area at the tip of the Cotentin peninsula, with only small outliers farther east. *U. minor* is widespread outside this area in western and central France. In the Basque country and in north-west Spain there are indications of a repetition of a similar pattern.

Perhaps the most likely explanation of this remarkable distribution pattern is that the two species are so closely similar in ecological requirements that they are competing for the same ecological niche, and cannot coexist (except transitorily) in the same vegetation. With this in mind, it would be worth making systematic observations over a period of years in localities where the two species do occur together. At the moment it is hard to say whether the pattern is determined by present conditions of soil or climate, or whether it reflects past conditions, and has been 'frozen' by the fragmentation of heathland.

HYBRIDIZATION

Corillion (1950b) reported hybrids between *U. minor* and *U. gallii* from heaths in the zone of contact of the two species in Brittany†. As far as I know, this hybrid has never been reported from England (see Millener, 1952), and hybridization does not appear to enter as a complication into the problem of distinguishing the two species. It is possible that some hybridization may take place where the two species meet; I have not looked critically for evidence of it. Hybrid individuals might be expected to show intermediate characters in the size of flowers and other parts—perhaps with some modification due to hybrid vigour. As *U. minor* has $2n = 32$ and *U. gallii* $2n = 80$ (Castro 1941, 1943) the most satisfactory evidence of hybridity would be provided by chromosome number, and perhaps sterility.

ACKNOWLEDGMENTS

I would like to thank all the correspondents, too numerous to mention individually, who so readily answered my questions about *Ulex* specimens and localities.

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* The occurrence of the species in the following vice-counties may be taken as satisfactorily established:
U. minor: 7–17, 20–28, 32, 70.

U. gallii: 1–9, 15–17, 25, 27, 34–53, 55–60, 63–65, 69–73, H 1–13, 15, 16, 19–21, 27, 32, 37, 38.

Confirmation of either identification or status in other vice-counties is desirable.

† See also Lambinon, J. (1962). Note sur les *Ulex* du Massif Armoricaïn. *Lejeunia* **NS 9**, 64–66.

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DIPLOIDS IN THE GENUS *COCHLEARIA*

By J. J. B. GILL

Department of Genetics, University of Liverpool

ABSTRACT

Three new counts of diploid *Cochlearia* are reported. (*C. aestuaria* (Lloyd) Heywood $2n = 12$, *C. alpina* Wats. $2n = 12$ and *C. arctica* Schlecht $2n = 14$.) It is suggested that the previous count for *C. alpina* of $2n = 28$ is wrong and was probably made on a mis-identified specimen of *C. officinalis* L. containing accessory chromosomes.

INTRODUCTION

The chromosome counts in the genus *Cochlearia* have been reviewed recently by two authors (Saunte, 1955, and Löve & Löve, 1961). Both these reviews show the genus to consist of polyploid series based on the numbers $x = 6$ and $x = 7$.

The $x = 6$ series contains the diploid ($2n = 12$) *C. pyrenaica* DC., the tetraploid ($2n = 24$) *C. officinalis* L., the hexaploids ($2n = 26$) *C. micacea* Marshall and *C. polonica* Borb. and the octoploid ($2n = 48$) *C. anglica* L. Decaploids ($2n = 60$) ascribed to *C. anglica* have also been reported (Lövkvist, 1963 a & b). In the $x = 7$ series there have been reported the diploids ($2n = 14$) *C. groenlandica* L., *C. oblongifolia* DC., and *C. scotica* Druce, the tetraploid ($2n = 28$) *C. alpina* Wats. and the hexaploids ($2n = 42$) *C. danica* L. and *C. tatarae* Borb. (For all references except those which are individually noted see Saunte (1955) and Löve & Löve (1961).)

In the course of a cytogenetical investigation of the genus it has been shown that *C. aestuaria* (Lloyd) Heywood and *C. alpina* (Wats.) are diploids of the $x = 6$ series and *C. arctica* Schlecht is a diploid of the $x = 7$ series.

METHOD

The plants were grown in pots in a cold frame and mitotic chromosome preparations were obtained from root tips pre-treated for four hours in a saturated solution of para-dichloro-benzene, fixed in 1 : 3 acetic alcohol, stained by Feulgen's method and squashed in aceto-carmin. Meiotic preparations were made from pollen mother cells fixed in Carnoy's fixative and stained and squashed in aceto-carmin.

In all cases the preparations were made permanent by the dry-ice method (Conger & Fairchild, 1953) but were mounted in Canada balsam instead of euparal.

RESULTS

Seed of *C. aestuaria* was obtained from Galicia in Northern Spain. Only one plant developed from this seed and squashes of root tips from this plant showed it to be a diploid of the $x = 6$ series ($2n = 12$). The somatic chromosomes (Plate 12, A) vary after pre-treatment from $1-2\mu$ in length and all have more or less median centromeres. The longest chromosome forms about 10 per cent. and the shortest about 6.5 per cent. of the total length of the karyotype. The somatic count was verified from PMC squashes which showed the presence of 6 bivalents (Plate 12, B).

Two samples of English *C. alpina* were obtained, one from Malham Tarn Field Centre and the other from Helvellyn. Both samples gave chromosome counts of $2n = 12$ but the populations also contained plants with accessory chromosomes.

Root-tip squashes of 17 plants from Helvellyn showed that 16 of them were normal with $2n = 12$ (Plate 12, C) but one was $2n = 12+1$ accessory with the extra chromosome distinguishable from the other members of the karyotype by its smaller size (Plate 12, D). The normal somatic chromosomes of this material were very similar to those of *C. aestuaria* in that they varied from $1-2\mu$ in length and were more or less metacentric. The longest formed about 11 per cent. and the smallest about 6.5 per cent. of the total length of the



EXPLANATION OF PLATE

- A. Root-tip cell of *C. aestuaria* showing $2n = 12$.
 B. PMC of *C. aestuaria* showing 6 bivalents.
 C. Root-tip cells of *C. alpina* from Helvellyn showing $2n = 12$.
 D. Root-tip cell of *C. alpina* from Helvellyn showing $2n = 12 + 1$ accessory.
 E. PMC of *C. alpina* from Helvellyn showing 6 bivalents.
 G. Root-tip cell of *C. alpina* from Malham showing $2n = 12 + 1$ accessory.
 H. Root-tip cell of *C. alpina* from Malham showing $2n = 12 + 2$ accessories.
 J. PMC of *C. alpina* from Malham showing 6 normal bivalents + paired accessory chromosomes, the accessories being indistinguishable from the normal bivalents.
 K. PMC of *C. alpina* from Malham showing 6 bivalents + 3 non-associated accessories.
 L. PMC of *C. alpina* from Malham showing 6 normal bivalents + 1 pair associated accessories + 1 single accessory.
 M. PMC of *C. alpina* from Malham showing 6 normal bivalents (one slightly out of focus) + 1 pair accessories + 2 non-associated accessories.
 N. Root-tip cell of *C. pyrenaica* showing $2n = 12$.
 O. PMC of *C. pyrenaica* showing 6 bivalents.
 P. Root-tip cell of *C. arctica* showing $2n = 14$.
 R. PMC of *C. arctica* showing 7 bivalents.

All $\times 1,000$.

karyotype. No accessory chromosomes were visible in any of the PMCs of this material examined, all showing six bivalents only (Plate 12, E).

Accessory chromosomes are extremely common in the Malham population and root-tip squashes of 20 plants gave the following results $2n = 12$ (2 plants), $2n = 12+1$ (14 plants) and $2n = 12+2$ (4 plants). The accessories were again distinguishable from the normal members of the karyotype by their smaller size (Plate 12, G and H). The normal karyotype members again varied from $1-2\mu$ in length and had median centromeres. The longest formed about 11 per cent. and the shortest about 7 per cent. of the total karyotype length. Accessories were present in all the PMCs of Malham material examined and varied in number from 1 to 4 per cell. When more than one were present they could be paired so that the accessory pair could not be distinguished from the other pairs (Plate 12, J), not associated at all (Plate 12, K) or associated in such a way that the accessory pair was evident (Plate 12, L and M). Frequently when the accessories were associated their separation at anaphase I was completed before that of the normal pairs.

The somatic chromosomes of all the above collections were compared with those of *C. pyrenaica* from South-West Westphalia (Plate 12, N). No differences were apparent. In *C. pyrenaica* the chromosomes again vary from $1-2\mu$ in length and are all approximately metacentric. The longest forms about 10.5 per cent. and the smallest about 6.5 per cent. of the total karyotype length. No accessories were present in any of the root-tip cells examined and all the PMCs showed only 6 bivalents (Plate 12, O).

Seeds of *C. arctica* were obtained from Leningrad. Cytological examination of the plants developed from this seed showed the plant to be a diploid of the $x = 7$ series. All root-tip squashes gave a count of $2n = 14$ (Plate 12, P). The chromosomes, like those of the $x = 6$ series varied in length from about $1-2\mu$ and all were approximately metacentric. This count was verified from PMC squashes which showed 7 bivalents (Plate 12, R).

CONCLUSIONS

The only previous report of a diploid *Cochlearia* of the $x = 6$ series was that of *C. pyrenaica* (Rohner, 1954). The range of this group is therefore extended. All counts of diploids of the $x = 7$ series come from farther north and it appears that the $x = 6$ diploids have a more southerly distribution than those of the $x = 7$ series.

The count previously reported for *C. alpina* is $2n = 28$ (Crane & Gairdner, 1923). Saunte (1955) has, however, pointed out that Crane & Gairdner's count could be interpreted as $2n = 24+4$ accessories because one of their illustrations shows 4 chromosomes which are smaller than the other karyotype members. If their count is interpreted as $2n = 24+4$ accessories, then their specimen can be recognized as *C. officinalis* with accessory chromosomes. This occurrence of accessory or supernumerary chromosomes in *C. officinalis* is common (Saunte, 1955; Lökvist, 1963a, 1963b). The true identity of Crane & Gairdner's material cannot, however, be determined as they do not give the locality of their collection and it has therefore been impossible to re-collect. It has also proved impossible to trace any of their voucher specimens. It is, however, suggested that the true chromosome count for *C. alpina* is $2n = 12$.

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NATURAL HYBRIDIZATION BETWEEN THE COWSLIP (*PRIMULA VERIS* L.) AND THE PRIMROSE (*P. VULGARIS* HUDS.) IN BRITAIN

By S. R. J. WOODELL
Botany School, University of Oxford

ABSTRACT

A population comprising *Primula vulgaris*, *P. veris* and hybrids between them has been found in a wood near Oxford. In contrast to the common situation, where only first generation hybrids occur, second generation and later segregants, including backcrosses to each species, have been found. In most cases where these two species meet, genetic and temporal barriers to hybridization are reinforced by ecological isolation. In this wood *P. veris* is growing in an atypical habitat in close proximity to *P. vulgaris*. The ecological barriers have thus been lowered, and some hybridization has resulted from the proximity, combined with frequent disturbance. So far as can be seen little introgression has taken place. Thus, although conditions appear to be very favourable for introgression, the two species remain almost entirely distinct.

INTRODUCTION

It has been shown by Valentine (1955) that there is considerable seed incompatibility between *Primula vulgaris* and *P. veris*. The cross between these species is successful only when *P. veris* is used as seed parent, and the maximum germination obtained has been 37 per cent. Woodell (1960) showed that when the cross is made in this direction, seed development is abnormal; the inner integument is hypertrophied, and the endosperm is reduced in quantity, with a concomitant reduction in embryo size. In the reciprocal cross the seeds are large, with a poorly developed integument, a minute quantity of highly aberrant endosperm, and an undifferentiated embryo which dies early.

The F_1 hybrids from the successful cross are moderately fertile; Valentine (1955) found a mean pollen fertility (percentage grains stained in aceto-carmin) of 32 per cent. with a range from 14.5 to 45 per cent. In the wild the number of seeds per capsule in putative F_1 plants is about 20 per cent. of that in the two parents.

Valentine (1955) obtained experimental backcrosses to each parent with a partial restoration of fertility. Germination of the backcross to *P. veris* ranged up to 75 per cent., compared with up to 41 per cent. for the backcross to *P. vulgaris*.

Though the putative F_1 appears in almost all instances where the two species grow near to each other in the wild, it rarely forms more than 1–2 per cent. of the population. Backcrosses are apparently very rare. Until the population to be discussed here was found, I had only seen three plants which were clearly backcrosses. This has been the experience of other workers (Harrison 1931, Clifford 1958). This apparent rarity of backcross or F_2 plants is rather surprising, since field observation shows that the F_1 hybrids set seed, and they also provide pollen for fertilization of the parent species.

Clifford (1958) attempted to detect introgression between these two species by comparing means and variability of the two species in 'pure' and 'mixed' populations. There was no detectable introgression, but Clifford showed that the wild F_1 plants were more variable than some artificial ones from the garden, and suggested that hybrid segregates other than F_1 were present, but that they resembled the F_1 so closely that they had been included among them by him. I shall comment on this view later.

Mowat (1961) studied some mixed populations in Fife, using a simplified hybrid index technique. Her results suggest that in one population some sort of hybrid swarm was present. This population would be worth further investigation.

In the spring of 1963 a large mixed population was discovered in a wood ten miles

east of Oxford, and in one small area in particular, the scene of recent coppicing, there was a mixture of many hybrid types as well as apparent F_1 s. It is the plants from this small area that are to be discussed here.

MATERIALS AND METHOD

The area of the woodland floor that contained the hybrid swarm was marked out with string, and every plant within this area was sampled. No selection of plants was made. The largest flower and the largest leaf was taken from each plant. On the fresh material the following five characters were measured (see Fig. 1): (1) corolla diameter, (2) petal width, (3) calyx circumference, (4) calyx tooth length, (5) leaf angle. In addition four qualitative characters were scored: (6) throat pattern, (7) calyx hair, (8) leaf hair, and (9) pedicel hair. For comparison, a characteristic population of primrose from Marley Wood, Berks, and one of cowslip from Dickleburgh, Norfolk, were scored similarly.

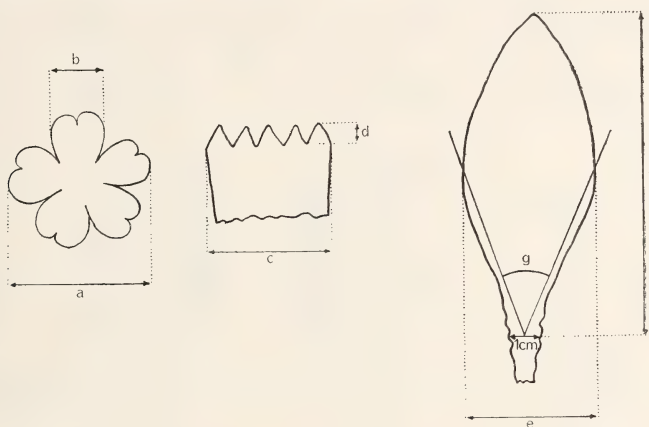


Fig. 1. Diagram showing measurements made

- (a) corolla diameter
- (b) petal width
- (c) calyx circumference
- (d) calyx tooth length
- (e) leaf width
- (f) leaf length
- (g) leaf angle

After scoring, the flowers were preserved in 70 per cent. alcohol for subsequent determination of pollen fertility. The frequency of 'good' pollen was estimated by teasing out anthers in acetocarmine, and counting the percentage of rounded, stainable pollen grains.

It is realized that the characteristic populations may have themselves been introgressed in the past; indeed in Britain it is very possible. However, one is comparing an *obviously* hybrid population with populations that are clearly referable to the parent species; i.e. comparing relative, not absolute differences.

A population at Cockayne Hatley, Cambs, was sampled in two successive years at different times in the season, and comparison of the measurements indicated differences between the two years (Table 1). Consequently a population was sampled at weekly intervals through the following spring to determine seasonal differences in the characters used. The results, shown in Table 2, indicate that there are seasonal differences, and that care must be taken to sample at the height of the season when dimensions are likely to be more stable. The populations used in this study were sampled in late April.

It should be noted here that Clifford (1958) pooled his results from many populations, and therefore probably masked any environmental differences between his populations. His

TABLE 1. Means and standard errors of certain characters in the samples of 30 pin and 30 thrum plants of *Primula vulgaris* from the same population (Cockayne Hatley Wood, Cambs.) in two successive years.

Date	Corolla diam.	Petal width	Calyx circ.	Calyx tooth-length
<i>Pin</i>				
22.4.59	34.6 ± 0.097	12.5 ± 0.035	19.8 ± 0.060	7.6 ± 0.041
23.3.60	28.7 ± 0.109	10.8 ± 0.061	15.2 ± 0.080	5.9 ± 0.032
<i>Thrum</i>				
22.4.59	34.03 ± 0.123	12.7 ± 0.067	18.18 ± 0.051	7.37 ± 0.041
24.3.60	30.1 ± 0.090	10.7 ± 0.061	16.0 ± 0.055	6.3 ± 0.038

TABLE 2. Means and standard errors of certain dimensions in samples of pin and thrum plants of *Primula vulgaris* in each of eight successive weeks in one year.

Date	No. of plants	Corolla diameter	Petal width	Tooth length
<i>Pin</i>				
31.1.61	8	26.00 ± 0.44	9.50 ± 0.18	5.75 ± 0.14
7.2.61	14	25.80 ± 0.19	10.50 ± 0.07	6.25 ± 0.06
14.2.61	18	27.66 ± 0.22	10.77 ± 0.10	5.64 ± 0.04
20.2.61	20	32.15 ± 0.17	12.55 ± 0.06	6.03 ± 0.05
28.2.61	29	31.17 ± 0.14	12.36 ± 0.06	5.83 ± 0.03
6.3.61	30	30.73 ± 0.16	11.22 ± 0.05	6.55 ± 0.03
14.3.61	28	28.63 ± 0.14	11.59 ± 0.05	6.13 ± 0.04
24.3.61	29	32.23 ± 0.18	12.95 ± 0.07	7.21 ± 0.05
<i>Thrum</i>				
31.1.61	7	29.50 ± 0.36	10.50 ± 0.21	6.75 ± 0.07
7.2.61	10	26.50 ± 0.15	9.50 ± 0.10	6.25 ± 0.07
14.2.61	13	27.69 ± 0.29	10.69 ± 0.22	5.92 ± 0.08
20.2.61	23	30.70 ± 0.14	11.48 ± 0.07	6.09 ± 0.04
28.2.61	28	29.48 ± 0.19	10.36 ± 0.05	6.04 ± 0.03
6.3.61	30	30.40 ± 0.13	11.62 ± 0.06	6.83 ± 0.04
14.3.61	28	28.91 ± 0.19	11.96 ± 0.07	6.17 ± 0.06
24.3.61	29	34.90 ± 0.09	12.59 ± 0.03	7.15 ± 0.03

garden experiment to test the effects of environment was based on too few families to provide a reliable indication of environment influences.

The results in Tables 1 and 2 indicate that pin and thrum flowers are very little different in their dimensions, and they have been considered together in the scatter diagrams.

RESULTS

Comparison of 'characteristic' and mixed populations

The populations of *P. veris* from Dickleburgh, and of *P. vulgaris* from Marley Wood are plotted on the scatter diagram in Fig. 2 and the Boarstall Wood population in Fig. 3. It can be seen that there is a clear separation of the two species, using the characters chosen, particularly corolla size and calyx tooth length. Although these two species are so distinct in the field that no one could confuse them, individual quantitative measurements that distinguish them absolutely are not easy to find. However, when the scatter diagram for the Boarstall Wood population (Fig. 3) is compared with those for the species (Fig. 2) it is clear that here the distinctions have broken down, and there is present a series of types ranging between the species.

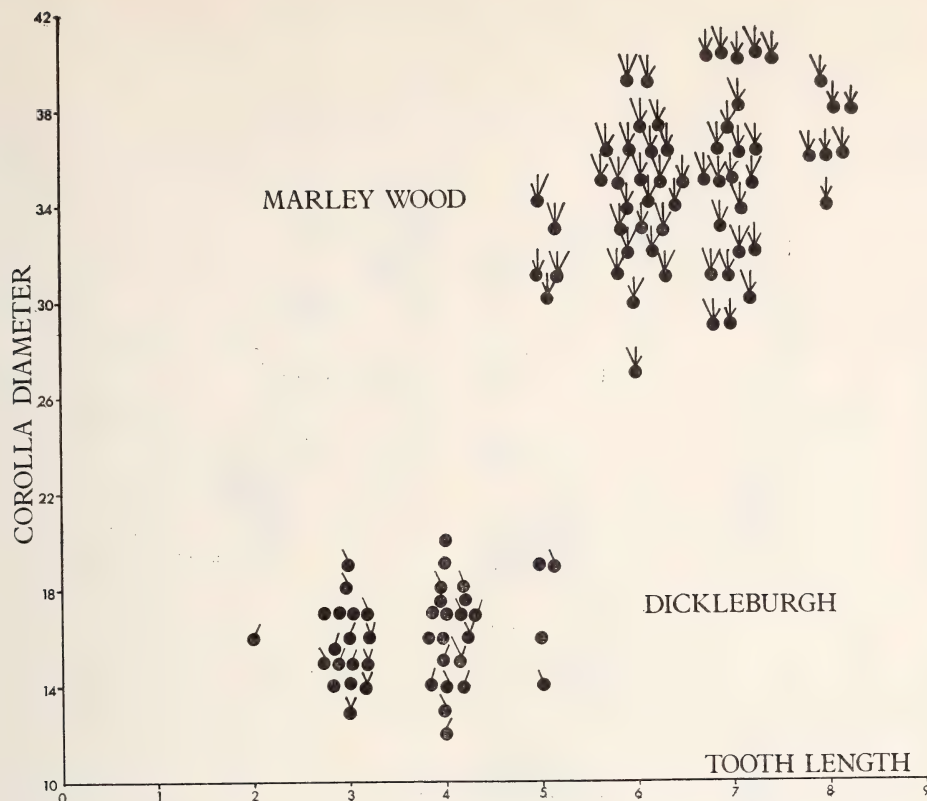


Fig. 2. Scatter diagram representing populations of *Primula vulgaris* from Marley Wood, Berkshire, and *P. veris* from Dickleburgh, Norfolk. (For key see Fig. 3.)

The data on the scatter diagram are plotted so as to show five groups of plants, distinguished on the basis of the marking of the throat and flower colour (termed together, 'throat pattern'). These five groups are as follows (see key to Fig. 3):

- C. Flowers of typical cowslip colour and throat marking; bright yellow, with distinct, deep orange spot at the base of each petal.
- CCP. Flowers larger than those of cowslip; slightly paler yellow, inflorescence less nodding, orange spot less distinct.
- CP. Flowers intermediate in size between cowslip and primrose, colour medium yellow. Orange throat spot diffuse.
- PPC. Flowers large, almost as large as those of primrose; pale yellow, with very diffuse and pale orange spot at base of each petal.
- P. Flowers pale sulphur-yellow, very large, with greenish marking at throat of corolla tube. Typical primrose flower colour and pattern.

These groupings were made before plotting the diagram, and it is interesting to note that the quantitative measurements place the plants in the positions that might be expected if the throat pattern distinctions are correct.

Fig. 3 does give the impression that the putative F_1 plants are nearer to *P. vulgaris* than to *P. veris*. This is, I think, a chance effect, and not an indication that the plants that I have classified as F_1 individuals are in fact backcrosses to *P. vulgaris*. This opinion is based partly on the evidence of pollen fertility, which will be discussed later, and partly on a

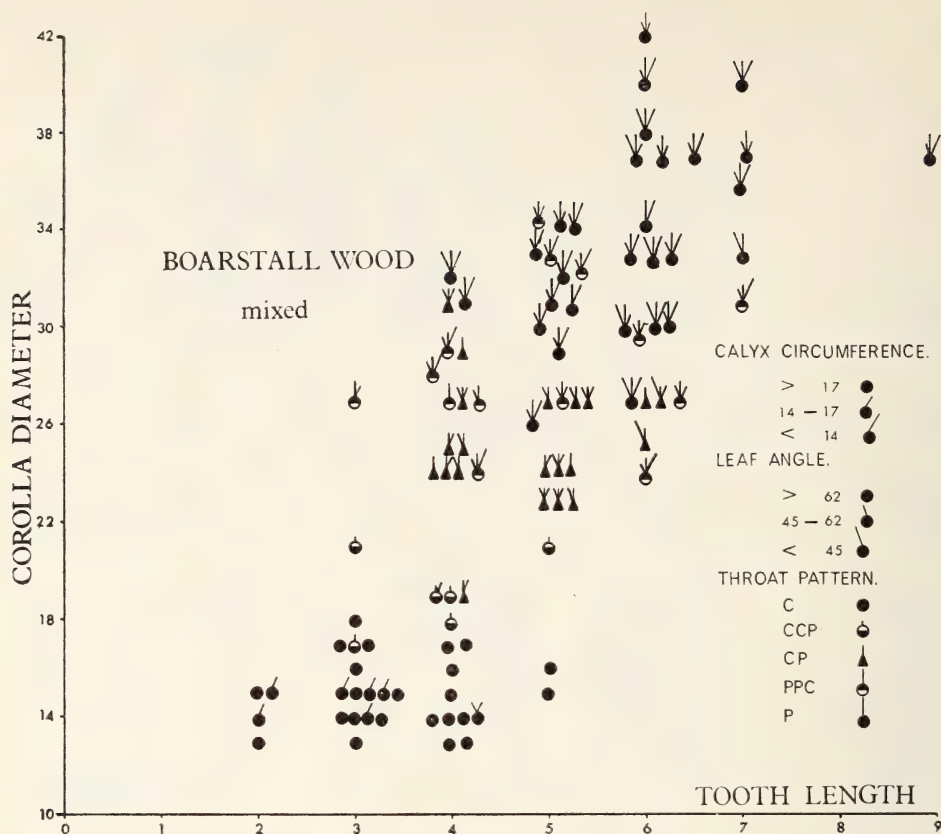


Fig. 3. Scatter diagram representing the hybrid population from Boarstall Wood, Buckinghamshire.

comparison with artificial hybrids. There appear to be more backcrosses to *P. vulgaris* than to *P. veris*, and this may be pure chance or the result of the ecological situation. This will be discussed later.

Fig 4 shows histograms that have been constructed using four of the characters measured, and again they illustrate that whereas some characters give good separation between these two species, others do not. Throat pattern, being subjectively classified, naturally gives the best distinction. The histograms for the Boarstall Wood population show that there is a range, varying for different characters, between the two parental forms, and that in some cases hybridization has resulted in increased variability, e.g. leaf angle.

Fig. 5 is a histogram constructed from a hybrid index, the characters used being set out in Table 3. It is clear from this that there is a peak in the histogram representing the F_1 , and again that there is more apparent variation toward *P. vulgaris* than to *P. veris*.

Pollen fertility

The pollen fertility of all the individuals was measured from the three populations, except for three plants in Boarstall Wood, which lacked anthers. The populations of the parent species show a consistently high pollen fertility (Table 4) suggesting that they have not been involved in interspecific hybridization. Indeed, even if it has occurred in the past, the individuals that remain are very close to the recurrent parents, and are genotypically balanced.

The Boarstall Wood population has a wide range of pollen fertility, and the results are set out in detail in Table 4. They are of interest for several reasons. Firstly, they show that

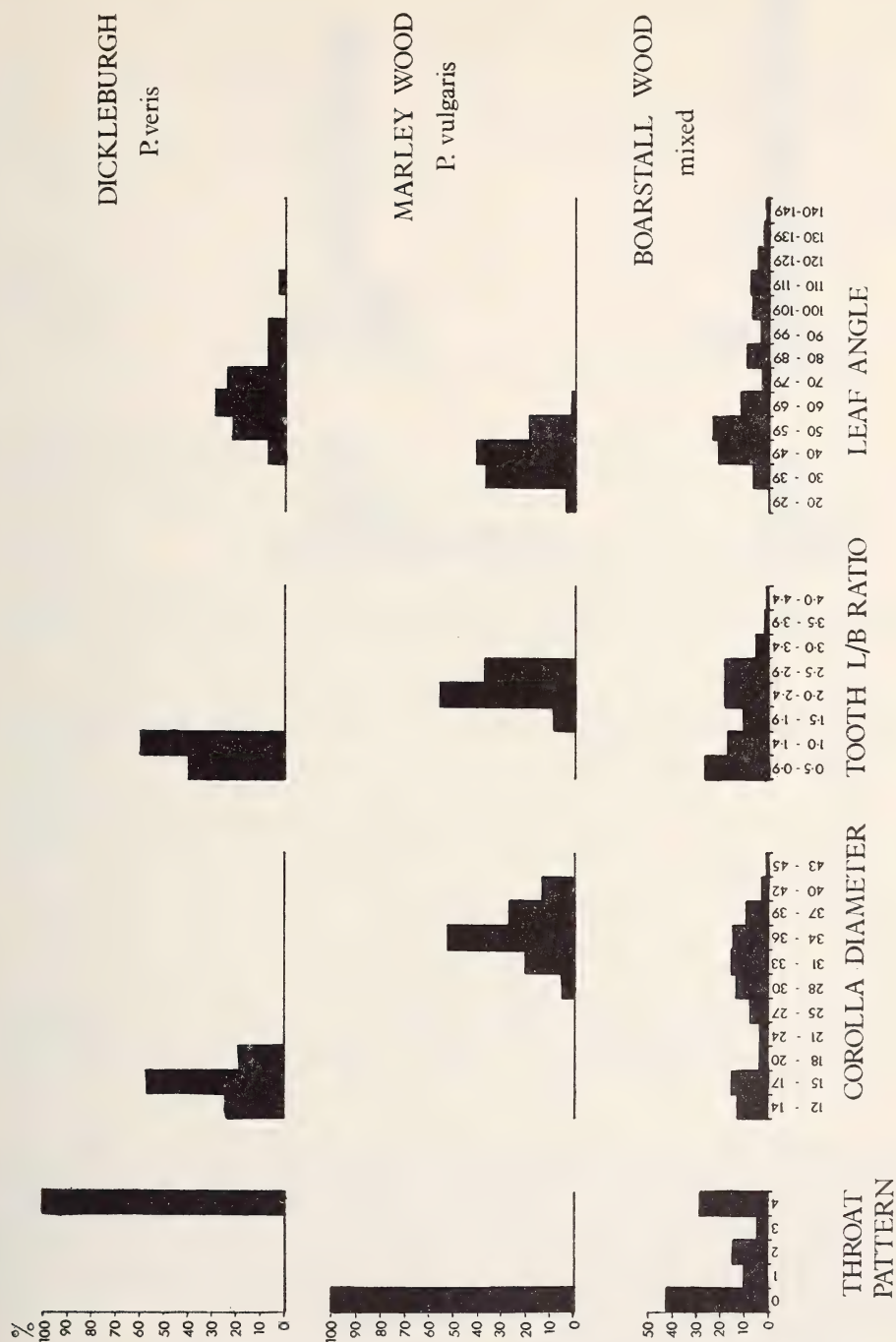


Fig. 4. Frequency distributions for four characters in the three population samples.

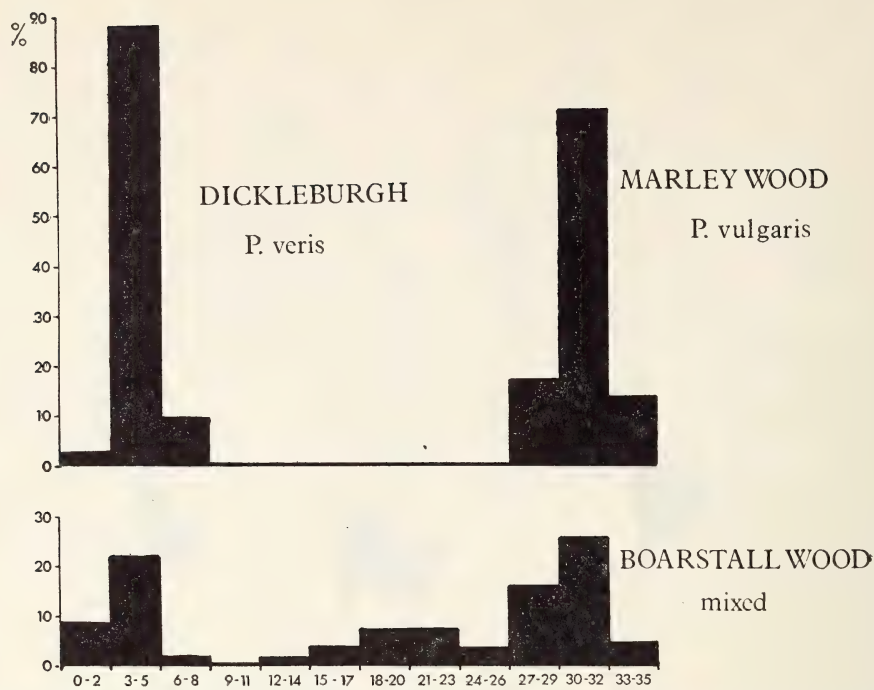


Fig. 5. Frequency distribution of scores calculated using a hybrid index. Characters used to construct the hybrid index are given in Table 3.

TABLE 3. Characters used in construction of hybrid index.

Character	Score	<i>veris</i>					<i>vulgaris</i>				
		0	1	2	3	4	5	6	7	8	9
1. Corolla diameter (mm.)		12-14	15-17	18-20	21-23	24-26	27-29	30-32	33-35	36-38	39-41
2. Calyx circumference (mm.)		24-22	21-19	18-16	15-13	12-10					
3. Calyx tooth length (mm.)		2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10		
4. Throat pattern		C	C(P)	CP	(C)P	P					
5. Calyx hair		C	C(P)	CP	(C)P	P					
6. Pedicel hair		C	C(P)	CP	(C)P	P					
7. Leaf hair		C	C(P)	CP	(C)P	P					

Note: In characters 4-7, C = *P. veris*; C(P) = putative backcross to *P. veris*; CP = putative F₁; (C)P = putative backcross to *P. vulgaris*; P = *P. vulgaris*. The minimum score, representing 'pure' *P. veris*, would be 0, that representing 'pure' *P. vulgaris* would be 36.

the plants regarded as parent species individuals, using the throat pattern criterion, have high fertility, equivalent to that of the plants from 'characteristic' populations. Secondly, the putative F₁ plants have a low average fertility, and thirdly, the putative backcross plants have an average fertility much higher than that of the F₁ individuals, and, with one exception, an individual value above the majority of individual F₁ plants. This indicates that pollen fertility, at least, is rapidly restored to a level not falling very far short of that of the parents; in some cases to 100 per cent, even in recognizably hybrid plants.

DISCUSSION

The data presented in this paper indicates that under some circumstances *P. vulgaris* and *P. veris* hybridize fairly freely, and that as well as F₁ plants, a proportion of backcross

TABLE 4. Pollen fertility of all plants sampled from Marley Wood, Dickleburgh and Boarstall Wood.

Species	Locality	No. of plants	Mean of fertility	Individual values
<i>P. vulgaris</i>	Marley Wood	60	99.97	99, 99, 58 at 100
	Boarstall Wood	60	99.98	99, 59 at 100
<i>P. veris</i>	Dickleburgh	42	99.93	98, 99, 40 at 100
	Boarstall Wood	39	99.95	99, 99, 37 at 100
<i>P. veris</i> × <i>vulgaris</i>	Boarstall Wood	20	43.45	9, 17, 20, 24, 31, 33, 33, 35, 38, 40, 45, 46, 50, 50, 51, 60, 60, 62, 63, 65, 70
Putative backcross to <i>P. veris</i>	Boarstall Wood	6	88.15	63, 70, 98, 99, 99, 100
Putative backcross to <i>P. vulgaris</i>	Boarstall Wood	12	77.33	2, 62, 63, 72, 75, 80, 85, 95, 95, 96, 99, 100

or F_2 segregants may be formed. This is in contrast to the situation normally found, where the barriers to hybridization between these species appear to be strong. In this discussion I will consider what these barriers may be; why they have broken down to some extent in this wood; and further, whether the data show that introgression is occurring between the species.

A consideration of the behaviour of these two species suggests that any large amount of hybridization would be unlikely. As has been shown by Valentine (1955) and Woodell (1960) the cross between them is only successful when *P. veris* is the seed parent (see introduction). The low viability will be unlikely to result in many hybrid plants in the field, and in most populations they form a minute percentage of populations where the species come into contact; usually less than 1 per cent. (Clifford 1958, and personal observation). Even this number is likely to give a false impression of the amount of hybridization occurring, since there is some evidence from garden cultivation of these plants that the F_1 hybrid almost always outlives the parent species. Of course, extrapolation of this situation to field conditions is dangerous, but it is suggestive. Thus it is possible that even less hybridization occurs, since hybrids will be over-represented by virtue of living longer.

A second isolating factor is flowering period. In the Oxford area *P. vulgaris* flowers from early spring until May, while *P. veris* flowers from mid-April to June so that the overlap in flowering periods is relatively small, and although pollinating insects have been observed visiting both species in the same area, I have no idea how frequent this is. Apparent F_1 hybrids do have a flowering season that overlaps both parent species, so once they are established there are opportunities for backcrossing to take place. Experimental work on pollinating insects is now in progress, and may lead to a better knowledge of the amount of pollen transfer that takes place between these species.

In my view habitat differences constitute the most important isolating factors. In England, *P. veris* is a plant of unshaded or lightly shaded habitats, rarely found in woodland, though often along the margins of woods and in broad woodland rides. *P. vulgaris* is a plant of much more mesic environments, found in open conditions in western districts, but in eastern England mainly a woodland plant. Normally the species only meet along wood margins, in hedgerows, and along woodland rides and paths. Thus the opportunities for pollen transfer are not great. As Clifford (1958) pointed out, these meeting places are often disturbed, and it is in disturbed habitats that introgression is favoured (Anderson 1949). But very often the disturbance is short-lived, and here lies one possible reason for such limited hybridization.

If a species cross takes place, and the cowslip thus pollinated sets seed, it is unlikely that the plants resulting from such seed will flower before their second year, even under very

favourable conditions. It may well be later than this. In many areas where F_1 plants occur, such as woodland rides after clearance has taken place, hedgerows after ditching, etc., the ground usually becomes rapidly grassed over after a couple of years, and the establishment of any new plants, either of the species or of hybrids, will be greatly reduced. Hybrids are likely to be ill-adapted and at a great selective disadvantage. The fact that the F_1 plants are likely to be with the cowslip, i.e. in the grassy areas, will increase this effect. In meadows which are grazed, and therefore subject to some disturbance, backcross or F_2 plants are very rare, indicating that even here the hybrids are ill-adapted.

Harper & Chancellor (1959) and Cavers & Harper (1964) have demonstrated that even in meadowland conditions where they occur naturally, it is difficult to establish several species of *Rumex* from seed, and Sagar & Harper (1964) have shown that the same holds true for *Plantago*. Such difficulties of establishment are likely to be much greater for hybrids.

There are therefore fairly strong genetic barriers between these two species, operating after fertilization; there is some temporal isolation, and there is very considerable ecological isolation. From a consideration of these isolating factors, one could perhaps forecast that the most important factor leading to an extension of hybridization would be a breakdown of the ecological isolation. If one considers a mixed population in grassland, where primrose has emerged from its usual shaded habitat, the establishment of hybrids would be inhibited in the manner suggested above. On the other hand, if cowslips occurred in woodland, then the hybrid seed would be given a greater chance of establishment, since ground cover in woodland is less complete. (It is relevant here to note that in woods containing Oxlip (*P. elatior*) seed is often set, and seedlings are common, indicating a greater chance of seedling establishment in woodland.) Further, if that woodland is disturbed not once, but frequently, then the proximity of the two species, together with regular disturbance, might be expected to favour an increase in hybridization. This situation is just that which exists in Boarstall Wood.

Boarstall Wood is an oakwood (*Quercus robur*), with well-spaced oaks, and a very dense understory of coppiced hazel (*Corylus avellana*). The soil is yellow-brown clayey loam, with a pH of from 5.0–5.7 (four samples) and a cation exchange capacity of 26.1 me/100g.

Under the dense shrub layer the field layer is sparse. Immediately adjoining the sample area, in 1964 both *P. veris* and *P. vulgaris* were present, with occasional hybrids. So few were in flower here that no estimate of the percentage of hybrids could be obtained in 1964. Table 5 gives a list of species present, in a 10 sq m area, estimated on the Domin cover-abundance scale. Also given is a list from a 10 sq m area in the region sampled for *Primula*. This part of Boarstall Wood had been cleared completely of undershrubs in the winter of 1962–63. The great increase in ground cover is evident from the Table. Yet there was still a good deal of bare ground, which presumably was providing potential sites for establishment of hybrids. Some weedy species had already invaded (*Plantago major*, *Rumex sanguineus*). At the time of writing, the area of the wood in question has been completely cleared of trees and shrubs, and the operation has been accompanied by tremendous disturbance. It will be watched with interest over the next few years.

There is no difference in ground flora associated with *P. veris* and *P. vulgaris*; at least no obvious difference. The two species are interspersed with each other over the sample area, which extends for about 150 m inward from the eastern edge of the wood. This is a contrast to the situation described by Valentine (1948) for *P. elatior* and *P. vulgaris* in Buff Wood, Cambs. In Boarstall Wood the cowslip is in an atypical habitat, and its invasion of the wood may have been correlated with an earlier complete clearance. An examination of the felled oaks in early 1965 disclosed that they were all the same age; about 100 years. This suggests that 100 years ago the area was cleared and replanted. Such an occasion may have facilitated the invasion of *P. veris*. Once established, its survival will have been helped by regular coppicing. Cowslips, identifiable by their leaf shape, were present under the 10–12 year old shrub canopy adjacent to the sample area. In recently coppiced areas they

TABLE 5. Species present in a 10 sq m area of Boarstall Wood, (a) in an area untouched for about ten years (b) in an area coppiced 18 months previously. Estimates of cover-abundance on the Domin Scale.

	(a)	(b)
<i>Corylus avellana</i>	9	3
<i>Euonymus europaeus</i>	3	
<i>Ligustrum vulgare</i>		
<i>Lonicera periclymenum</i>	3	
<i>Prunus spinosa</i>	3	
<i>Rosa arvensis</i>	2	
<i>R. canina agg.</i>	2	
<i>Rubus fruticosus agg.</i>	4	2
<i>Thelycrania sanguinea</i>	1	3
<i>Ajuga reptans</i>	2	2
<i>Carex sylvatica</i>	3	3
<i>Cirsium vulgare</i>		2
<i>Deschampsia cespitosa</i>	3	8
<i>Dryopteris filix-mas</i>	2	
<i>Galium aparine</i>		1
<i>Geum urbanum</i>	1	2
<i>Hypericum tetrapterum</i>		1
<i>Juncus communis</i>	1	4
<i>Plantago major</i>		1
<i>Potentilla sterilis</i>	1	2
<i>Primula veris</i>	2	3
<i>P. vulgaris</i>	3	3
<i>Hybrids</i>	2	2
<i>Rumex sanguineus</i>		1
<i>Atrichum undulatum</i>		2
<i>Cirriphyllum piliferum</i>	2	
<i>Eurhynchium praelongum</i>	4	3
<i>E. striatum</i>	2	1
<i>E. swartzii</i>	1	
<i>Fissidens taxifolius</i>	1	
<i>Funaria hygrometrica</i>		3 (on site of fire)
<i>Mnium undulatum</i>	1	1
<i>Thamnium alopecurum</i>	2	
<i>Thuidium tamariscinum</i>	4	3
<i>Bare ground</i>	8	5

flower freely, and the opportunities for hybridization, establishment of hybrids, and maintenance of cowslips in the population are obvious. The disturbance caused by clearing leaves bare ground that persists for several years. It might not be thought surprising that hybrids other than F_1 forms are found in such a situation.

Clifford (1958) suggested that selection was maintaining each of the species and a third phenotype resembling the F_1 hybrid. He based this view on two facts; that in wild populations only F_1 hybrids are normally found and that the wild putative F_1 plants are more variable than artificial F_1 plants grown in a garden. In my opinion, these facts cannot be taken to suggest that selection is operating in this manner. My reasons for this are as follows:

1. The artificial F_1 plants that were used as a basis for comparison of variability were from four families, grown in the same garden. The wild plants were from 15 field popula-

tions. One would expect the wild hybrids to be more variable, even if they are all true F_1 plants. They will have come from many more than four crosses; they will have been growing in a variety of environments, and we have seen that environmental effects are demonstrable. It is likely that differences in variability of the order shown by Clifford could have been produced by these two causes alone.

2. For selection to act in the way suggested by Clifford, one would have to suppose that the F_1 plants were adapted to a set of conditions that prevail almost everywhere that the two parent species meet, and that this intermediate habitat was in fact almost exactly intermediate; an ' F_1 habitat' in fact. This is clearly not so, and F_1 hybrids can be found in quite a wide variety of conditions. What is often true of F_1 hybrids is that because they can only be produced from cowslip mothers, they generally occur in habitats more like those of cowslip than those of primrose. One would expect selection to favour backcrosses to cowslip, if anything.

3. For reasons stated above, ecological conditions appear to be operating against the establishment of hybrids other than F_1 plants, and the widespread presence of these F_1 plants is more a result of this than of positive selection for them.

A study of the pollen fertility of the putative F_1 plants found by Clifford in the wild might have given a better indication of their true nature.

The pollen fertility results from the populations studied here indicate that there is a considerable loss of fertility in the first generation hybrid, followed by a restoration to a high level in later generations (cf. Moore 1959, Heiser 1951, Gajewski 1957). Peto (1933) found in hybrids between *Festuca pratensis* and *Lolium perenne* that a much reduced pollen fertility in the first generation was restored, in some cases to a level near to that of the parents, in the backcrosses. He found among his backcrosses one or two plants with very low pollen fertility or complete sterility. It is interesting to note that in my sample one of the putative backcrosses has a pollen fertility of 2 per cent. (Table 4).

Finally we have to consider whether introgression is taking place in this situation where everything seems to be in its favour. In an attempt to determine this I have extracted from my original sample in Boarstall Wood, which was a complete sample from a circumscribed area, the plants which were, on subjective grounds, 'characteristic' primroses or cowslips, and compared their variability with that of the 'characteristic' populations from Dickleburgh and Marley Wood. The results are set out in Table 6.

The results in this Table indicate that while thrum *P. vulgaris* is significantly more variable in Boarstall Wood than in Marley Wood, the species in Boarstall Wood are not in general more variable.

Introgression, in the sense of Anderson (1949) is the transfer of genes across an incomplete genetic barrier, and the establishment of well adapted backcross types, resembling

TABLE 6. The variances for selected characters of plants in 'pure' and 'mixed' populations of *Primula vulgaris* and *P. veris*.

Species	Locality	Corolla diameter	Calyx circumference	Calyx tooth length	Leaf length/breadth ratio
<i>P. veris</i> thrum	Dickleburgh	4.18*	9.05	0.38*	0.053
	Boarstall	1.82*	5.1	0.86*	0.042
<i>P. veris</i> pin	Dickleburgh	3.22	4.45	0.48	0.117
	Boarstall	2.67	6.12	0.68	0.121
<i>P. vulgaris</i> thrum	Marley	7.18***	2.72	0.42**	0.39***
	Boarstall	11.90***	2.55	1.26**	0.13***
<i>P. vulgaris</i> pin	Marley	11.55	2.91	0.65	0.09
	Boarstall	11.15	4.72	0.72	0.13

* = differences significant at 5 per cent. level. ** = at 1 per cent. level.

*** = at 0.1 per cent. level.

either or both parents. If such has happened, one would expect greater variability in the parent species from an area where introgression has occurred. The results from Boarstall Wood indicate that with the exception of thrum primrose, they are hardly more variable.

There are two alternative interpretations of this situation. Either introgression has not proceeded very far, or it is so complete that the methods used for detecting variability, and the characters selected, do not show it. Let us examine these alternatives a little more closely.

When introgression has occurred in the past it is often difficult to detect (Stebbins, 1950). In view of the strength of stabilizing selection this is not perhaps surprising. If one accepts this, then one cannot rule out the possibility that the small amount of extra variability in the Boarstall Wood primroses is a real indication of complete introgression. One does not know what characters in these two species are of real selective value, and those used in the analyses were selected merely because they were those that gave the clearest distinction between the species. Even among these there are some partially common to both species, and the detection of introgression in such cases is especially difficult.

The presence of a number of individuals that are either second generation segregates or backcrosses indicates at least that introgression is in progress. (These individuals are more likely to be backcrosses in view of the likelihood that fertilization of hybrids will take place mainly by parental pollen.) Without knowing the detailed history of this wood it is difficult to know how often disturbance has allowed a burst of flowering and subsequent hybridization.

The evidence at hand does not seem to be conclusive enough to enable one to decide with certainty whether introgression is well advanced or in an early stage. It does not really matter; what does matter is that it is clear that introgression does not occur readily between these two species. It requires very exceptional habitat conditions, and these have been met in Boarstall Wood. This area will be watched closely from now on, in an attempt to follow the course of events in the train of the recent catastrophic disturbance.

Has introgression occurred elsewhere between these two species? Literature records for continental Europe are very scanty, but they indicate that backcrosses are rare (Pugsley 1927). In Britain, although Harrison (1931) refers to the presence of occasional backcrosses, he states that the vast majority of hybrids in the field are first generation progeny. The only two investigations of possible introgression have been those of Clifford (1958) and Mowat (1961).

It is not surprising that Clifford failed to detect introgression, in view of the fact that he pooled material from different localities, thus masking seasonal and environmental differences. The present investigation indicates the importance of individual habitat conditions. Mowat's data were based on populations from three localities in Fife. She used a hybrid index based on ten characters, each being given a score of 0 for typical *P. vulgaris* and 1 for *P. veris*; thus 'typical' *P. vulgaris* would have a score of 0 and 'typical' *P. veris* one of 10. One of Mowat's populations appeared to be 'characteristic' *P. vulgaris*. Her third population had 43 per cent. of the plants differing from the *P. veris* standard by one character, and she took this to be evidence of introgression. I think that this deviation is unlikely to reflect more than the usual variation pattern; characters distinguishing these species are not of the 'all or none' type that Mowat has suggested.

Her second population clearly contained hybrids, and although they are grouped in such a way that suggests that most are F_1 individuals, there may be a few backcross types. In the absence of pollen fertility data it is difficult to say whether any introgression had occurred.

It would thus appear that hybridization between primrose and cowslip beyond the first generation is very rare. The internal isolating barriers are strong, and unless a particular and very unusual set of ecological conditions operates, the possibility of backcrossing and subsequent introgression is remote, in Britain at least. Even in such a favourable situation as that in Boarstall Wood, there is little evidence for the occurrence of introgression.

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BOOK REVIEW

Vascular Plants of the Pacific Northwest. C. L. Hitchcock, A. Cronquist, M. Ownbey and J. W. Thompson. Part 2: *Salicaceae to Saxifragaceae*, by C. L. Hitchcock and A. Cronquist. Drawings by Jeanne R. Janish. Pp. 597. University of Washington Press, Seattle. 1964. Price \$15.00.

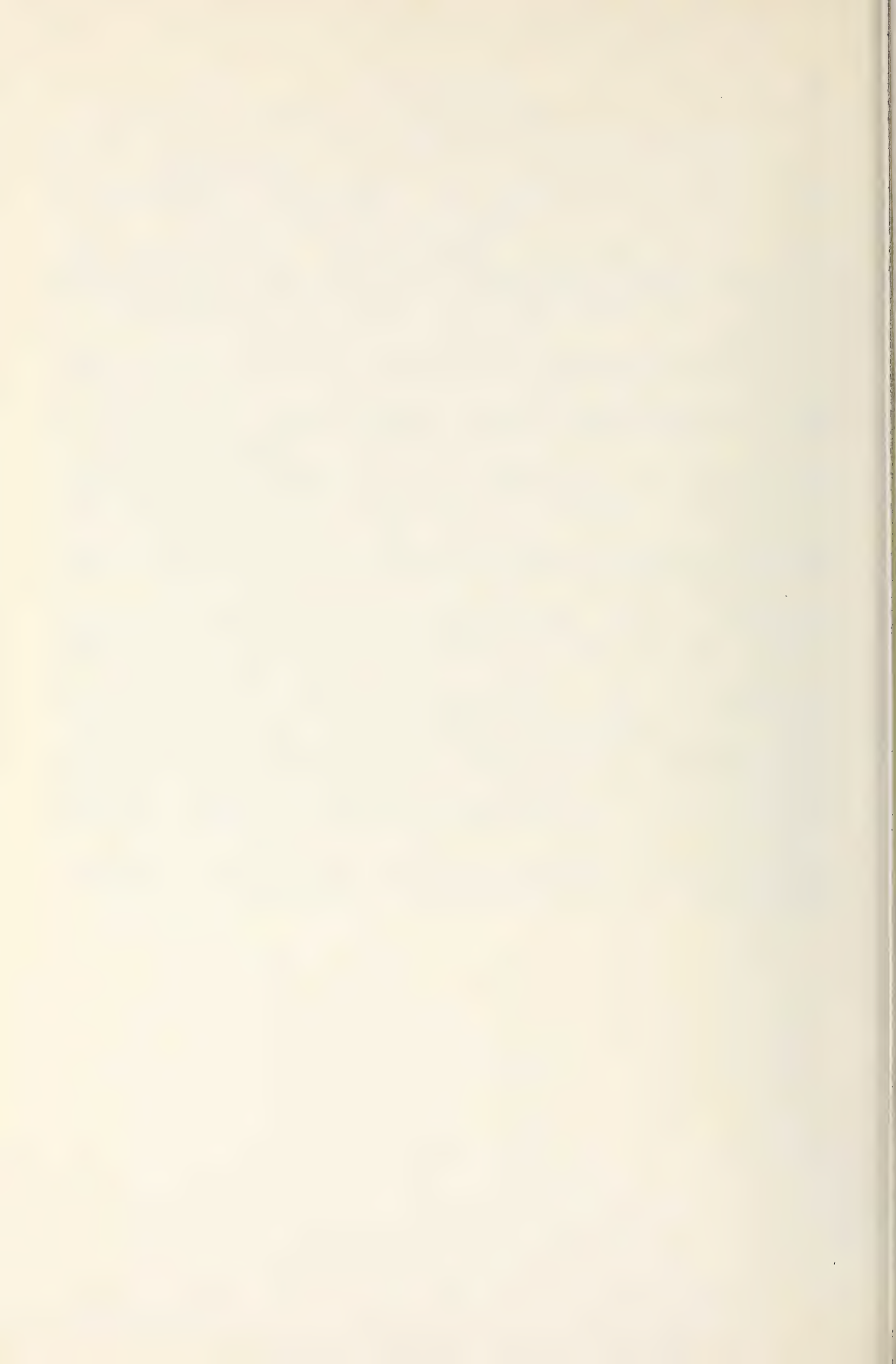
This is the fourth volume to appear of a flora covering the State of Washington, northern Oregon, Idaho north of the Snake River plains, the mountainous western part of Montana, and southern British Columbia. The parts are being published in reverse order and only one, the fifth, remains to come. The previous volumes were Part 5, *Compositae*, by Cronquist (1958); Part 4, *Ericaceae* through *Campanulaceae*, by Hitchcock, Cronquist and Ownbey (1959); and Part 3, *Saxifragaceae to Ericaceae*, by Hitchcock and Cronquist (1961).

The families, with some exceptions, follow the Engler system and every species is beautifully illustrated, often with its varieties and also with analytical drawings of important parts such as flowers, fruits or types of indumentum. Among the great merits of this flora are the indented keys, the elaborate descriptions and synonymy, the valuable critical notes, the treatment of varieties and intergrades, and the comments on the horticultural value of many taxa. Type collections are cited, even of taxonomic synonyms, and the derivation of generic names is given. Much less acceptable to most of us here is the placing of both genera and species in alphabetical order. Dare we whisper, this seems scarcely more intelligent than the similar arrangement of the covers in a herbarium. It makes a mockery of the indexes at the end of the volumes, where synonyms (in italics) and the relative accepted names (in roman) are ranged in strange parallel vertical columns, page references being confined to accepted specific names (a minority), those of families and genera, and common names. A further disadvantage of this system is that the illustrations also appear in alphabetical order, so that the drawings of closely allied species may well be on different pages.

The present volume, since it completes the treatment of the Dicotyledons, begins with two keys (synoptical and artificial) to the orders and families dealt with in Parts 2-5: the synoptical key amplifies the phylogenetic chart based on Cronquist's system which is included in the introduction to this Part. Among the important families of which we find accounts in this volume are the *Cruciferae*, *Ranunculaceae*, *Cras-sulaceae*, *Polygonaceae*, *Caryophyllaceae*, *Portulacaceae*, *Chenopodiaceae*, *Salicaceae* and the order *Urticales*. The treatments of critical genera are often wisely conservative and, now and then, one is reminded of remarks or confessions by contributors to *Flora Europaea*: for instance, *Erysimum* seems as difficult in this area as in Europe and it seems that part of the confusion results from the maintenance of several taxa that represent no more than extremes in a nearly continuous series of variation; the genus is badly in need of monographic study. But, in contrast to *Flora Europaea*, the rank of variety is retained for the more common kind of infraspecific taxon, that of subspecies being restricted to a 'hierarchical category (i.e. a group of varieties)'.

British students of *Amaranthus* may not like the reduction of *A. blitoides* S. Wats. to *A. graecizans* L., and among other points to be noted by British botanists are the maintenance of generic status for *Tillaea* and the appearance of *Chenopodium pratericola* Rydb. as a synonym of *C. leptophyllum* (Moq.) S. Wats. var. *oblongifolium* S. Wats.

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A LIST OF INFRASPECIFIC TAXA OF BRITISH PHANEROGAMS TESTED IN CULTIVATION

By D. E. ALLEN

In recent years interest in infraspecific taxa has greatly declined among British botanists both amateur and professional. This is undoubtedly a reflection of the scanty, if not non-existent, treatment of named variants below subspecific rank in the standard floras and check-lists published since the war, in understandable reaction to the excessive naming of trivial variants by earlier generations and the accompanying nomenclatural chaos. Modern experimental work has in many cases exposed the futility of attempting to give names where the variation is more or less continuous in character. It has also shown how inevitably misleading taxonomic treatment can be in terms of genetics, limited as it must be to readily discernible external differences and so liable to recognise a highly conspicuous variant due to the effect of a single gene, while at the same time bound to ignore different chromosome types which, as in *Lathyrus pratensis* (Larsen 1957), cannot be separated morphologically with any consistency.

While recognizing these limitations, however, there may still be a case for keeping up many of the existing taxa, provided this is done with more discrimination than in the past. Surprisingly little is known about the British distribution of even the more conspicuous of these variants and, to put the argument at its lowest, unless they receive recognition in the form of Latin epithets they are likely to continue to pass largely unrecorded, particularly by amateur botanists, to whom a great part of such recording must inevitably fall. On scientific grounds the task of working out the distribution of even relatively trivial variants is surely justifiable if it results in greater recognition and more detailed knowledge of, for example, polymorph-ratio clines (as demonstrated by New (1958) in *Spergula arvensis* L.), of the spread of certain variants (such as the inland radiate forms of *Senecio vulgaris* L.), of variation betraying cryptic introgression between species, and of the existence of local races which, perhaps representing incipient subspecies, contribute to an understanding of the phytogeographical relationships of different areas.

Basic to such work, however, is more precise and extensive information on the very validity of many taxa that have been described. *Oenanthe lachenalii* var. *minima* Camus & Rouy, for example, is a dwarf variant reported from maritime localities in Co. Cork, Co. Wexford, Anglesey and the Isle of Man; it has never, apparently, been tested in cultivation and so it remains uncertain whether it is an interesting race peculiar to the shores of the Irish Sea or a mere ecad. On the other hand, far too much has been written in the past and records are still today being published for variants (such as the terrestrial state of *Polygonum amphibium* L.) that have been exposed, more or less conclusively, as ecads—and thus surely do not merit taxonomic recognition. Because of the absence of any list of reported experiments, many variants have been tested repeatedly, while others whose status could have been much more usefully checked have been continually ignored. If it serves no further purpose than to redirect efforts in future, therefore, the list that follows may prove to be of use.

The list has been compiled over fifteen years primarily from British publications, and except possibly for published reports of British experiments it cannot be regarded as exhaustive. It is confined to variants that have received taxonomic recognition (with one or two exceptions) and to those that have been reported as occurring in the British Isles. Albinos and semi-albinos have been ignored, as these have only partially and inconsistently had Latin epithets bestowed on them. A number of names new to British botanists inevitably appear, but in general no attempt has been made to establish earliest legitimate names, and new combinations have been deliberately avoided, not least because general

agreement has yet to be reached on the appropriate infraspecific rank (if any) to be given to each category of variant.

The list, inevitably, has a number of pitfalls and must be used with caution. Many of the experiments reported on are, by modern standards, crude in the extreme, and most of those performed (by all except specialists in genetics) before about 1930 probably need re-checking. Some of the results reported in the last century (for example, *Anagallis arvensis* var. *azurea* and *Leontodon hispidus* var. *glabratus*) are almost certainly misinterpretations resulting from unawareness of the existence of heterozygotes. Too limited a progeny and too short a period of observation may also have led to errors. In many cases, as observed in *Plantago coronopus* by Böcher, Larsen & Rahn (1955) and in *Mentha* by Morton (1956), cultivation has a "levelling-out" effect, the variation noted in the field being still recognizable but greatly reduced. Sometimes, too, the variation may differ in intensity from year to year, as reported by Riddelsdell (1948) in cultivated plants of *Viola odorata* var. *sulfurea*. Most important of all, non-genetic effects can be closely simulated, perhaps even exactly duplicated, by hereditary variants (genocopies), so that it is sometimes impossible to be sure without breeding experiments whether a particular variant is genotypic or phenotypic. Cook (1962) has described an instance of this in alpine specimens of *Ranunculus trichophyllus* Chaix, some retaining their original character when cultivated in lowland conditions, while others come to resemble lowland material. A similar situation in *Veronica anagallis-aquatica* L. has been recorded by Burnett (1955). Examples in the list of conflicting data which may be explicable on this basis are :

Caltha palustris var. *minor*

Chenopodium rubrum f. *pseudobotryodes*

Sarothamnus scoparius subsp. *maritimus*

Aethusa cynapium var. *agrestis*

Heracleum sphondylium var. *angustifolium*

Plantago lanceolata var. *capitata*

P. coronopus var. *pygmaea*.

Test results are placed in the list in one of four categories abbreviated as follows :

- CC Constant "in cultivation", i.e. all cases in which raising from seed is not explicitly mentioned, ranging from elaborate transplant experiments to mere transfers from the wild to a garden.
- RC Reverted to type "in cultivation".
- CS Constant when grown from seed.
- RS Reverted to type when grown from seed.

Fuller genetical details can be obtained in many cases by referring to the original source.

Unless a horticultural origin is clearly indicated, experiments reported in British journals can almost without exception be assumed to have been carried out on wild material of Britannic origin, although very often this has not been specifically stated. It is possible that results reported on non-Britannic material may not invariably be applicable to taxa bearing the same name in this country, due to a differing genetic make-up or more simply to taxonomic confusion. Equally, results may conceivably vary for apparently identical variants originating from different areas even within the British Isles.

Of all the infraspecific variants ever reported as British, the great majority of which are cited in G. C. Druce's *British Plant List* (Ed. 2, 1928), probably less than a third are now revealed to have been tested so far by cultivation.

CALTHA PALUSTRIS var. MINOR (Mill.) DC. CC—Christy, *Mag. Nat. Hist.* (1833) 54 ; Graebner ex Druce, *New Phytol.* (1912) 357. RC—Hunnybun ex Moss, *Cambr. Brit. Fl.*, 3, (1920) 105 ; var. GUERANGERII (Bor.) Syme. CC—Linton, *Rep. Bot. Exch. Club* for 1893, 399.

For cultivation experiments on the species as a whole see Reese, *Planta* (1954) 203–268.

- TROLLIUS EUROPAEUS var. RELICTUS (H.-Harrison) Druce. CC—Heslop-Harrison, *Trans. Nat. Hist. Soc. Northumb., Durh. and Newc.* (1917) 136.
- ANEMONE NEMOROSA var. PURPUREA DC. CC—Butler ex Riddelsdell, Hedley & Price, *Fl. Glos.*, 4 (1948).
- RANUNCULUS ACRIS subsp. ACRIS (*R. boraeanus* Jord.) and subsp. FRIESIANUS (Jord.) Rouy & Fouc. (*R. vulgatus* Jord. ex Bor.; *R. stevenii* auct.). CC—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1930, 474; var. PUMILUS Wahlenb. (subsp. *borealis* (Trautv.) Nyman?). CC—Druce, *J. Bot.* (1890) 40; Graebner ex Druce, *New Phytol.* (1912) 357; Turesson, *Hereditas* (1925) 179–184; Böcher, *Dansk Bot. Arkiv* (1945), 12 (3), 1–16.
- R. REPENS var. PROSTRATUS (Poir.) Gaud. (var. *subacaulis* Bréb.; *R. reptabundus* Jord.). CC—Shoobred, *Rep. Bot. Soc. and Exch. Club* for 1913, 444, and for 1915, 309.
- R. BULBOSUS var. VALDEPUBENS (Jord.) Corb. (var. *dunensis* Druce?; var. *maritimus* Lange?). CS—Jordan, *Ann. Soc. Linn. Lyon* (1861) 450. CC—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1931, 736; Rossiter, *Proc. Bot. Soc. Br. Is.* (1956) 78.
- R. ARVENSIS var. ETUBERCULATUS Sér. (var. *inermis* Nees; var. *reticulatus* (Schmitz & Regel) Rouy & Fouc.). CS—Godron, *Mém. Acad. Stanislas* (1873) 77; Hoffmann, *Bot. Zeit.* (1884) 244. Recessive—Saunders in Bateson, Saunders & Punnett, *Rep. Evol. Comm. Roy. Soc.* (1904) 54–55.
- R. SARDOUS var. PARVULUS (L.) Lange. RC—Hailstone ex Wilkinson, *Rep. Yorks. Phil. Soc.* (1895) 12.
- R. FLAMMULA subsp. FLAMMULA var. MAJOR Schult. CC—Padmore, *Watsonia* (1957) 20; var. RADICANS Nolte (var. *tenuifolius* Wallr.). RC—Beeby, *J. Bot.* (1887) 370 and *Scot. Nat.* (1888) 210; Padmore, *Watsonia* (1957) 25–26; subsp. MINIMUS (A. Benn.) Padmore. CS—Padmore, *Watsonia* (1957) 23; subsp. SCOTICUS (E. S. Marsh.) Clapham. CC—Marshall, *J. Bot.* (1889) 230; Padmore, *Watsonia* (1957) 23.
- R. FICARIA var. INCUMBENS F. W. Schultz. CS: more or less recessive—Marsden-Jones & Turrill, *J. Genet.* (1952) 530.
- NYMPHAEA ALBA f. TERRESTRIS Schuster. RC—Brand ex Hegi, *Ill. Fl. Mitteleur.*, ed. 1, 3, 44 (1911).
- PAPAVER RHOEAS var. STRIGOSUM Boenn. Partially CS—Dixon, *J. Bot.* (1892) 309. Single dominant gene—Winge, *Bull. Acad. Sci. URSS, Genet.* (1932) 115–120; var. PRYORII Druce. Dominant—Philp, *J. Genet.* (1933) 194; var. CHELIDONIOIDES O. Kuntze. Dominant, probably two factors involved—Philp, *J. Genet.* (1933) 197–199.
- BRASSICA RAPA var. BRIGGSII H. C. Wats. ex Briggs. CS—Varenne, *J. Bot.* (1881) 360; Watson ex Brown, *Engl. Bot.*, ed. 3, *Suppl.* 22 (1892).
- RAPHANUS RAPHANISTRUM var. OCHROLEUCUS (Stokes) Peterm. (var. *flavus* (S. F. Gray) Schübler & Mart.). CS—Druce, *Rep. Bot. Soc. and Exch. Club* for 1917, 210.
- LEPIDIUM HETEROPHYLLUM var. ALATOSTYLUM (Townsend) Thurston & Vigurs. CS—Townsend, *J. Bot.* (1903) 97–98.
- COCHLEARIA DANICA var. PRAECOX Le Jolis. CC—Wheldon, *Rep. Bot. Soc. and Exch. Club* for 1916, 557.
- CARDAMINE PRATENSIS var. UNIFLORA Sternb. & Hoppe (var. *acaulis* (Berg) Hallier). RC—Sternberg & Hoppe, *Denkschr. Kgl. Baier. Ges. Regensb.* (1815) 157.
- C. IMPATIENS var. POTERIOFOLIA Druce. CC—Stuart ex Druce, *Rep. Bot. Soc. and Exch. Club* for 1927, 301.
- BARBAREA VULGARIS var. TRANSIENS Druce. CS—White, *Rep. Bot. Soc. and Exch. Club* for 1923, 374. var. with variegated leaves. Single recessive gene—Tilney-Bassett, *J. Hered.* (1963) 545.
- CARDAMINOPSIS PETRAEA var. GRANDIFOLIA (Druce). CC—Druce, *Rep. Bot. Exch. Club* for 1888, 200, *J. Bot.* (1890) 40 and *Ann. Scot. Nat. Hist.* (1892) 255.
- NASTURTIUM OFFICINALE var. SIFOLIUM Reichb. RC—Howard & Lyon, *J. Ecol.* (1952) 228.
- SISYMBRIUM OFFICINALE var. LEIOCARPUM DC. CS—Jordan, *Ann. Soc. Linn. Lyon* (1861) 507.

- ARABIDOPSIS THALIANA var. BREVICAULIS (Druce). CS—Wilson ex Druce, *Rep. Bot. Soc. and Exch. Club* for 1923, 27.
- CAMELINA SATIVA var. INTEGRIFOLIA Wallr. Double recessive—Tedin, *Hereditas* (1925) 290.
- RESEDA LUTEOLA var. CRISPATA (Link) Müller Arg. CC—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1931, 738.
- VIOLA ODORATA var. IMBERBIS (Leight.) Hensl. CC—Leighton, *Fl. Shropshire*, (1841) 116. CS—White, *Fl. Bristol* (1912) 171 ; var. RUBROPURPUREA Greg. CC—Gregory, *Rep. Bot. Soc. and Exch. Club* for 1917, 148B ; var. SUBCARNEA (Jord.) Parl. CS—Gregory, *British Violets*, (1912) 4 ; var. SULFUREA (Cariot) Rouy & Fouc. CC—Riddelsdell ex Riddelsdell, Hedley & Price, *Fl. Glos.* (1948) 68.
- V. HIRTA subsp. HIRTA f. ROSEA Beeby. CS—Hanbury & Marshall, *Fl. Kent* (1899) 46 ; subsp. CALCAREA (Bab.) E. F. Warb. CC—Baker ex White, *Fl. Bristol*, (1912) 175.
- V. RIVINIANA f. VILLOSA Neum., Wahlst. & Murb. RC—White, *Fl. Bristol* (1912) 176 ; Gregory, *British Violets*, (1912) 59 ; subsp. RIVINIANA and subsp. MINOR (Greg.) Valentine CS—Valentine, *J. Ecol.* (1939) 420 and *New Phytol.* (1941) 191. CC—Dizerbo, *Bull. Soc. Sci. Bretagne* (1960) 103.
- V. REICHENBACHIANA var. PUNCTATA (Rouy & Fouc.) Wilmott (*V. canina* var. *maculata* Boenn.?). CC—Gregory, *British Violets*, (1912) 40.
- HYPERICUM PERFORATUM var. ANGUSTIFOLIUM DC. CC—Westcott, *Phytol.* (1843) 427.
- H. PULCHRUM var. PROCUMBENS Rostr. CC—Beeby, *Scot. Nat.* (1888) 212 ; Druce, *Rep. Bot. Soc. and Exch. Club* for 1921, 481.
- HELIANTHEMUM CHAMAECISTUS f. PARVIFLORUM Druce. CC—Anon. ex Druce, *Ann. Scot. Nat. Hist.* (1911) 98 and *Rep. Bot. Soc. and Exch. Club* for 1920, 16. subvar. PALLIDUM Druce. CC—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1931, 738.
- H. CANUM subsp. LEVIGATUM Proctor. CS—Proctor, *Watsonia* (1957) 31, 37.
- SILENE VULGARIS var. HIRSUTA (S. F. Gray). (var. *pubescens* DC.). Dominant, several genes involved—Marsden-Jones & Turrill, *Kew Bull.* (1931) 125 ; var. RUBRA (Ramond ex Sér.). Single dominant gene—Turrill, *Brit. Plant Life*, (1948) 198.
- S. DIOICA subsp. ZETLANDICA (Compton) Tutin. CS—Baker, *J. Ecol.* (1947) 284 and *New Phytol.* (1948) 134. CC—Darimont ex Lambinon, *Bull. Soc. Sci. Bretagne* (1962) 100. Dwarf var., probably this : CC—McNab, *Proc. Bot. Soc. Edinb.* (1838) 57 ; var. ALPESTRIS (Fries ex Blytt). Single recessive gene—Saunders in Bateson & Saunders, *Rep. Evol. Comm. Roy. Soc.* (1902) 15–19 ; De Vries, *Species and Varieties* (1906) 283 and 585.
- AGROSTEMMA GITHAGO var. HIEMALIS Compton. CS—Nathansohn, *Jahrb. Wissensch. Bot.* (1913) 125–153.
- CERASTIUM FONTANUM subsp. TRIVIALE (Link) Jalas var. PRATENSE (Diard). CC—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1931, 739 ; var. HANBURYENSE (Druce). Druce, *Rep. Bot. Soc. and Exch. Club* for 1930, 258.
- STELLARIA NEMORUM subsp. GLOCHIDISPERMA Murb. CS—Peterson, *Bot. Not.* (1936) 323.
- S. MEDIA var. GYMNOCALYX Trautv. Single dominant gene—Peterson, *Bot. Not.* (1936) 312.
- S. NEGLECTA var. ELISABETHAE (F. W. Schultz) Bég. Single dominant gene—Peterson, *Bot. Not.* (1936) 322 ; var. DECIPIENS E. S. Marsh. Simply recessive, 1–2 factors involved—Peterson, *Bot. Not.* (1936) 320.
- SAGINA MARITIMA var. CILIATA Norsdt. CS—Elliston Wright, *J. Bot.* (1935) App. 8.
- S. PROCUMBENS var. SPINOSA S. Gibs. RS—Elliston Wright, *J. Bot.* (1935) App. 6.
- SPERGULA ARVENSIS var. SATIVA (Boenn.) Mert. & Koch. CS—Griffiths, *J. Bot.* (1922) 229. Single gene without dominance ; no genetical association between seed-coat and hairiness characters—New, *Ann. Bot.* (1959) 25–26 ; var. NANA E. F. Linton. CS—Linton, *J. Bot.* (1907) 380.
- CHENOPODIUM ALBUM f. CYMIGERUM (Koch) Schinz & Thell. (*C. viride* auct.). CS—Boreau, *Fl. Centre Fr.*, 2, (1857) 545.
- C. URBICUM var. INTERMEDIUM (Mert. & Koch) Koch. CC—Koch, *Syn. Fl. Germ.*, ed. 1, (1837) 603. CS—Bickham, *Rep. Wats Bot. Exch. Club* for 1905–06, 63.

- C. RUBRUM f. PSEUDOBOTRYODES (H. C. Wats. ex Syme) (Druce, RS—Bromfield, *Phytol.* (1849) 751 ; Watson, *J. Bot.* (1869) 142 ; Hume ex Lousley, *Rep. Bot. Soc. and Exch. Club* for 1932, 444 ; Elliston Wright, *Rep. Bot. Soc. and Exch. Club* for 1932, 267. But see *Rep. Bot. Soc. and Exch. Club* for 1945, 165, for an instance where apparently CS.
- HALIMIONE PORTULACOIDES var. PARVIFOLIA (Rouy). CC—Chapman, *Ann. Bot.* (1937) 305–309.
- MALVA MOSCHATA var. INTEGRIFOLIA Lej. CC—Borrer ex Woods, *Tourist's Fl.* (1850) 62.
- LINUM CATHARTICUM var. DUNENSE Druce. RC—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1931, 741.
- GERANIUM PRATENSE var. LILACINUM Čelak. CC—Heginbotham ex Grose, *Fl. Wilts.* (1957) 173.
- G. ENDRESSII var. THURSTONIANUM Turrill. CC—Rilstone, *Rep. Bot. Soc. and Exch. Club* for 1937, 653.
- G. SANGUINEUM var. MICRANTHUM F. B. White. CC—Bennett, *Sci. Gossip* (1892) 199 ; var. PROSTRATUM (Cav.) Pers. (var. *decumbens* Druce). CC—Lawson ex Ray, *Fascic. Brit.* (1688) ; Syme, *Engl. Bot.*, ed. 3, 2, (1866) 192 ; Druce, *Rep. Bot. Soc. and Exch. Club* for 1923, 32 ; Bolam, *Trans. Nat. Hist. Soc. Northumb., Durh. and Newc.* (1923–26) 84 ; N. D. Simpson ined. Mostly CC but merely extreme of a more or less continuous geo-ecocline—Böcher & Lewis, *Biol. Skr. K. Danske Vidensk. Selsk.* (1962), 11 (5), 1–25 ; var. LANCASTRIENSE (With.) S. F. Gray. Corolla colour: CS—Syme, *Engl. Bot.*, ed. 3, 2, (1866) 192. Recessive—Sansome, *J. Genet.* (1936) 361. Stansfield, *Gard. Chron.* (1928) 208, describes a case of wholesale reversion after forty years of constancy in cultivation.
- G. ROBERTIANUM subsp. CELTICUM Ostenf. CS—Ostenfeld, *Rep. Bot. Soc. and Exch. Club* for 1919, 552 ; Baker, *Watsonia* (1956) 276 ; subsp. MARITIMUM (Bab.) H. G. Bak. CS—Wilmott, *J. Bot.* (1921) 95 ; Baker, *Watsonia* (1956) 275.
- G. PURPUREUM subsp. FORSTERI (Wilmott) H. G. Bak. CC—Pugsley, *Rep. Wats. Bot. Exch. Club* for 1927–28, 427. CS—Baker, *Watsonia* (1955) 165 and *New Phytol.* (1957) 189.
- ERODIUM MOSCHATUM var. MINUS Rouy. RC—Miller ex White, *Proc. Bristol Nat. Soc.* (1928) 53.
- E. CICUTARIUM subsp. CICUTARIUM and subsp. DUNENSE Andreas. CS—Larsen, *Biol. Medd. K. Danske Vidensk. Selsk.* (1958), 23 (6), 17–19.
- OXALIS ACETOSELLA var. CAERULEA Pers. (var. *subpurpurascens* DC.). CC—Leighton, *Fl. Shropshire*, (1841) 196. CS—Wolley-Dod, *Fl. Sussex* (1937) 100.
- EUONYMUS EUROPAEUS var. LEUCOCARPUS Druce. RS—Roper, *Rep. Bot. Soc. and Exch. Club* for 1924, 710.
- ULEX EUROPAEUS var. STRICTUS (Mackay) Webb (*U. hibernicus* G. Don ex Loud.). CS—Cameron, *Phytol.* (1841) 76. CS, but not invariably—Babington ex Syme, *Engl. Bot.*, ed. 3, 3, 5 (1866).
- SAROTHAMNUS SCOPARIUS subsp. MARITIMUS (Rouy) Ulbr. RS—Mitten ex Reid, *Origin Brit. Fl.*, (1899) 4. CS—Jackson, *Gard. Chron.* (1939) 387 ; Böcher, *Bot. Tidsskr.* (1955) 129 ; Adams, *Watsonia* (1957) 17 ; P. F. Yeo ined.; Alderney material CC—M. C. F. Proctor ined.; Dungeness plants CC but genetically distinct from Lizard and Pembroke-shire plants—Gill & Walker ex Ford, *Ecol. Genetics*, (1964) 293.
- ONONIS REPENS var. HORRIDA Lange. CS—Bennett, *Rep. Bot. Exch. Club* for 1889, 245. CS, but spines disappeared subsequently—Henslow, *Heredity of Acquired Characters in Plants*, (1908) 33 (as *O. spinosa* L.).
- TRIFOLIUM ARVENSE L. Stature, head-length, etc. genotypic, but described variants merely extremes of clines—Böcher, Larsen & Rahn, *Biol. Skr. K. Danske Vidensk. Selsk.* (1955), 8 (3), 13, 26.
- T. REPENS var. CARNEUM S. F. Gray (var. *rubescens* Sér.). Single dominant gene—ex Turrill, *Brit. Plant Life*, (1948) 206. For genetics of other, unnamed variants see Daday, *Heredity* (1954) 61–72.

- LOTUS CORNICULATUS var. HIRSUTUS Koch. CC—Larsen, *Bot. Tidsskr.* (1954) 206 ; var. CRASSIFOLIUS Pers. CC, only with respect to fleshiness of leaves—Larsen, *Bot. Tidsskr.* (1954) 206.
- ONOBRYCHIS VICHIFOLIA Scop. Indigenous chalk-down form : CC—Grose, *Fl. Wilts.* (1957) 206.
- VICIA SYLVATICA var. CONDENSATA Druce. CS—Druce, *J. Bot.* (1911) 235.
- LATHYRUS MONTANUS var. TENUIFOLIUS (Roth) Garcke. CC—Don, *Mem. Wernerian Nat. Hist. Soc.* (1821) 302. RS—Koch, *Syn. Fl. Germ.*, ed. 3, (1857) 176. CS—Anon. ex Druce, *Rep. Bot. Soc. and Exch. Club* for 1915, 337.
- FILIPENDULA ULMARIA var. DENUDATA (Hayne). CC—Beeby, *Rep. Bot. Exch. Club* for 1887, 170 ; Yapp, *Ann. Bot.* (1912) 840. CS—Druce, *New Phytol.* (1911) 311.
- RUBUS IDAEUS f. OBTUSIFOLIUS (Willd.) W. Wats. (var. *obtusifolius* (Willd.) Focke. var. *anomalous* Arrhen). Single recessive gene—Crane & Lawrence, *J. Genet.* (1931) 254 ; var. ASPERRIMUS E. Lees. Single dominant gene—Crane & Lawrence, *Genetics of Garden Plants*, (1938) 130.
- POTENTILLA ANSERINA var. SERICEA (Hayne) Koch. RC—Trail, *Ann. Scot. Nat. Hist.* (1906) 38.
- P. REPTANS var. MICROPHYLLA Tratt. CC—Anon. ex Druce, *Fl. Berks.*, (1897) 192. RC—Fraser, *Rep. Bot. Soc. and Exch. Club* for 1926, 260.
- FRAGARIA VESCA var. BERCHERIENSIS (Druce) Druce. CC—Von Solms Laubach ex Druce, *J. Bot.* (1910) 198 ; f. ALBA (Ehrh.) Rydb. (var. *leucocarpa* Druce). Recessive—Richardson, *J. Genet.* (1923) 152.
- CRATAEGUS MONOGYNA var. XANTHOCARPA Lange (var. *aurea* (Hort. ex Loud.) Druce). CS—Druce, *Rep. Bot. Soc. and Exch. Club* for 1911, 91.
- SEDUM TELEPHIUM var. FABARIA (Koch) Kirschleger. CC—Britton, *J. Bot.* (1932) 317.
- PARNASSIA PALUSTRIS var. CONDENSATA Travis & Wheldon. CC—Graebner ex Druce, *New Phytol.* (1912) 359 ; Travis & Wheldon, *J. Bot.* (1913) 88. RC—Salisbury, *Downs and Dunes* (1952) 278.
- PEPLIS PORTULA var. LONGIDENTATA Gay. CS—Gay ex Allen, *Watsonia* (1954) 86.
- EPILOBIUM HIRSUTUM var. VILLOSISSIMUM Koch. CS—Compton, *Rep. Bot. Soc. and Exch. Club* for 1913, 469.
- E. TETRAGONUM f. STENOPHYLLUM Hausskn. CS—Druce, *Rep. Bot. Soc. and Exch. Club* for 1913, 469.
- E. PALUSTRE var. LAVANDULAEFOLIUM Lec. & Lam. CC—Marshall, *J. Bot.* (1910) 122.
- E. ANGUSTIFOLIUM var. BRACHYCARPUM Leight. CC—Syme, *Engl. Bot.*, ed. 3, (1866) 4, 9. CS—Ockendon & van den Driessche, *Proc. Bot. Soc. Br. Is.* (1963) 172.
- HEDERA HELIX var. ARBORESCENS Loud. RS—Turesson, *Bot. Not.* (1961) 443.
- ANTHRISCUS SYLVESTRIS (L.) Hoffm. All leaf forms CS but form a continuous clinical series—Petersen, *Dansk Bot. Arkiv.* (1915) 1 (6), 149. Dissected-leaved extreme (*Chaerophyllum sylvestre* var. *angustisectum* Druce). CS—Hall, *J. Bot.* (1928) 25.
- PIMPINELLA SAXIFRAGA var. DISSECTA (Retz) Spreng. CS, but only one extreme of a topocline—Peterson, *Bot. Tidsskr.* (1921) 240.
- AETHUSA CYNAPIUM var. AGRESTIS Wallr. RS—Hoffmann, *Bot. Zeit.* (1878) 273. CS, though other dwarf plants that might pass under this name RS—Weimarck, *Bot. Not.* (1945) 351–380 ; var. GIGANTEA Lej. (var. *elata* (Friedl.) Gaud.). CS—Weimarck, *Bot. Not.* (1945) 380.
- HERACLEUM SPHONDYLIIUM var. ANGUSTIFOLIUM Huds. RC—Hudson, *Fl. Anglica*, ed. 2, (1778) 117 ; Bagnall, *Fl. Warwicks.*, (1891) 128. CS—Green ex Grose, *Fl. Wilts.*, (1957) 304.
- DAUCUS CAROTA subsp. GUMMIFER Hook f. CS except for stature—J. E. Lousley ined.; Nehou, *Bull. Soc. Sci. Bretagne* (1961) 97–98.
- MERCURIALIS PERENNIS var. SALISBURYANA Mukerji. CS—Mukerji, *J. Ecol.* (1936) 42.
- EUPHORBIA EXIGUA var. RETUSA Roth. CS—Dunn, *Rep. Rugby Sch. Nat. Hist. Soc.* (1897) 43.

- POLYGONUM AMPHIBIUM var. AQUATICUM Wallr. and var. TERRESTRE (Leyss.) Boenn. RC—Massart, *Bull. Jard. Bot. Bruxelles* (1902) 76.
- P. LAPATHIFOLIUM L. Numerous variants, named and unnamed, CS—Danser, *Rec. Trav. Bot. Neerl.* (1921) 125–210 ; Timson, *Watsonia* (1963) 387.
- RUMEX CRISPIUS var. ULIGINOSUS Le Gall (var. *elongatus* Trimen & Ley, non Guss.). CC—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1931, 753 ; Lousley, *J. Bot.* (1935) 256–260. Most trivial variants of this species CS—Lousley, *Rep. Bot. Soc. and Exch. Club* for 1941–42, 556.
- URTICA PILULIFERA var. DODARTII (L.) Aschers. CS—Bickham, *Rep. Wats. Bot. Exch. Club* for 1905–06, 63. Single recessive gene—Crane in Huxley, *New Systematics* (1940) 531.
- QUERCUS ROBUR var. CRISTATA A. Henry. CS—Yates ex Grose, *Fl. Wilts.*, (1957) 504.
- SALIX REPENS L. Leaf and habit variants. RC—Howitt & Howitt, *Fl. Notts.*, (1963) 184.
- CALLUNA VULGARIS var. ERIKAE Aschers. CC—Graebner ex Druce, *New Phytol.* (1911) 315.
- ERICA TETRALIX var. FISSA Druce. RC—Hall, *J. Bot.* (1928) 25 ; Rayner, *Suppl. Fl. Hampshire* (1929) 67.
- E. VAGANS var. KEVERNENSIS Turrill. RC—Turrill, *Kew Bull.* (1922) 176.
- VACCINIUM VITIS-IDAEA var. PUMILUM Hornem. (subsp. *minus* (Lodd.) Hultén). CC—Nicholson ex Beeby, *Scot. Nat.* (1890) 215.
- PRIMULA FARINOSA var. LITTORALIS H.-Harrison. CS—Heslop-Harrison, *Vasculum* (1921) 22.
- P. VULGARIS f. CAULESCENS (Koch) Schinz & Thell. RC—De Vries, *Species and Varieties* (1906) 635. CC—White, *Fl. Bristol*, (1912) 493.
- ANAGALLIS ARVENSIS var. AZUREA Wilmott. RS—Grindon, *Phytol.* (1842) 130 ; Henslow, *Phytol.* (1849) 651 ; var. PALLIDA Hook. f. CS—Pugsley, *Rep. Wats. Bot. Exch. Club* for 1927–28, 435.
- Corolla colour forms : scarlet dominant over pink, pink over white, white over purple, purple over blue—Marsden-Jones & Weiss, *Proc. Linn. Soc. London* (1938) 146–154. Allen, *Proc. Bot. Soc. Br. Is.* (1954) 157, cites data suggestive of linkage in these colour forms. Var. VERTICILLATA Diard. CS—Diard, *Cat. Pl. Rais. Pas-de-Calais* (1852) 130.
- PULMONARIA OFFICINALIS var. IMMACULATA Opiz (subsp. *obscura* (Dumort.) Murb.) CC—Marshall, *J. Bot.* (1908) 288.
- LITHOSPERMUM OFFICINALE var. PSEUDOLATIFOLIUM C. E. Salmon (var. *latifolium* Gremli?). CC—Salmon, *J. Bot.* (1906) 367 and *Rep. Bot. Exch. Club* for 1908, 390. CS—Marshall, *Rep. Bot. Soc. and Exch. Club* for 1910, 579.
- HYOSCYAMUS NIGER var. PALLIDUS (Waldst. & Kit. ex Willd.) Fries. Recessive—De Vries, *Species and Varieties*, (1906) 283. CS—Jackson, *J. Bot.* (1910) 283.
- SOLANUM DULCAMARA var. MARINUM Bab. CC—Turesson, *Hereditas* (1922) 107, 229–231. CS—Marsden-Jones & Turrill, *J. Ecol.* (1945) 80.
- S. NIGRUM var. FLAVUM Dumort. (var. *chlorocarpum* (Spenn.) Boiss.; *S. luteovirescens* C. C. Gmel.) Single recessive gene—De Vries, *Species and Varieties*, (1906) 282, 298. CS—Britton, *Rep. Bot. Soc. and Exch. Club* for 1935, 94.
- DATURA STRAMONIUM var. TATULA (L.) Torr. Single dominant gene—Saunders in Bateson & Sanders, *Rep. Evol. Comm. Roy. Soc.* (1902) 21–32, Safford, *J. Hered.* (1921) 178–190 ; var. INERMIS (Jacq.). Single recessive gene—Naudin, *Nouv. Arch. Mus.* (1865) 41 ; Saunders in Bateson & Saunders l.c.
- LINARIA VULGARIS var. LATIFOLIA Bab. RC—Watson, *Cybele Brit.*, 3, (1852) 473.
- CHAENORHINUM MINUS var. PRAETERMISSUM (Delastre) Rouy. Single dominant gene—Champagnat, *Bull. Soc. Bot. Fr.* (1952) 301–304.
- SCROPHULARIA NODOSA var. PALLESCENS Döll (var. *bobartii* Pryor). CC—Baxter, *Brit. Phaenog. Bot.*, (1835) 385.
- DIGITALIS PURPUREA var. NUDICAULIS Saunders. Single dominant gene—Saunders, *J. Genet.* (1918) 215–228.
- VERONICA OFFICINALIS var. INTEGRALIS (Druce) Druce. CC—Smith, *Engl. Fl.*, (1824) 1, 23 ; Druce, *Ann. Scot. Nat. Hist.* (1911) 170. Differences in leaf shape and pubescence CS

- but form a more or less continuous geo-ecocline—Böcher, *Dansk Bot. Arkiv* (1944), **11** (7), 1–20.
- V. SERPYLLIFOLIA subsp. SERPYLLIFOLIA var. OBSCURA Drabble & Salmon. CC—Drabble & Salmon, *J. Bot.* (1929) 213 ; subsp. HUMIFUSA (Dickson) Syme. CC—Marshall, *Rep. Bot. Soc. and Exch. Club* for 1917, 235.
- V. ARVENSIS var. NANA (Lam.) Poir. (var. *eximia* Towns.). CS—Townsend, *Fl. Hampshire*, ed. 1, (1883) 232. CC—Druce, *Fl. Berks.* (1897) 377.
- V. PERSICA var. ASCHERSONIANA (Lehm.) C. E. Britton and var. CORRENSIANA (Lehm.) C. E. Britton. CS—Lehmann, *Österr. Bot. Zeitschr.* (1909) 255
- V. POLITA var. POLITA (subsp. *ludwigiana* Lehm.) and var. THELLUNGIANA (Lehm.) Hayek & Hegi. CS—Lehmann, *Österr. Bot. Zeitschr.* (1909) 258.
- V. AGRESTIS var. MICRANTHA Drabble. CS—Drabble, *J. Bot.* (1926) 25 and *Rep. Bot. Soc. and Exch. Club* for 1932, 442.
- MENTHA PULEGIUM var. ERECTA Mill. RC—Fraser ex Salmon, *Fl. Surrey*, 515 (1931).
- ORIGANUM VULGARE var. VIRENS Gren. & Godr. CS—Larsen, *Biol. Skr. K. Danske Vidensk. Selsk.* (1960), **11** (3), 42.
- BETONICA OFFICINALIS var. NANA (Druce). CC—Druce, *Rep. Bot. Soc. and Exch. Club* for 1918, 299 ; C. D. Pigott ined.
- LAMIUM PURPUREUM var. LUMBII Druce. CS—Lumb, *Rep. Bot. Soc. and Exch. Club* for 1914, 156.
- GALEOPSIS TETRAHIT var. NIGRICANS Bréb. RS—Britton, *Rep. Bot. Soc. and Exch. Club* for 1927, 584 and *J. Bot.* (1928) 44.
- TEUCRIUM SCORODONIUM var. ACROTOMUM L. B. Hall. CC—Hall, *Rep. Bot. Soc. and Exch. Club* for 1929, 236.
- PLANTAGO MAJOR var. ROSEA Boenn. (var. *bracteata* Druce). CS—White, *Fl. Bristol* (1912) 501 ; Orme ex Druce, *Rep. Bot. Soc. and Exch. Club* for 1928, 634 ; var. MINOR Roth (var. *minima* (DC.) Schlecht., var. *intermedia* auct.) RS—Schultz, *Arch. Fl. Fr. Allem.* (1869) 376. RC—Marsden-Jones & Turrill, *J. Ecol.* (1930) 372–375 ; var. MAXIMA Schlecht. CS, perhaps recessive—Griffiths, *J. Bot.* (1922) 230 ; var. SCOPULORUM Fries (subsp. *intermedia* (Godr.) Lange). CC—Bureau, *Fl. Centre Fr.*, ed. 3, (1857) 2, 537 ; Turesson, *Hereditas* (1925) 160 ; Koch, *Ber. Schweiz. Bot. Ges.* (1928) 45–61.
- P. LANCEOLATA var. ANTHOVIDIRIS W. Wats. CS—Watson, *J. Bot.* (1937) 231–233. var. CAPITATA Schum. (var. *sphaerostachya* Mert. & Koch var. *lanuginosa* Boenn.; *P. eriophora* Hoffm. & Link ; var. *capitellata* Sonder ex Koch). RC—Lawson, *Bot. Gaz.* (1849) 35 ; Druce, *Rep. Bot. Soc. and Exch. Club* for 1910, 583 and *J. Bot.* (1911) 235. RS—Griffiths, *J. Bot.* (1922) 229. CS as one extreme of an ecocline—Böcher, *Dansk Bot. Arkiv* (1943), **3**, 1–18. CC—Nehou, *Bull. Soc. Sci. Bretagne* (1955) 113–133 ; var. ALTISSIMA Schum. (var. *sylvatica* Pers.; var. *major* Syme). CS as one extreme of an ecocline—Böcher, l.c.
- P. MARITIMA var. LINEARIS Syme. CC—Hosking ex Davey, *Fl. Cornwall*, (1909) 372 and ex Williams, *Prodr. Fl. Brit.* (1910) 363 ; var. PUNCTATA Neum. Single dominant gene—Gregor, *New Phytol.* (1938) 31. Other variants CS, but part of more or less continuous ecoclines—Gregor, *New Phytol.* (1938) 15–49, (1939) 293–322.
- P. CORONOPUS var. MARITIMA Gren. & Godr. (var. *ceratophyllum* Rapin). CS—Wheldon, *Rep. Bot. Soc. and Exch. Club* for 1915, 366 ; Turrill in Wilmott, *Brit. Fl. Plants and Modern Syst. Methods*, (1949) 18. CC—M. E. Gillham ined ; var. PYGMAEA Lange (*Astero-geum laciniatum* var. *capitatum* S. F. Gray). RC—Salisbury ex Moss, *Rep. Wats. Bot. Exch. Club* for 1914–15, 505 and in Huxley, *New Systematics*, (1940) 333 ; Watson ex Thurston & Vigurs, *Suppl. Fl. Cornwall*, (1922) 114. RS to some extent—Gravis, *Bull. Biol. Fr. Belg.* (1932) Suppl. xiv, 66. Some populations RS, others CS, forming one extreme of an ecocline—Böcher, Larsen & Rahn, *Hereditas* (1955) 440–442.
- CAMPANULA GLOMERATA var. MINOR S. F. Gray (var. *nana* C. Bailey). RC—Bromfield, *Phytol.* (1849) 527 ; Druce, *Fl. Berks.*, (1897) 325.

- GALIUM APARINE* var. *MARINUM* Fries (var. *confertum* Westerlund ; var. *condensatum* Druce). CS—Böcher, Larsen & Rahn, *Biol. Skrift. K. Danske Vidensk. Selsk.* (1955), 8 (3), 21 ; F. H. Perring & R. G. West ined.
- VALERIANELLA LOCUSTA* var. *DUNENSIS* D. E. Allen. CS—Young ex Allen, *Watsonia* (1961) 45.
- SUCCISA PRATENSIS* var. *NANA* Bolle (*S. subacaulis* Bernardin). CC—Turesson, *Hereditas* (1922) 222–225. RC—N. D. Simpson ined.
- BIDENS CERNUA* f. *RADIATA* (Roth) Larsson. CS—De Vries, *Species and Varieties*, (1906) 158.
- SENECIO JACOBAEA* var. *FLOSCULOSUS* DC. (var. *discoideus* Wimm. & Grab.). CS—Schultz Bipont, *Arch. Fl. Fr. Allem.* (1855) 128. A “mid-ray” form (*S. dunensis* var. *breviradius* Dumort.) appears when this variety is crossed with the type—Trow, *J. Genet.* (1912) 250 ; it has been observed in the field or in cultivation by Dumortier, *Fl. Belg.* (1827) 66 ; Jordan, *Cat. Jard. Bot. Dijon* (1848) 30 ; and Rosser ex Harper & Wood, *J. Ecol.* (1957) 630 ; var. *STENOGLOSSUS* Brenan & Simpson. CS—N. D. Simpson ined.
- S. AQUATICUS* var. *INTERMEDIUS* Druce. CS—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1932, 437.
- S. SQUALIDUS* f. *SUBINTEGER* Druce. CS—Druce, *Rep. Bot. Soc. and Exch. Club* for 1928, 914.
- S. VULGARIS* var. *DENTICULATUS* (O. F. Müll.) Hyl. (var. *radiatus* Koch ; var. *lanuginosus* Druce). CS—Watson ex Briggs, *Fl. Plymouth* (1880) 205 ; Trow, *J. Bot.* (1909) 306 and *J. Genet.* (1912) 246 ; Druce, *Rep. Bot. Exch. Club* for 1908, 382 ; var. *HIBERNICUS* Syme (var. *radiatus* auct.). CS—Syme, *Rep. Bot. Exch. Club* for 1872–74, 27 ; Colgan, *Fl. Co. Dublin* (1904) 113 ; Young, *Yearbook Bot. Soc. Br. Is.* (1950) 92. Presence of ray florets : single gene without dominance, heterozygotes represented by a “mid-ray” form—Trow, *J. Bot.* (1909) 306 and *J. Genet.* (1912) 246.
- TUSSLILAGO FARFARA* var. *DENUDATA* Druce. CC—West ex Druce, *Rep. Bot. Soc. and Exch. Club* for 1916, 417.
- PULICARIA DYSENTERICA* var. *HUBBARDII* Turrill (var. *ramosissima* Lec. & Lam.?). CS—Turrill, *J. Ecol.* (1951) 221.
- SOLIDAGO VIRGAUREA* L. Continental material not certainly identifiable with taxa described from Britain has been tested as follows : var. *RETICULATA* DC. CC—Lange, *Naturhist. Foren. Vidensk. Medd.* (1861) 115–116 ; var. *ALPESTRIS* (Walst. & Kit.) DC. (var. *plukenetiana* Druce?). CC—Turesson, *Hereditas* (1925) 204–215 ; subsp. *RUPICOLA* (Rouy) Lambinon (var. *corymbosa* Druce?). CC—Lambinon, *Lejeunia* (1962) 64.
- ASTER TRIPOLIUM* var. *DIFFUSUS* DC. (var. *arcticus* Fries). CS—Turesson, *Hereditas* (1922) 221.
- BELLIS PERENNIS* var. *CAULESCENS* Lej. RS—Carano & Bambacioni, *Ann. di Bot.* (1923) 32.
- ACHILLEA MILLEFOLIUM* var. *CONTRACTA* Schlecht. (var. *crustata* Koch). CS—Clausen, Keck & Hiesey, *Exper. Studies on Nature of Species*, (1940) 1, 304 ; f. *ROSEA* (Desf.) Rand & Redf. RS—De Vries, *Species and Varieties*, (1906) 133. RC—N. D. Simpson ined.
- TRIPLEUROSPERMUM MARITIMUM* subsp. *INODORUM* (L.) Hyl. ex Vaarama. CS—Turesson, *Hereditas* (1922) 232 ; Nehou, *Bull. Soc. Sci. Bretagne* (1954) 146–152 ; var. *SALINUM* (Wallr.). RS—Lloyd, *Fl. Loire-Inf.*, (1844) 139 ; Massart ex Cuénot, *L’Espèce* (1934) 74. RC—Drabble & Drabble, *J. Bot.* (1910) 154.
- CIRSIMUM ARVENSE* var. *SETOSUM* (Willd.) C. A. Meyer. CC—Druce, *Fl. Berks.*, (1897) 303.
- C. ACAULON* var. *CAULESCENS* (Pers.) DC. RS—Trow, *Fl. Glamorgan*, 97 (1911).
- C. DISSECTUM* var. *BIFLORUM* (Desp.) (var. *ambiguum* (Rouy) Sledge ; *C. anglicum* subvar. *polycephalum* Coss & Germ.). CC—Linton, *Rep. Bot. Exch. Club* for 1885, 131.
- CENTAUREA SCABIOSA* var. *INTEGRIFOLIA* Gaud. (var. *succisifolia* E. S. Marsh.) CS—Marshall, *J. Bot.* (1901) 268.
- HYPOCHOERIS GLABRA* var. *EROSTRIS* Coss & Germ. CS and uniform in F_1 .—Turrill, *Kew Bull.* (1918) 304 ; var. *ROSTRATA* Coss. & Germ. RS—Lloyd, *Fl. Loire-Inf.*, (1844) 151 and *Fl. Ouest Fr.*, ed. 1, (1854) 266.

- LEONTODON AUTUMNALIS var. PRATENSIS (Link) Koch (var. *nigrolanatus* Fries ; var. *sordidus* Bab.). CC—Turesson, *Hereditas* (1925) 177–179 ; var. SALINUS (Aspegren) Lange. CC—Turesson, *Hereditas* (1922) 236.
- L. HISPIDUS var. GLABRATUS (Koch) Bisch. RS—(but from data cited could be a recessive)—Crépin, *Man. Fl. Belg.*, ed. 1, (1850) 135.
- L. TARAXACOIDES f. DUBIA (Bab.) (*L. leysseri* f. *lasiolaena* (Bisch.) F. N. Will.). CS—Watson ex Salmon, *Fl. Surrey*, 424 (1931).
- PICRIS HIERACIOIDES var. GRACILIS (Jord.). RS—Drabble, *Rep. Bot. Soc. and Exch. Club* for 1931, 747.
- SONCHUS OLERACEUS var. GLANDULOSUS (Coss., Germ. & Wedd.) Druce. CS—Ostenfeld, *Bot. Tidsskr.* (1917) 343 ; var. TRIANGULARIS Wallr. (var. *runcinatus* Koch). CS—Ostenfeld, *Bot. Tidsskr.* (1917) 343 ; var. LACERUS (Willd.) Wallr. (*S. ciliatus* Lam.). CS—Boreau, *Fl. Centre Fr.*, ed. 3, (1857) 2, 381 ; Ostenfeld, *Bot. Tidsskr.* (1917) 344 ; f. ALBESCENS Neum. CC—Ostenfeld, *New Phytol.* (1912) 120 and *Bot. Tidsskr.* (1917) 345.
- S. ASPER var. ASPER (var. *pungens* Bisch.,; *S. spinosus* Lam.) and var. MOLLIS Coss. & Germ. (var. *inermis* Bisch.). CS—Ostenfeld, *Bot. Tidsskr.* (1917) 346 ; var. GLANDULOSUS (Coss., Germ. & Wedd.) Beckh. CS—Druce, *Rep. Bot. Soc. and Exch. Club* for 1920, 236.
- HIERACIUM UMBELLATUM var. DUNENSE Reyn. (var. *litorale* Lindeb.). CC—Turesson, *Hereditas* (1922) 109.
- H. PELETERANUM var. TENUISCAPUM Pugsl. CC—Darimont ex Lambinon, *Bull. Soc. Sci. Bretagne* (1962) 107.
- CREPIS CAPILLARIS var. DIFFUSA (DC.) Druce. RS—Lloyd, *Fl. Ouest Fr.*, ed. 1, (1854) 273. For genetics of various other characters see Collins, *Univ. Calif. Publ. Agr. Sci.* (1924) 249–296.
- BALDELLIA RANUNCULOIDES var. REPENS Davies. CC—Glück ex Druce, *Rep. Bot. Soc. and Exch. Club* for 1910, 509.
- ASPARAGUS OFFICINALIS subsp. PROSTRATUS (Dumort.) E. F. Warb. CC except for stature—Wilson, *Bot. Miscell.* (1831) 413.
- ENDYMION NON-SCRIPTUS var. BRACTEATUS (Hort. ex Baker). CC—Watson, *Phytol.* (1850) 808 and *Rep. Bot. Exch. Club* for 1869, 14 ; White, *Fl. Bristol*, (1912) 594 ; Turrill in Wilmott, *Brit. Fl. Plants and Modern Syst. Methods*, (1949) 18 ; var. LECAILLEI (Corb.). CC—Lecaille ex Senay, *Rep. Bot. Soc. and Exch. Club* for 1929, 38.
- JUNCUS EFFUSUS var. SPIRALIS McNab. CS—McNab, *Trans. Bot. Soc. Edinb.* (1873) 502 ; Druce, *Rep. Bot. Soc. and Exch. Club* for 1909, 419.
- J. ARTICULATUS var. LITTORALIS Patze, Meyer & Elkan (var. *nigritellus* auct.) CC—Clapham, *S. E. Nat. and Antiq.* (1943) 29–32 ; Richards, *New Nat.* (1949) 44.
- MOLINIA CAERULEA var. DEPAUPERATA (Lindl.) Bab. and var. ARUNDINACEA (Schränk) Aschers. CC—Guinochet & Lemée, *Rev. Gén. Bot.* (1950) 578.
- DACTYLIS GLOMERATA var. COLLINA Schlecht. (var. *abbreviata* (Bernh. ex Reichb.) Drej.). CS—Stapledon, *J. Ecol.* (1928) 94. Dwarf sea-cliff form : CS—Gregor & Sansome, *J. Genet.* (1927) 357 ; Stapledon, *J. Ecol.* (1928) 100 ; Böcher, *Bot. Tidsskr.* (1961) 319.
- AVENA STRIGOSA subsp. GLABRESCENS Marq. and subsp. ORCADENSIS Marq. CS—Marquand, *Rep. Bot. Soc. and Exch. Club* for 1921, 322–325.
- ARRHENATHERUM ELATIUS var. BULBOSUM (Willd.) Spenn. (*A. tuberosum* F. W. Schultz). CS—Druce, *Fl. Berks.* (1897) 571.
- DESCHAMPSIA CESPITOSA var. BREVIFOLIA (Parn.) Druce. RC—Druce, *J. Bot.* (1890) 46.
- AGROSTIS TENUIS var. HUMILIS (Aschers. & Graebn.) Druce. CC—Philipson, *J. Linn. Soc. London* (1937) 110. Variation in this species consists of a continuous series of ecotypes, without clear clines—Bradshaw, *New Phytol.* (1959) 208.
- A. STOLONIFERA var. STOLONIFERA. CC—Philipson, *J. Linn. Soc. London* (1937) 110 ; var. MARITIMA (Lam.) Koch, var. COARCTATA (Ehrh. ex Hoffm.) Čelak. and subvar. SALINA Jans. & Wacht. All RC—Philipson, *J. Linn. Soc. London* (1937) 109–110.

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THE BREEDING RELATIONSHIPS OF SOME EUROPEAN EUPHRASIAE

By P. F. YEO

University Botanic Garden, Cambridge

ABSTRACT

Previous chromosome counts on *Euphrasia* are summarized, and one new count is reported. Two chromosome numbers, $2n = 22$ and $2n = 44$ are known in the genus.

Euphrasia species are not apomictic but are fully self-fertile, producing viable seed. Crosses were carried out between different populations of the same species, and between different species, both alike and unlike in chromosome number. When chromosome numbers of the parents differed, partially developed seeds were produced, but no hybrids were obtained.

All other crosses gave a good seed set. However, when the parents were in different Subsections of the genus, seed development was variable. In most samples hybrid progeny were raised. Crosses within Subsections produced progeny ranging from almost normal in fertility (meiosis, pollen, seed and progeny) to somewhat sterile. Crosses between Subsections gave highly sterile progeny. Some crosses were carried through several generations; where fertility was initially reduced, it tended to rise in later generations.

The morphology of all the F_1 hybrids, and of later generations of three crosses, is partially described. The F_1 was usually intermediate in most but not all characters, while segregation in later generations suggested polygenic control of most characters. In one cross morphologically divergent lines were selected in later generations.

The flowers of *Euphrasia* are entomophilous but much selfing takes place, the amount probably depending on floral behaviour and flower size. Insect visits are rarely seen in nature, but can be effective in causing cross-pollination in cultivation. The occurrence of natural hybrids indicates the availability of cross-pollination to *Euphrasia* in Britain, but the frequency of hybrids is much affected by ecological conditions.

The ecological and distributional characters of the British species are summarized. Diploids are represented by fewer species and are less wide-ranging and less frequent in occurrence than tetraploids.

Sources of taxonomic difficulty in the genus, and the factors which may at present be maintaining the distinctness of the species are indicated. The appropriate taxonomic treatment of the *Euphrasiae* and their genecological status are briefly discussed.

CHROMOSOME NUMBER

The normal chromosome numbers of British *Euphrasiae* are $n = 11$ and $n = 22$. I have previously published a tabulation of the known chromosome numbers in the genus (Yeo 1954), and it is now possible to add to this list the count $n = 22$ for *E. salisburgensis* var. *hibernica* Pugsl., which I have obtained from metaphase II of meiosis. The count was made on a second-generation cultivated plant of a stock from near Lough Bunny, County Clare, v.c. H 9, Ireland (Tutin, 52129; my serial no. E230, specimen in CGE). Further counts are those of $n = 22$ for *E. stricta* Lehm. (Reese 1952), *E. brevipila*, *E. curta*, *E. rotundifolia* and *E. davidssonii* Pugsl. (Löve 1956). These authors state the origin of their material, though they do not say where voucher specimens are preserved. Instances of pairing failure at meiosis, leading to the occurrence of two univalents, have already been reported for a hybrid of *E. anglica* and for two of the three populations of *E. brevipila* investigated (Yeo 1954, p. 103; 1956, p. 263); the same irregularities have since been found in a sample of *E. brevipila* (from west of Bowes, N.W. York, v.c. 65, no. E247, specimens in CGE and Herb. Univ. Leicester) collected as *E. borealis*. One of the samples for which a count was given in my earlier paper (1954) was misidentified; it is no. E136, listed as *E. pseudokernerii*, and is in fact *E. confusa*.

The diploid species of *Euphrasia* belong to Subsection *Ciliatae*, Series *Hirtellae*, and are weakly differentiated morphologically from the tetraploids of the same Subsection, which are distributed in three other Series. The tetraploid number also occurs in Subsection

Angustifoliae, which is rather strongly separated morphologically from the other tetraploids. The only species counted in this Subsection is *E. salisburgensis*.

APOMIXIS

In order to find out whether apomixis could occur, I cut the anthers and stigmas out of some flowers just before they opened, using plants growing in a greenhouse (Yeo 1964). In a few cases, no observations could be made because of death or disease. In every other flower treated in this way, the capsule failed to develop normally or to dehisce; the capsules grew to only half to two-thirds the length of the calyx and did not swell. In nearly all cases, other capsules at the same node or a later one developed normally. This showed that enough time had been allowed for the unfertilized ovaries to develop before the observations

TABLE 1. *Euphrasia* species tested for apomixis.

	<i>Number of capsules of treated flowers failing to develop</i>
Tetraploid Species	
<i>micrantha</i> E112A	2
<i>occidentalis</i> E73	8
<i>nemorosa</i> E74	1
<i>nemorosa</i> E161	1
<i>pseudokernerii</i> E70	1
<i>pseudokernerii</i> E77	1
<i>brevipila</i> E81	3
Diploid Species	
<i>anglica</i> E71	12
<i>anglica</i> E76	4
<i>rivularis</i> E123	2
Total	35

ended. These unfertilized ovaries eventually died; one, 2 mm long, belonging to *E. anglica* (E76) was opened after death, 7½ weeks from the time of the excisions, and was found to contain eleven undeveloped ovules .25 mm long or less. The number of flowers of each species for which this result was obtained is given in Table 1. Fertile capsules enlarge in about two weeks, becoming somewhat swollen and attaining approximately the length of the calyx; they dehisce after four to five weeks, and the seeds are usually about 1.5 to 2 mm long.

I concluded from these results that apomixis does not play a significant part in the reproduction of *Euphrasia*. Later hybridizing work on these and allied species has not cast doubt on this conclusion.

SELF-FERTILITY

Self-fertility was tested by bagging the flowers of plants growing in the greenhouse, and in some instances assisting the transfer of pollen from anthers to stigma. In Table 2 the results are compared with those of open-pollination in the greenhouse. Extraction of seeds was facilitated by moistening the contents of the capsule first, wet seeds being much easier to handle than dry. Sometimes an unknown number of seeds appeared to have been lost from the capsules when they were first found to have dehisced. These capsules are not included in Table 2. The great majority of bad seeds produced by the selfed plants were very small empty ones, similar to those produced by the unpollinated capsule described earlier. Their occurrence is presumably due to failure of fertilization. As they are rather difficult to extract and detect I have put a dash in the table when I did not record any.

TABLE 2. Seed production with enforced self-pollination and with open-pollination, 1952-57.

	No. of capsules	Total good seed	Total bad seed	Mean no. good seeds per capsule
Self-pollinated				
<i>micrantha</i> E185A	3	28	8	9.3
<i>occidentalis</i> E192*	3	34	2	11.3
E561	10	151	6	15.1
<i>nemorosa</i> E608	10	104	4	10.4
E650*	7	94	13	13.4
<i>confusa</i> E601	4	26	—	6.5
<i>pseudokernerii</i> E42	2	24	—	12.0
E226*	10	99	6	9.9
E609*	6	50	4	8.3
<i>salisburgensis</i> E515 Bavaria	4	46	—	11.5
<i>salisburgensis</i> var. <i>hibernica</i> E230	2	13	3	6.5
<i>anglica</i> E180	8	82	3	10.3
E616	3	26	1	8.7
E663*	9	95	7	10.6
<i>hirtella</i> E559* Brittany	3	18	2	6.0
Open-pollinated				
<i>pseudokernerii</i> E42	38	274	—	7.2
<i>anglica</i> E71	28	265	—	9.5
E76	26	269	5	10.3
E663	4	24	20	6.0

*Pollination assisted in some or all of the flowers.

The remaining bad seeds from selfed capsules comprised a few that were undersized with much-reduced contents and two full-sized testas with no perceptible contents.

Full-sized but empty testas are the characteristic product of the pollination of diploid *Euphrasia*s by tetraploids, and among the open-pollinated seeds recorded in Table 2 all the bad ones of E76, and 19 of those of E663, were of this type. Probably most of these seeds resulted from cross-pollination with tetraploids by insects. The production of good seed by open-pollinated E663 has thus been abnormally reduced. The table shows a high degree of self-fertility, approximately equal to fertility under open-pollination. The greatest number of good seeds in a single selfed capsule was 21 for *E. nemorosa*, 18 for *E. occidentalis*, 16 for *E. anglica* and 15 for *E. pseudokernerii*. Capsules with very few seeds are sometimes undersized, and their dehiscence is probably somewhat delayed.

Fifteen samples of seed resulting from self-pollination of eight species were later sown and germination took place in ten samples representing six species. Figures for some of these samples are given by Yeo (1961); germination ranged from one seed out of 31 to 24 out of 49. Poor germination or complete failure may not necessarily indicate infertility connected with selfing, as germination is often unexpectedly poor in *Euphrasia* (Yeo, l.c.).

CROSS-FERTILITY

Method

The anthers were removed from the flowers by cutting the filaments with a small pair of curved scissors. In large-flowered forms this was sometimes done as the flower was opening, but it is preferable to do it the day before the flower is due to open, and occasionally it was necessary to do it even earlier than this. Cuts in the corolla were usually unavoidable but they had no ill-effects. After extraction the anthers were examined and if they had begun to dehisce, or had been broken, the fact was noted, but the flower could still be used for cross-pollination provided there appeared to be little or no pollen on the stigma.

The resulting seeds were kept separate from those produced by flowers where there was not this slight possibility of selfing. The stigma was pollinated at the time of emasculation or up to three days after the flower had opened. Pollen was transferred on a mounted needle and a lens was used to see that the stigma was well pollinated. The flowers were protected by small paper bags, the lower ends of which were blocked by cotton wool.

Crosses were made between species alike and unlike in chromosome number and, among the latter, between species in the same Series and species in different Series. In addition, different populations of the same species were cross-pollinated. Of the species used, *E. pseudokernerii* (a British endemic) hybridises in nature with *E. nemorosa* and *E. occidentalis*, but shows a marked geographical and ecological separation from *E. brevipila*, *E. micrantha* and *E. scottica*; *E. anglica*, another British endemic, could not meet *E. hirtella*, which I do not believe occurs in Britain, but *E. confusa* and *E. micrantha*, which crossed spontaneously in cultivation, are known to cross in nature, as also are *E. brevipila* and *E. scottica*; *E. salisburgensis* var. *hibernica* appears to cross in nature with *E. nemorosa* and it could conceivably also come into contact with *E. occidentalis*.

Seed production and germination

The seed production from cross-pollinations between diploid and tetraploid species is given in Table 3; this includes figures for capsules where an unknown number of seeds was lost. However, there are few of these, because bad seeds, which predominated, do not fall out of the capsules as easily as good ones. Where there was definitely no selfing, good seed production was almost nil.

TABLE 3. Seed production from cross-pollination of species differing in chromosome number.

<i>Euphrasias</i>	<i>Selfing impossible</i>		<i>Selfing possible</i>	
	<i>No. of capsules</i>	<i>No. of seeds</i>	<i>No. of capsules</i>	<i>No. of seeds</i>
		<i>Bad</i> <i>Good</i>		<i>Bad</i> <i>Good</i>
Diploid female × tetraploid male				
<i>anglica</i> × <i>brevipila</i> E76 × E81	1	13 0	3	15 6
<i>anglica</i> × <i>confusa</i> E76 × E179	1	13 0	2	22 2
E76 × E209	—	— —	3	38 0
E135 × E179	—	— —	5	41 2
<i>anglica</i> × <i>micrantha</i> E180 × E185A	7	79 0	3	38 0
<i>anglica</i> × <i>nemorosa</i> E76 × E154	1	16 0	1	14 0
E168 × E154	3	18 0	4	17 0
E135 × E196	—	— —	2	10 10
E135 × E154	1	16 0	8	36 27
E180 × E196	12	151 1 or 2	2	32 0
<i>anglica</i> × <i>pseudokernerii</i> E76 × E77	2	25 0	1	13 0
E168 × E77	1	2 0	3	10 0
<i>anglica</i> × <i>scottica</i> E76 × E120	1	18 0	3	25 0
Totals	30	351 1 or 2	40	311 47
(Mean per capsule = 11.7) (Mean per capsule = 9)				
Tetraploid female × diploid male				
<i>micrantha</i> × <i>anglica</i> E185A × E493	2	16 0	—	— —
<i>nemorosa</i> × <i>anglica</i> E129 × E76	—	— —	5	0 0
E196 × E180	1	11 0	—	— —
E474 × E493	2	? 0	—	— —
<i>nemorosa</i> × <i>rostkoviana</i> E474 × E520	10	14 0	5	10 0
<i>pseudokernerii</i> × <i>anglica</i> E42 × E76	—	— —	2	10 3
E77 × E76	1	0 0	—	— —
	—	— —	2	0 0

The type of bad seed produced depended on whether the diploid or the tetraploid was the ovule parent. In the first case, the capsules developed normally and dehisced, though sometimes rather belatedly. As a rule they contained normal numbers of full-sized but empty, or nearly empty, testas. When the ovule parent was tetraploid, full-sized empty seeds were not produced. Many of the capsules were undeveloped, and doubtless contained minute empty ovules, which were seen in a number of cases though not usually counted. Occasionally, partially developed seeds were found; these had considerably undersized testas but some development of contents, though much less than in a normal seed, even when it nearly filled the testa. Usually several such seeds occurred in the same capsule which was itself partially developed (for example, the 24 bad seeds of *E. nemorosa* $\times$ *E. anglica*, E474 $\times$ E493, were produced by only three of the fifteen flowers pollinated). Seeds of this type were formed in all the crosses shown in the lower part of Table 3 except the two between *E. pseudokernerii* and *E. anglica* (they also appear in a number of later tables under the heading 'partly filled').

A possible interpretation of these results is that, when the diploid is female, fertilization takes place readily and seed-development begins; but although the testa reaches full size there is practically no development of the embryo and endosperm. The initiation of seed-development seems to stimulate the development of the capsule. When the tetraploid is the female, fertilization perhaps takes place more rarely, but when it does the development of seed-contents goes further than in the reverse cross. Perhaps, therefore, there is a better chance of getting a triploid from the cross with the tetraploid as female, although at first the reverse type of cross seemed more promising.

All the apparently good seeds from these pollinations were sown. Where selfing was thought to have been impossible one seed (of the cross *E. anglica* $\times$ *E. nemorosa*, E180 $\times$ E196) germinated but the seedling died at an early stage. A total of 58 seeds was sown where there was a possibility of selfing; of these 14 germinated and ten plants were raised, all of them like the seed-parents, and presumably resulting from accidental self-pollination. This failure to obtain hybrids between diploid and tetraploid species is not surprising in view of the fact that I have only once found a triploid in nature; this was a hybrid between *E. anglica* and *E. micrantha* (Yeo 1954, 1956).

The seed production in crosses between parents alike in chromosome number is given in Table 4. There are two types of cross here, namely those between two populations of the same species (*E. anglica*) and those between different species. The total seed production was moderate, and so also was the production of good seed, since only about one-ninth of all seeds were bad.

Most of the bad seeds that were produced were the minute empty ones described previously, but in the cross *E. occidentalis* $\times$ *E. salisburgensis* var. *hibernica*, E192 $\times$ E230, two of the bad seeds were half-filled and large; in the similar cross *E. nemorosa* $\times$ *E. salisburgensis*, E608 $\times$ E515, there was one large empty seed in a capsule in which the good seeds varied in size and shape; and in the reverse cross between these species, E515 $\times$ E608, one bad seed had contents but was only about half the normal thickness, while some of the seeds classed as good in the same capsule were also rather thin. In *E. anglica* $\times$ *E. anglica*, E663 $\times$ E649, four of the total of ten bad seeds were large empty ones. In the cross *E. pseudokernerii* $\times$ *E. micrantha*, E609 $\times$ E185A, most seeds appeared well-filled and looked normal, but it was noticed that they were distinctly smaller than artificially self-pollinated seeds of *E. pseudokernerii* and open-pollinated seeds of *E. micrantha*; they were, however, classed as good seeds.

Germination of these seeds is shown in Table 5. Although the crosses between Subsections (i.e. those involving *E. salisburgensis*) produced seeds of varying development, germination was quite good when compared with that of crosses within Subsection *Ciliatae*.

Meiosis in the hybrids

E. pseudokernerii $\times$ *E. nemorosa*, E42 $\times$ E154. Only one slide of pollen mother cell meiosis was made of this hybrid. Notes were made on 17 cells at various stages, but in none

TABLE 4. Seed production from cross-pollination between forms alike in chromosome number.

Parents (female × male)	Selfing impossible			Selfing possible		
	No. of capsules	No. of seeds		No. of capsules	No. of seeds	
		Bad	Good		Bad	Good
One species						
<i>anglica</i> × <i>anglica</i> E76 × E71	—	—	—	1	0	13
E76 × E168	2	0	38	1	0	16
E663 × E649	5	4	28*	3	6	36
Species in same Series						
<i>anglica</i> × <i>hirtella</i> E616 × E559	4	1	7*	4	0	15*
<i>pseudokernerii</i> × <i>nemorosa</i> E 42 × E154	2	0	13	2	0	15
E609 × E608	3	5	36	—	—	—
<i>pseudokernerii</i> × <i>occidentalis</i> E226 × E192	2	1	7*	4	0	15*
Species in different Series of same Subsection						
<i>pseudokernerii</i> × <i>brevipila</i> E70 × E81	—	—	—	1	0	5
E609 × E623†	1	0	10	—	—	—
<i>brevipila</i> × <i>scottica</i> E81 × E120	—	—	—	3	3	20
<i>pseudokernerii</i> × <i>micrantha</i> E609 × E185A	4	4	49	—	—	—
E699 × E185A	4	8	34*	1	6	8
<i>pseudokernerii</i> × <i>scottica</i> E42 × E120	1	0	8	1	0	11
Species in different Subsections						
<i>salisburgensis</i> var. <i>hibernica</i> × <i>occidentalis</i> E230 × E192	7	7	28*	3	4	19
<i>occidentalis</i> × <i>salisburgensis</i> var. <i>hibernica</i> E192 × E230	6	4	42*	4	2	24
<i>salisburgensis</i> × <i>nemorosa</i> E515‡ × E608	—	—	—	2	4	22
<i>nemorosa</i> × <i>salisburgensis</i> E608 × E515‡	1	1	11	2	1	20
Totals	42	35	311	32	26	239

(Mean per capsule = 8.2) (Mean per capsule = 8.3)

*Some other seeds lost, or probably lost.

†From Germany.

‡From France.

TABLE 5. Germination of hybrid seed, and plants raised from it.
(Parents alike in chromosome number)

	No. of seeds sown	No. of seedlings	Plants raised	
			hybrid	non-hybrid
Inter-population crosses of <i>E. anglica</i>	139	30	25	0
Interspecific crosses within Subsection Ciliatae	203	45	28	0
Interspecific crosses between Subsections Ciliatae and Angustifoliae	159	30	12	1

was the interpretation quite clear. No definite irregularities were seen, and it is possible that meiosis was normal in this hybrid. It seems clear that, if there were any irregularities, they could not have involved more than one bivalent.

E. pseudokernerii × *E. scottica*, E42 × E120. About 65 cells derived from three plants were examined. The preparations were slightly better than those of the preceding hybrid. It was rarely possible to get a complete interpretation of a cell, but it seems that meiosis may occasionally have been normal, as it was not always possible to detect irregularities. Usually, however, univalents were visible at Metaphase I (Fig. 1), most frequently two in number, and six at the most. Very little was seen of other stages of meiosis, but in one Anaphase II a group clearly consisting of 22 chromosomes was counted, and at Telophase

II it was noted in one cell that two chromosomes had not quite joined their nearest re-forming nuclei, while in another more advanced cell there were no stray chromosomes.

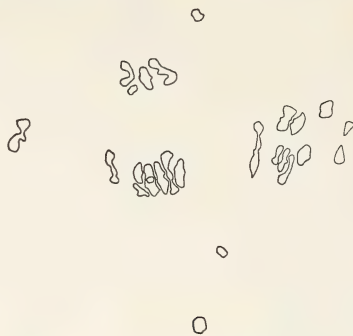


Fig. 1. Metaphase I of meiosis in the F_1 hybrid *Euphrasia pseudokernerii* $\times$ *E. scottica*, E42 $\times$ E120, showing 20 bivalents and 4 univalents. $\times$ 1100.

E. salisburgensis var. *hibernica* $\times$ *E. occidentalis*, E230 $\times$ E192. Notes were made on about 110 cells derived from two plants. Most of the preparations were good, and definite interpretations of some cells were obtained. All stages of meiosis were seen. There were always many univalents present at Metaphase I (Fig. 2); these were counted as accurately as possible, and the results for 40 cells were as follows:

1	cell	had	12	univalents
4	cells	had	16	„
6	„	„	18	„
10	„	„	20	„
11	„	„	22	„
7	„	„	24	„
1	cell	„	28	„

Where an odd number of univalents was visible, one was added to the count, on the assumption that they always occur in pairs. When the chromosomes resulting from the disjunction of bivalents were congregating at the poles at late Anaphase I, some of the univalents came into the equatorial region and divided (Fig. 3), while others were to be seen in the peripheral region and probably did not divide. Finally, all chromosomes joined one or other of the Telophase nuclei.

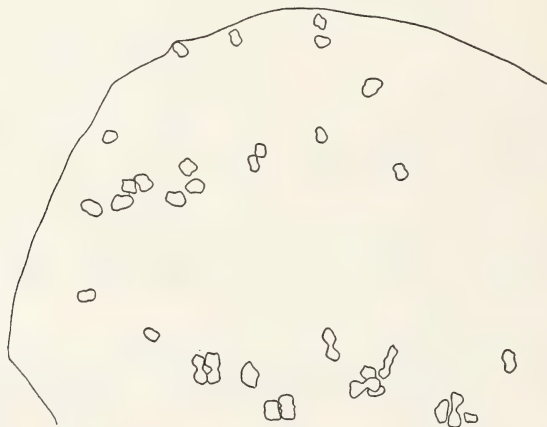


Fig. 2. Metaphase I of meiosis in the F_1 hybrid *Euphrasia salisburgensis* var. *hibernica* $\times$ *E. occidentalis*, E230 $\times$ E192, showing 12 bivalents and 20 univalents (mostly carried away from the equatorial region in squashing the cell). $\times$ 1100.



Fig. 3. Anaphase I of meiosis in E230 $\times$ E192. Univalents dividing in the equatorial region; the rather indefinite outlines which the univalents showed are not indicated by this method of drawing. $\times$ 1100.

At Metaphase II the chromosomes that divided at the first division of meiosis did not line up on the equator but remained scattered and appeared as laggards at Anaphase II (Fig. 4). However, nearly all the laggards eventually joined a nucleus (Fig. 5). Such an irregular meiosis can rarely lead to the production of a pollen grain with a normal set of chromosomes, and any grains which contain 22 chromosomes may well lack some members of the normal set and possess others in duplicate. Some counts were made at Anaphase II and Telophase II which confirmed the inconstancy of the final chromosome numbers. In one cell there were probably 24, 21, 22, and 20 chromosomes in the four nuclei, plus one stray chromosome; other chromosome counts for individual nuclei were 16 or 17, 18, 22 or 23, 24, and for cells at Anaphase II, in which the nuclei could only be counted in pairs, 41 + 47, 39 + 49, 36 + 52, 40 + 48, 42 + 46.

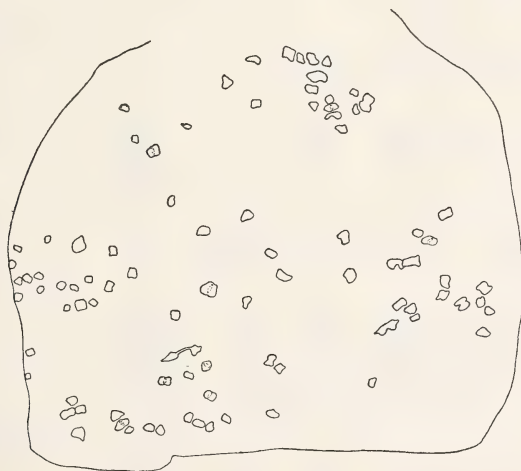


Fig. 4. Anaphase II of meiosis in E230 $\times$ E192. (As the figure shows 89 bodies, it may be that some other matter had been mistaken for a chromosome.) $\times$ 1100.

Production of normal pollen in the hybrids

Pollen counts of hybrids and their parents were obtained by breaking up the anthers in cotton-blue in lactophenol. The numbers of good and bad grains were counted, the good ones being rounded and darkly stained, and the bad ranging from minute to fairly large without contents, or having darkly stained contents but being markedly undersized. These counts were made during July and August 1954; on 6 October 1954, it was discovered



Fig. 5. Late Anaphase II of meiosis in E230 $\times$ E192. Nearly all the chromosomes have joined one of the re-forming nuclei. $\times$ 1100.

TABLE 6. Production of normal pollen in species and hybrids of *Euphrasia*.

	Production of normal pollen (approx.)
	per cent.
Parents	
<i>pseudokernerii</i> E42 $\times$ E70	100
E226	95
<i>occidentalis</i> E192	? 100
<i>salisburgensis</i> var. <i>hibernica</i> E230	? 100
Cross within one species	
<i>anglica</i> $\times$ <i>anglica</i> E76 $\times$ E168	100
Crosses within one Series	
<i>pseudokernerii</i> $\times$ <i>nemorosa</i> E42 $\times$ E154	? 100
<i>pseudokernerii</i> $\times$ <i>occidentalis</i> E226 $\times$ E192	? 90-95
Crosses between Series	
<i>pseudokernerii</i> $\times$ <i>brevipila</i> E70 $\times$ E81	85
<i>pseudokernerii</i> $\times$ <i>scottica</i> E42 $\times$ E120	c. 70
<i>brevipila</i> $\times$ <i>scottica</i> E81 $\times$ E120	85
<i>micrantha</i> $\times$ <i>confusa</i> E185A $\times$ E183C	85
Cross between Subsections	
<i>salisburgensis</i> var. <i>hibernica</i> $\times$ <i>occidentalis</i> E230 $\times$ E192	17-24

that all the counts had been lost and all that remained was a list of pollen samples taken. However, I could remember most of the counts approximately and at once wrote them down. They are given in Table 6.

In the hybrid *E. pseudokernerii* $\times$ *E. scottica* pollen counts were first made from three plants; two of them produced about 70 per cent of normal pollen, and the third produced considerably more. Additional pollen counts were made on anthers collected about two weeks later from two of these plants in order to see whether the discrepancy would be repeated. Both plants gave very much lower proportions of normal pollen than before.

It seemed, therefore, that the production of normal pollen was lower at the later date. If this was so, pollen fertility must fluctuate and one must not expect to assign fixed values to the production of normal pollen in hybrids. Probably, counts showing little or no bad pollen in plants that are not hybrids are more reliable. Table 6 shows a fairly good correspondence between pollen fertility and the affinity of the hybrid's parents although, in view of what has been said, such a conclusion must be regarded as tentative.

Finally, it should be pointed out that these counts are of visually normal pollen, and that the correlation between this and physiologically good pollen is not known.

TABLE 7. Seed production and germination of seed of F_1 hybrids when selfed, open-pollinated or back-crossed, 1954-1958.

Parentage of hybrid	Pollination	No. of plants of the hybrid	No. of capsules	Seeds produced			No. of good seeds per capsule	Germination
				Good	Small empty	Large empty, or partly filled		
Species in same Series								
<i>pseudokernerii</i> × <i>nemorosa</i>								
E609 × E608	selfed	1	2	15	5	0	7.5	+
E609 × E608	× E609 ♀	1	4	24	3	1	6	+
<i>pseudokernerii</i> × <i>occidentalis</i>								
E226 × E192	selfed	1	6	66	1	3	11	+
<i>anglica</i> × <i>hirtella</i>								
E616 × E559	selfed	1	23	57	70	7	2	+
E616 × E559	× E616 ♂	1	1	5	0	5	5	+
Species in different Series, same Subsection								
<i>micrantha</i> × <i>confusa</i>								
E185 × E183	selfed	1	28	227	5	7	8	—
<i>pseudokernerii</i> × <i>brevipila</i>								
E70 × E81	selfed	1	8	85	2	3	10.5	—
E609 × E623	selfed	2	17	174	19	5	10	+
E609 × E623	× E699 ♀	1	4	45	2	0	11.3	+
	(<i>pseudokernerii</i>)							
<i>pseudokernerii</i> × <i>scottica</i>								
E42 × E120	selfed	3	13	100	34	18	7.5	—
<i>pseudokernerii</i> × <i>micrantha</i>								
E609 × E185	selfed	1	17	100	99	4	6	+
E609 × E185	× E185 ♂	1	4	23	24	1	6	+
E609 × E185	× E609 ♀	1	4	18	26	0	4.5	+
E609 × E185	× E699 ♀	1	1	9	2	0	9	—
Species in different Subsections								
<i>salisburgensis</i> var. <i>hibernica</i> ×								
<i>occidentalis</i> E230 × E192	selfed	2	13	8	4	2	<1	—
E230 × E192	open-poll.	1	13	18	14	3	1.5	+
<i>salisburgensis</i> × <i>nemorosa</i>								
E515 × E608	selfed	3	29	4	many	2	<1	—
E515 × E608	open-poll.	4	17	14	c. 100	19	<1	+
E515 × E608	× E701 ♀							
	(<i>nemorosa</i>)	2	3	1	7	3	<1	+*
<i>nemorosa</i> × <i>salisburgensis</i>								
E608 × E515	× E608 ♀	1	4	0	10	9	0	+*
E608 × E515	open-poll.	1	21	7	many	2	<1	+*

*Including seed from additional capsules where accidental selfing was possible.

Seed production and germination in hybrids

Seed production and germination is the conclusive test of fertility in hybrids, and this is shown in Table 7; pollination was artificially assisted in nearly all flowers covered by the table. This shows that normally developed seed was obtained from the F_1 of all crosses. The number of good seeds per capsule was quite high in all but one of the hybrids whose parents belonged to the same Subsection. The exception was *E. anglica* $\times$ *E. hirtella* and it is difficult to account for its infertility. The seeds produced by five open-pollinated capsules of this cross were also counted: these capsules were similarly infertile and contained only one to six seeds each. However, most of the estimates of F_1 fertility in this work are based on single individuals and could therefore easily be biased. The somewhat low rates of seed production in *E. pseudokernerii* $\times$ *E. scottica* and *E. pseudokernerii* $\times$ *E. micrantha* and the low rate in *E. anglica* $\times$ *E. hirtella*, are associated with a large proportion of small empty seeds similar to those found in unpollinated capsules; their occurrence here could be caused by inviable embryo sacs, which would be equivalent to inviable pollen grains. The production of large empty or partly filled seeds by hybrids (which must be due to inviability after fertilization) is probably also a reflection of sterility in the F_1 , as it is particularly noticeable in *E. pseudokernerii* $\times$ *E. scottica*, which would be expected to show some effects of its rather unbalanced meiosis. *E. micrantha* is closely related to *E. scottica* and produced a slightly more sterile hybrid with *E. pseudokernerii* than *E. scottica* did. However, *E. pseudokernerii* (E609) itself had a rather low fertility (Table 10).

The crosses between species of different Subsections were very much more sterile than the others. The plants produced so few seeds that it was necessary to collect seeds resulting from open-pollination, as it was feared there might otherwise be no progeny at all. In E230 $\times$ E192 many of the capsules covered by Table 7 were quite undeveloped and failed to dehisce; those with good seeds, large empty or partly filled ones were more or less well-developed, while those which contained only small empty seeds were more or less undeveloped at first, but later in the season even this class of capsule developed quite well. Capsule development in E515 $\times$ E608 was very much the same, but the sterility was even greater. Both crosses gave more seed under open-pollination than when selfed.

It can be seen from Table 7 that several large samples of seed failed to germinate; since F_2 seed of comparable hybrids germinated in other years, these failures are most

TABLE 8. Seed production and germination of seed of generations later than F_1 , when selfed (cont. in Table 9).

Hybrid generation and year grown	No. of plants	No. of capsules	Seeds produced			No. of good seeds per capsule	Germination
			Good	Small empty	Large empty, or partly filled		
<i>pseudokernerii</i> $\times$ <i>nemorosa</i> E609 $\times$ E608							
F_2 (1958)	1	4	19	23	1	5	+
back-cross to E609 (1958)	1	9	58	43	0	6.5	+
<i>anglica</i> $\times$ <i>hirtella</i> E616 $\times$ E559 F_2 (1958)	4	11	51	11	1	5	—
<i>pseudokernerii</i> $\times$ <i>brevipila</i> E609 $\times$ E623							
F_2 (1958)	1	12	113	36	4	9	+
F_3 (1959)	1	12	109	25	5	9	+
<i>pseudokernerii</i> $\times$ <i>micrantha</i> E609 $\times$ E185							
F_2 (1959)	2	19	101	82	1	5	+
back cross to E185 (1959)	1	7	46	15	7	7	+
back-cross to E609 (1959)	1	6	49	25	0	8	+
F_3 (1960)	{ 1	3	24	13	5	8	+
	{ 1	9	48	42	3	5	+
back-cross to E185 selfed (1960)	1	11	128	32	3	12	+

probably due to unfavourable conditions of seed storage. Three of the F_2 seedlings of *E. pseudokernerii* $\times$ *E. occidentalis* were very pale yellow and died about a week after they had germinated; this is the only occasion on which I have seen albino Euphrasias, either among hybrids or among species.

Seed production and germination in generations later than the F_1 is shown in Tables 8 and 9. Production in *E. pseudokernerii* $\times$ *E. nemorosa* was lower than in *E. pseudokernerii* $\times$ *E. brevipila*, as it was in the F_1 ; it was also still rather low in *E. anglica* $\times$ *E. hirtella*. In the *E. pseudokernerii* $\times$ *E. micrantha* group, fertility tended to rise after the F_2 , but one of the F_3 plants gave a low value and consistently had few (4–8) and large seeds in its capsules. The back-cross to *E. micrantha* selfed produced small and numerous seeds ((6–) 10–16 per capsule). In this cross, one plant of the F_2 in 1959 was male-sterile, and a plant of the F_3 in 1960 at first produced little pollen and later none. The cross *E. salisburgensis* $\times$ *E. nemorosa* is covered by Table 9. The fact that some generations were grown from open-pollinated seed means that further hybridization could have taken place, and evidence

TABLE 9. Seed production and germination of seed of generations later than F_1 (cont. from Table 8).

Generation	Polli- nation	No. of capsules	Seeds produced			Good seeds per capsule	Seeds sown	No. germi- nating
			Good	Small empty	Large empty, or partly filled			
<i>salisburgensis</i> × <i>nemorosa</i>								
E515 × E608 'F ₂ ', from F ₁	open-poll.							
open-poll. One plant	1958	31	1	c. 25	4	<1	1	0
E515 × E608 'F ₂ ', from F ₁	× E608♀							
open-poll. Two plants	1958	6	4	17	0	<1	4	2
E608 × 'F ₂ ' plant 6	selfed							
	1959	13	47	>83	5	3.5	47	29
E608 × 'F ₂ ' plant 6	open-poll.							
	1959	24	48	>146	17	2	48	23
E608 × 'F ₂ ' plant 7	open-poll.							
	1959	25	21	>97	5	<1	22	12
E608 × 'F ₂ ' plant 4	open-poll.							
	1959							
even less fertile								
Selfed progeny of plant 6 above.	selfed							
One plant	1960	14	131	74	3	9.5	128	48
<i>nemorosa</i> × <i>salisburgensis</i>								
E608 × E515 'F ₂ ', from F ₁	selfed							
open-poll. One plant	1959	13	15	>67	3	1	14	11
<i>nemorosa</i> × <i>salisburgensis</i>								
E608 × E515 'F ₂ ', from F ₁	open-poll.							
open-poll. One plant	1959	8	11	46	4	1.5	11	7

that it did so is given later. The most likely sources of pollen, judging by the characters of the progeny, were *E. pseudokernerii* and its hybrids. These belong to Subsection *Ciliatae* and are genomically similar to *E. nemorosa*. The accidental cross-pollination of the F_1 *E. salisburgensis* $\times$ *E. nemorosa*, and of the reciprocal hybrid, would thus be similar in effect to a back-cross. The figures for all the generations in Tables 8 and 9 show a gradual increase in fertility.

Occasionally the highly sterile hybrids involving *E. salisburgensis* produced some seeds which, though rather thin, and thus approaching the 'partly-filled' category, were thought to be worth sowing. The thinness of these seeds was presumably due to some

genetical defect; other seeds, apparently without any such defects, were exceptionally large, doubtless because they received extra nourishment through being so very few in each capsule. Eleven of the seeds produced by E515 $\times$ E608, open-pollinated in 1957, were sown; of these, six were thin and the rest large. They produced four particularly large seedlings and one particularly small one; it seems likely that the small seedling arose from one of the thin seeds and that such seeds are occasionally viable.

During the period when these hybrids were growing, some of the parent populations were maintained by enforced self-pollination, and detailed records were kept of the bad seeds produced. The results are shown in Table 10. It will be seen that *E. pseudokernerii* (E609) was consistently rather infertile, as mentioned earlier. Production of large empty seeds is appreciable though quite low, while partly filled seeds are very rare; this applied also in interspecific pollinations and in the resulting hybrid generations.

TABLE 10. Seed fertility in the parents of *Euphrasia* hybrids

Species	No. of capsules	Seeds produced			Partly filled or under-sized	No. of good seeds per capsule
		Good	Small empty	Large empty		
<i>pseudokernerii</i> E609, 1957, 2 plants	5	27	12	1	0	5
1958, 2 plants	20	143	80	6	1	7
1959, 1 plant	7	59	26	1	0	8
<i>pseudokernerii</i> E699, 1957, 1 plant	9	82	9	2	0	9
1958, 1 plant	5	57	3	1	0	11
<i>nemorosa</i> E701, 1957, 2 plants	16	213	3	0	1	13
<i>nemorosa</i> E608, 1958, 2 plants	14	180	11	5	1	13
<i>anglica</i> E616, 1958, 1 plant	11	140	3	3	0	13

THE MORPHOLOGY OF THE ARTIFICIAL HYBRIDS

Herbarium specimens have been preserved of all the hybrids raised, and in nearly every case specimens of the parents, grown under similar conditions, have also been kept. In addition, flowers and leaves of most plants have been mounted on cellulose tape and photographed by contact printing. A disadvantage of the herbarium specimens is that all plants used as seed parents were pressed much later than their sister plants and later than the best time for showing their characters. Their mounted flowers and leaves are, on the other hand, quite comparable with those of the other plants. This material shows that F_1 hybrids were usually intermediate between the parents, or exhibited combinations of characters of both parents, but that they were occasionally outside the range of both parents in certain characters.

Figs. 8 and 9 and Tables 11–15 show intermediacy of hybrids in number and direction of branches, length of internodes, size and shape of corolla, and node and date of flowering. When plants with glandular hairs on the leaves were crossed with eglandular (or almost eglandular) plants, some progeny were eglandular, some were intermediate in frequency of glands, and some had about as many glands as the glandular parent; this applied in full

TABLE 11. *E. anglica* $\times$ *E. hirtella*, comparison of flowers.

	Angle a (degrees)	Angle b (degrees)
<i>E. hirtella</i> , E559, 4 plants	13–18	60–80
F_1 hybrid, 2 plants	22–29	65–95
<i>E. anglica</i> , E616, 4 plants	35–45	85–100

TABLE 12. *E. pseudokernerii* × *E. nemorosa*.

	No. of plants	Node of last branch	Node of first flower
<i>E. nemorosa</i> , E608, 1958–9	7	8–12	12–16
F ₂ hybrid, 1958–9	3	17	18–24
Back-cross to E609, 1958	3	13–16	18–19
<i>E. pseudokernerii</i> , E609, 1958–9	10	11–25	20–26

TABLE 13. Node of first flower (F) and number of primary branching nodes (B) of *Euphrasia* hybrids and parents.

	<i>pseudokernerii</i> E42	<i>pseudokernerii</i> × <i>brevipila</i> E42 × E81	<i>pseudokernerii</i> × <i>scottica</i> E42 × E120	<i>brevipila</i> × <i>scottica</i> E81 × E120
No. of plants	5	3	10	3
Range of F	13–16	7–9	7–9	6–7
Range of B	3–10	3–5	2–4	0–1

TABLE 14. *E. pseudokernerii* × *E. brevipila*, E609 × E623.

	No. of plants	Start of flowering	Node of first flower	No. of primary branching nodes
E623, 1956	7	Late July–early Aug.	10–12	0–4
E609, 1956	8	Mid-Aug.	16–21	6–14
E609, 1957	6	Late Aug.–early Sept.	15–23	(3—) 9–12
E609, 1960	4	—	17–19	3–7
F ₁ hybrid, 1957	3	Late July–early Aug.	13–15	4–7
F ₂ hybrid, 1958	7	—	10–14	1–6
F ₄ hybrid, 1960	6	—	11–12	1–6
Back-cross: E699* × (E609 × E623), 1958	4	—	14–17	4–7
E699*, 1957–8	3	—	17–22	7–11

**E. pseudokernerii* of different origin from E609.

TABLE 15. Length of lower corolla lip, including tube, of hybrids and parents (in arbitrary units).

	<i>pseudokernerii</i> E609	Back-cross to E609	F ₂ hybrid	Back-cross to E185	<i>micrantha</i> E185
1956–8 number of plants	18				12
length	33–50				21–27
1959 number of plants	15	5	15	5	2
length	39–50	33–45	29–38	27–35	24–26

to the cross *E. pseudokernerii* $\times$ *E. occidentalis* (E226 $\times$ E192), where *E. occidentalis* is the glandular parent; it applied in part to *E. pseudokernerii* $\times$ *E. brevipila* (E70 $\times$ E81), where eglandular and sparsely glandular hybrids were produced, and also to *E. brevipila* $\times$ *E. scottica* (E81 $\times$ E120), where freely glandular and sparsely glandular plants were produced (*E. brevipila* being the glandular parent). An example of parental and hybrid leaf differences is seen in Fig. 11, and flower shape differences are seen in Figs. 6, 7 and 10. Leaf shape is fairly characteristic for species, though naturally each species shows some variation. Flower size is also characteristic within limits but the details of flower shape characterize populations rather than species; flower shapes are, therefore, useful as a form of easily presented evidence that hybrids have been obtained when the parents represent closely similar species, or populations within a species. Although marked differences from year to year in the flower shapes of wild plants growing at particular localities were observed by Wilkins (1963), this character has always appeared to me to be a reliable one in cultivated plants. I think that shape variations associated with size variations, such as described by Wilkins, have occurred in my cultures, but they did not seem to be great enough to affect the usefulness of details of corolla shape for purposes of identification.

Some details of the hybrid morphology will now be given, as evidence that hybrids were in fact raised, and in some cases to show the changes over more than one generation of hybrids.

E. anglica, inter-population hybrids (E76 $\times$ E168) and (E76 $\times$ E71): no plant of the female parent was raised under the same conditions as the F_1 , but both hybrids differed from the selfed progeny of the pollen parents in habit, leaf shape and flower shape (Fig. 6).

E. anglica $\times$ *E. hirtella* (E616 $\times$ E559): in *E. hirtella* the plants matured earlier and the branches developed later than in *E. anglica*; the hybrids were intermediate in these characters. The difference in flower shape was rather marked and the intermediate nature of the progeny is very clear from Fig. 7 and from Table 11, in which measurements are given for the angles which are explained in Fig. 7.

E. pseudokernerii $\times$ *E. nemorosa*: the plants of this hybrid raised in 1954 (E42 $\times$ E154) were more robust and larger leaved than the parental population of *E. nemorosa* (thus approaching *E. pseudokernerii*, as it grew in my cultures) and had more erect branches than *E. pseudokernerii* (being about the same as *E. nemorosa* in this respect). The flowers were

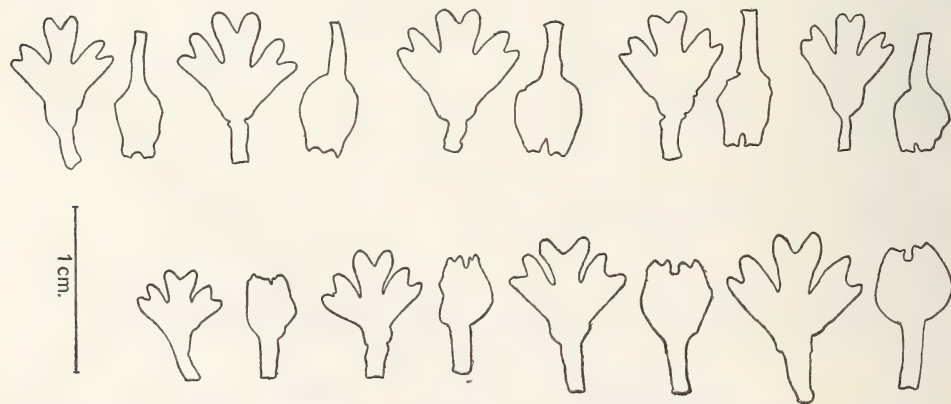


Fig. 6. Flowers of *Euphrasia*. The upper lip and tube, though often distorted in preparation, show overall length of flower and serve as a guide to the relative size of the lower lip, the shape of which is not distorted. Above, flowers of three populations of *E. anglica* and hybrids between them. Left to right, E71 (v.c. 11); E76 $\times$ E71; E76 (v.c. 17); E76 $\times$ E168; E168 (v.c. 55). Below, left to right, *E. nemorosa*, E608 (1956); *E. pseudokernerii* $\times$ *E. nemorosa*, E609 $\times$ E608, F_1 (1957); F_1 back-crossed to E609 (1958); *E. pseudokernerii*, E609 (1957). $\times 2.2$.

intermediate in shape between those of the parents but about the same size as those of *E. nemorosa*, which has smaller flowers than *E. pseudokerneri*. When this cross was repeated in 1956 (E609 $\times$ E608) the parents and hybrids showed much the same characters as before, although the features of the hybrid are known chiefly from the F_2 because only one very weak plant was raised of the F_1 generation. Some numerical data on this cross are given in Table 12, where the F_2 and the back-cross to *E. pseudokerneri* are alike in the characters considered; in other characters, seen in the dried plants, the back-cross approaches very closely *E. pseudokerneri*, and its flowers are closely similar to those of this species (Fig. 6). The F_2 and the back-cross were each selfed and the progeny differed in much the same way as their parents.

E. pseudokerneri $\times$ *E. occidentalis* (E226 $\times$ E192): some of the hybrids raised are shown in Fig. 8. Four F_1 and seven F_2 plants were raised; the F_2 plants shown in the figure represent the extremes of the variation.

E. pseudokerneri $\times$ *E. brevipila*: *E. brevipila* differs little from *E. pseudokerneri* in its flowers and upper leaves, but it has fewer branches and begins to flower earlier and at a lower node. This cross was carried out twice, and the behaviour of the plants in the characters just mentioned can be seen from Tables 13 and 14. No specimens of *E. brevipila* (E81), grown under comparable conditions to the other plants of the earlier cross (E42 $\times$ E81), were available. The *E. brevipila* for the second cross (E609 $\times$ E623) came from north-east Germany; its branches were particularly late in development, but their growth had started sufficiently for them to be counted in the dried specimens. The plants of E609 grown in 1960 were rather weak and branched less freely than those grown in other years and the F_3 hybrid generation is omitted from Table 14 as it consisted of only one plant.

E. brevipila $\times$ *E. scottica* (E81 $\times$ E120): no suitable specimens of either of the parents of this hybrid are available for comparison, but comparisons with other hybrids involving the same parents are given in Table 13. In shape, and in their small size, the flowers of the hybrids showed very strongly the influence of *E. scottica*.

E. pseudokerneri $\times$ *E. scottica* (E42 $\times$ E120): specimens involved in this cross between two widely different species are shown in Fig. 9 in which E120 is represented by a later gathering of wild-collected specimens from its original locality. In addition to the differences that can be seen in the figure, the hybrids differed from *E. pseudokerneri* in their cuneate-based floral leaves (not truncate) with fewer teeth, and in their small flowers; these differences were in the direction of *E. scottica* (see also Table 13).

E. micrantha $\times$ *E. confusa* (E185 $\times$ E183): a seedling grown in 1954, resulting from open-pollination of *E. micrantha* in 1953, proved to be this hybrid. It was particularly

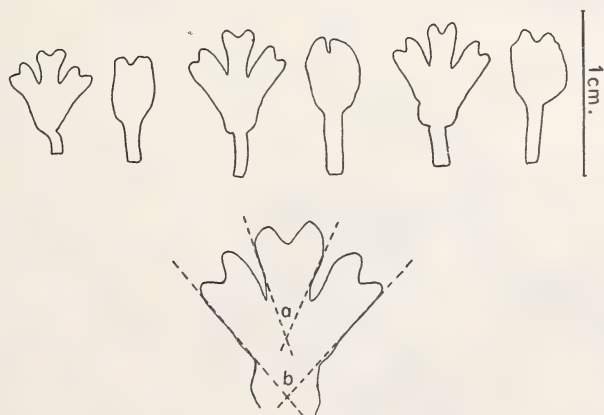


Fig. 7. Flowers of *Euphrasia*. Above, left, *E. anglica*, E616; right, *E. hirtella*, E559; centre, E616 $\times$ E559, F_1 ; all 1954. $\times 2.2$. Below, diagram to explain angles *a* and *b*, used in Table 11.



Fig. 8. Pressed specimens of *Euphrasia*. Right to left. *E. pseudokernerii*, E226 (1955); *E. occidentalis*, E192 (1953); E226 $\times$ E192, F_1 (1954); F_2 (1955), two plants. $\times \frac{1}{4}$.



Fig. 9. Pressed specimens of *Euphrasia*. Left, *E. pseudokerneri*, E42 (1954); right, *E. scottica*, E659, two wild plants from locality of E120 (1956); centre, E42 $\times$ E120, F₁ (1954). $\times \frac{1}{2}$.

interesting in that the flowers were yellow—a character which appeared to be dominant in inheritance, and which it must have received from the pollen parent, the rare yellow-flowered *E. confusa* forma *confusa* which I had grown in 1953.

E. pseudokerneri $\times$ *E. micrantha* (E609 $\times$ E185): the F₁ generation in this cross consisted of a single plant raised in 1958; this was selfed and back-crossed to both parents, and subsequently fresh generations were raised each year until 1961. Three successive generations of the back-cross to *E. micrantha* were grown; these remained fairly uniform and were morphologically close to *E. micrantha*, but they tended to be larger and bushier and had slightly larger flowers (Fig. 10; the leaves are shown in Fig. 11). The first back-cross to *E. pseudokerneri* showed a corresponding approach to that species, but differed from it in its smaller flowers with more lilac colouring in them, showing the influence of *E. micrantha*. The only offspring of this back-cross was a single weak individual. Two F₂ plants were selfed and the progeny kept as separate lines in the following two generations. These two lines (numbered I and III) differed consistently in both the 1960 (F₃) and 1961 (F₄) generations. Line I approached *E. pseudokerneri* in having the branches more spreading and the flowers larger than in Line III, and in having relatively broad leaves at node 9, while it approached *E. micrantha* in its obtuse leaf teeth. Line III approached *E. pseudokerneri* in its more acute leaf teeth, but it was more like *E. micrantha* in its more erect branches, smaller flowers, and (in 1961) slightly more elongated leaves at node 9 (leaf 9 was not available in 1960). The leaf differences are shown in Fig. 12 and habit differences in Fig. 13. Some figures for flower size in this cross are given in Table 15. It will be seen that the range of the F₂ hybrid does not overlap with that of either parent in 1959. The range of the back-cross to *E. micrantha* only just overlaps that of *E. micrantha*, while that of the back-cross to *E. pseudokerneri* overlaps considerably that of *E. pseudokerneri*. The table shows that the larger the flowers the greater the range of variation; probably the larger flowers are

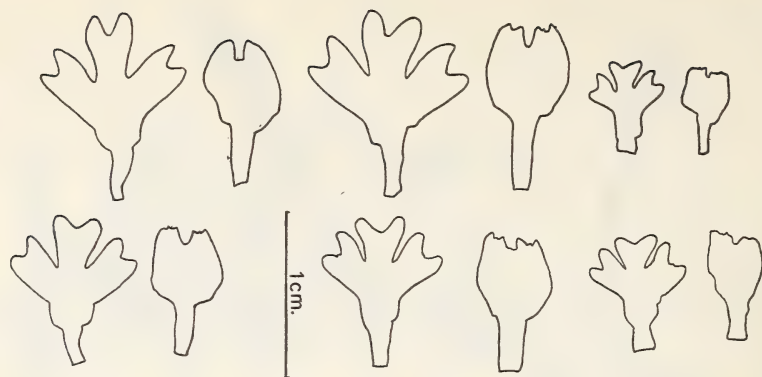


Fig. 10. Flowers of *Euphrasia*. Above, left to right, *E. pseudokernerii*, E609 (1959); the same (1956); *E. micrantha*, E185 (1956). Below, left to right, E609 $\times$ E185 back-crossed to E609 (1959); E609 $\times$ E185 (1958); E609 $\times$ E185 back-crossed to E185 (1959). $\times 2.2$.

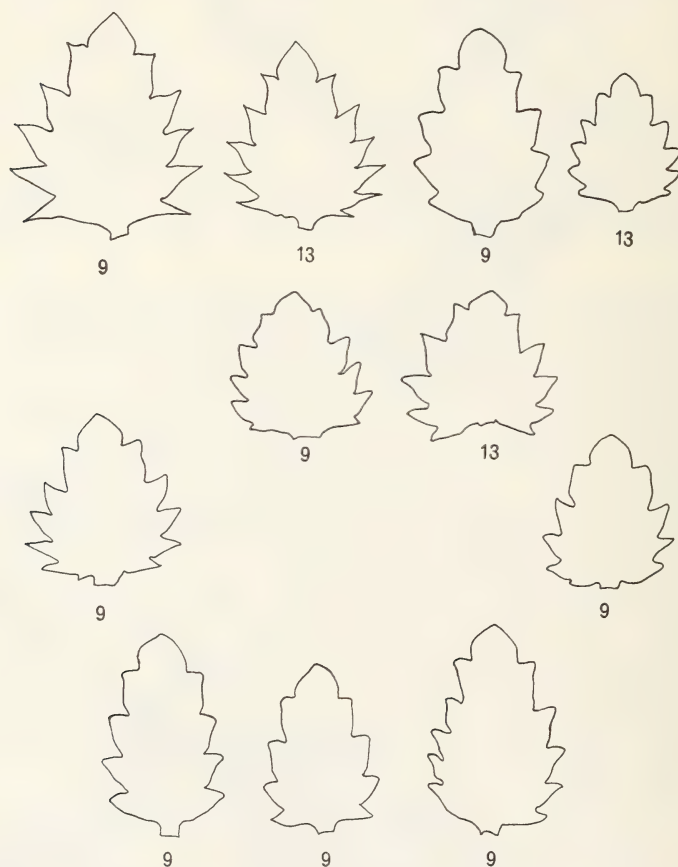


Fig. 11. Leaves of *Euphrasia*. Upper row, left, *E. pseudokernerii*, E609; right, *E. micrantha*, E185. Second row, E609 $\times$ E185, F_1 . Third row, left, F_1 back-crossed to E609; right, F_1 back-crossed to E185. Lower row, right, selfed offspring of back-cross to E185; centre and left, second generation selfed offspring of back-cross to E185, two plants. Numbers indicate node from which leaves were taken. $\times 2$, except lower left and centre which are $\times 3.6$.

more influenced in size by external conditions (chiefly water supply and humidity). The large overlap between *E. pseudokernerii* and the back-cross to it is therefore probably caused by this greater variability of large flowers, and is thus an environmental effect.

The cross *E. salisburgensis* var. *hibernica* $\times$ *E. occidentalis* (E230 $\times$ E192) produced vigorous offspring (Fig. 14). These hybrids differed from *E. salisburgensis* var. *hibernica* in their greater size, stouter stems and branches, and coarser foliage; they were no less freely branched than the female parent, and in this way did not approach the sparingly branched *E. occidentalis*. This development of branches may have been a reflection of the vigorous growth of the plants, which in turn appeared to be connected with their very poor seed production. Both the leaves (Fig. 15) and the flowers were larger than those of the parents but were intermediate in shape. The leaves of all four hybrid plants had a few stalked glands, and had more eglandular hairs than in the female parent (in *E. occidentalis* both glandular hairs and eglandular bristles were numerous).

In the comparable cross between *E. salisburgensis* and *E. nemorosa* (E515 $\times$ E608) the hybrids were very sparsely branched, imitating the form of *E. salisburgensis* which had been used, and showing scarcely any approach in this to *E. nemorosa*, which is freely branched. In the single plant of the reciprocal of this cross (E608 $\times$ E515), branching was intermediate between that of the parents. Although the plants were not particularly vigorous, two were still flowering on 14 October, probably as a result of their failure to set any appreciable quantity of seed. The leaves (Fig. 15) and flowers were intermediate in shape between those of the parents.

The only progeny that could be obtained from the cross E515 $\times$ E608 were the result of open-pollination. Seed produced in this way yielded two plants in 1958, both with flowers much larger than, and very different in shape from, those of the F_1 or the two parent samples. It seems likely, therefore, that both plants were crosses between the F_1 and something else, in one case probably *E. pseudokernerii*, and in the other *E. pseudokernerii* or one of its hybrids. In characters other than shape and size of flower, these probable parents are comparatively close to *E. nemorosa*, and the cross with them was, therefore, virtually

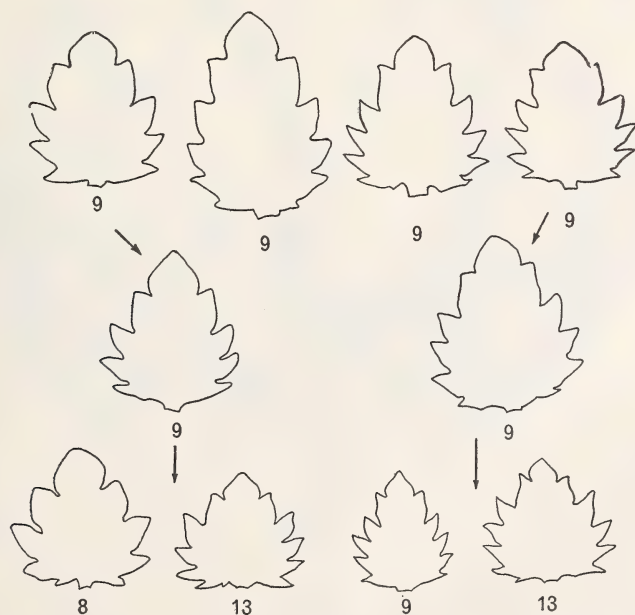


Fig. 12. Leaves of *Euphrasia*. Upper row, *E. pseudokernerii* $\times$ *E. micrantha*, E609 $\times$ E185, F_2 (1959), four plants; middle row, F_3 (1960), two plants; lower row, F_4 (1961), two plants. Arrows at left indicate Line I; at right Line III (the F_3 plant shown is a sibling of the actual parent of the F_4). $\times 2$.

a back-cross. Because of this, the foliar characters of *E. salisburgensis* were practically lost in one plant and only weakly evident in another. The reciprocal cross ($E608 \times E515$) was open-pollinated likewise, and gave rise to one offspring which also appeared to be the result of crossing with another plant.

The two back-cross plants: $E515 \times E608 \times ?$, were deliberately back-crossed to *E. nemorosa*, but with the possibility of selfing not excluded, and one of the three progeny



Fig. 13. Pressed specimens of *Euphrasia*. Above, left, *E. pseudokernerii*, E609 (1959); right, *E. micrantha*, E185 (1959); centre, second generation selfed offspring of back-cross of $E609 \times E185$ to E185 (1961).

Below, $E609 \times E185$, F_4 ; left, Line I; right, Line III (1961). $\times \frac{1}{2}$.

(1959) showed a close approach to this species in its flowers, while the other two could have resulted from accidental selfing. The leaves of all three plants had finer teeth than those of *E. nemorosa*, a feature which probably owed something to the *E. salisburgensis* element in the plant's ancestry. The sparingly branched habit was evident in this series of crosses down as far as this generation and again in 1961, but not in 1960. From the plant with flowers like *E. nemorosa* two further generations were bred by selfing; among these the leaf teeth were on the whole more antrorse than in *E. nemorosa* and *E. pseudokernerii*, while one plant of the final (1961) generation had flowers remarkably like those of E515. Otherwise these plants showed the effects of *E. salisburgensis* in their constitution only by their marked, but declining, sterility. Another plant of this second (1959) back-cross generation was open-pollinated and one of its offspring appeared to be the result of a cross with the hybrid *E. pseudokernerii* $\times$ *E. micrantha*.

In Table 15 it was shown that the F_2 generation of *E. pseudokernerii* $\times$ *E. micrantha* did not overlap with the parents in flower size. Failure to obtain segregants corresponding with the parental types suggests that the inheritance of this character is controlled polygenically (that is, by polymeric or multiple genes, in the sense of Clausen and Hiesey (1958)). Multiple gene inheritance is suggested for most characters in all the crosses by the inter-



Fig. 14. Pressed specimens of *Euphrasia*. Left, *E. occidentalis* E192 (1953); right, *E. salisburgensis* var. *hibernica* E230 (1954); centre, E230 $\times$ E192, F_1 (1954). $\times \frac{1}{2}$.

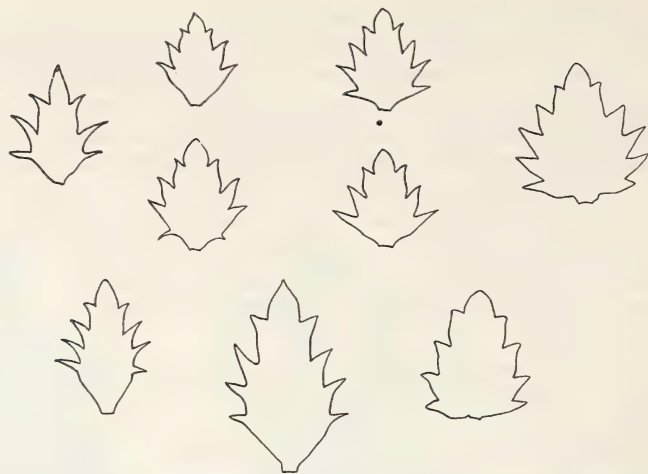


Fig. 15. Leaves of *Euphrasia*. Above, extreme left, *E. salisburgensis*, E515 (1956); extreme right, *E. nemorosa*, E608 (1956); centre, E515 $\times$ E608, F_1 (1957), four plants. All from node 13. Below, left, *E. salisburgensis* var. *hibernica* E230 (1954); right, *E. occidentalis*, E192 (1955); centre, E230 $\times$ E192, F_1 (1954). All from node 11. $\times 2$.

mediate condition of the F_1 (indicating absence of dominant genes of large effect) and by the absence of extreme segregation in the F_2 and back-crosses. This can be seen to some extent in the various figures and tables dealing with hybrids, and it also applied to flower colour in the cross *E. pseudokernerii* $\times$ *E. micrantha*, the former having a mainly white ground colour, and the latter a purplish one. A notable exception was the straw-yellow corolla colour in *E. micrantha* $\times$ *E. confusa*, which appeared to be dominant in the F_1 . There were indications that branching was controlled mainly by *E. salisburgensis* when this species was a parent.

It was found possible, in the course of five generations, to select different forms of the cross *E. pseudokernerii* $\times$ *E. micrantha* which bred reasonably true for different combinations of parental characters, and to obtain, by back-crossing, forms which showed chiefly the characters of the back-cross parent, somewhat modified. Rather uniform populations which appear to correspond to such different types can be found in nature, sometimes in situations giving direct evidence of hybridization and sometimes where there is no such evidence.

In order to amplify the picture of species relationships in *Euphrasia* an account of floral biology and natural hybridization will now be given.

FLORAL BIOLOGY

An account of the pollination mechanism of *Euphrasia* which is well supported by my own observations is that of Wettstein (1896) which is superbly illustrated. Wettstein grouped the flowers into three classes according to size and behaviour. In the species with large flowers, attaining 12–15 mm in length (exemplified by *E. rostkoviana*, *E. versicolor*, *E. picta* and *E. kernerii*) the individual flowers are at first female and later enter a male phase. When a flower of *E. rostkoviana* first opens, the stigma is held so that an insect seeking nectar will, if it is the right size, brush it with its back. Subsequently the corolla tube elongates and the anthers dehisce. An insect entering now strikes the prolongations of the anther cells, and shakes the pollen on to its back. If the insect then visits a flower at the female stage, it will cause pollination. The elongation of the corolla has led to the withdrawal of the stigma, so that the flower is functionally male. When a flower is in the second stage, there may be a flower in the first stage at the node above, so that self-pollination of the plant can occur. The large flowers are, however, primarily adapted to cross-pollination by insects.

The second type of flower is the middle-sized, exemplified by *E. stricta* and *E. pulchella*, in which the corolla reaches a length of 8–10 mm. In the half-opened flower, the stigma is in a position like that in the first stage of the large flowers, but the style is more curved. This short female phase lasts only until the flower is fully open, when the anthers dehisce. The flower is now functionally hermaphrodite. The style bends further bringing the stigma below the anthers. The stigma then withers and withdraws, while the anthers still produce pollen, so that the flower is functionally male.

In small-flowered species (*E. salisburgensis*, *E. micrantha* and *E. minima*) with flowers 4–7 mm long, the anthers have dehisced by the time the flower opens, so that the flower is initially hermaphrodite. The stigma lies immediately in front of or beneath the anthers, and self-pollination thus appears to occur regularly at the beginning of anthesis. However, the stigma soon withers, and the flower then enters a male phase.

Wettstein noted that the floral behaviour most strongly adapted to out-crossing was found in the largest flowers, while behaviour most strongly adapted to self-pollination was found in the smallest. Floral behaviour therefore corresponded with the conspicuousness of the flowers and their presumed attractiveness to insects. Since the basic morphology of the flowers is clearly adapted to insect pollination, Wettstein concluded that large flower size is primitive.

It was pointed out by Pugsley (1930) that in all Eyebrights the corolla grows during anthesis, and that this growth involves some elongation of the corolla tube. However, growth of the tube was considered by Pugsley to be disproportionately great in the large-flowered species, so that at maturity the corolla tube is exerted.

My observations have been made on *E. pseudokernerii*, *E. anglica*, *E. confusa*, *E. brevipila*, *E. nemorosa*, *E. micrantha* and *E. scottica* (this list is in order of decreasing corolla size, see Table 16). Detailed observations on floral development showed that this was subject to variation in the same species or even on the same plant.

TABLE 16. Length of corolla (mm), measured along the upper lip, of some samples of *Euphrasia*.

	<i>Initial</i>	<i>Final</i>
<i>E. pseudokernerii</i> , E42	6.5–7.0	8.5–9.5
<i>E. anglica</i> , E76	6.5–8.0	7.5–9.0
<i>E. anglica</i> , E71	5.0–7.0	7.0–8.0
<i>E. confusa</i> , E209	—	7.0–8.5
<i>E. brevipila</i> , E81	—	6.5–8.5
<i>E. nemorosa</i> , E196	—	6.0–7.0
<i>E. micrantha</i> , E185	—	5.5–6.0
<i>E. scottica</i> , E120	—	4.5–6.5

In *E. pseudokernerii* it was found that when the flower opens the stigma is curved through approximately a right angle but held well clear of the anthers, so that even if it is slightly below the level of the anther openings, it is out of the line of fall of pollen. If pollination does not take place the style remains in about the same position, or bends more to bring the stigma within reach of pollen falling from the anterior anther-loculi. After pollination the style straightens out and the stigma is usually withdrawn into the space between the anthers and the upper lip of the corolla. The withdrawal of the stigma is probably caused by the elongation of the corolla tube, but towards the end of anthesis the base of the style may wither, and as this probably results in shrinkage it may contribute to withdrawal of the stigma. Flowers usually open in the morning in *Euphrasia*, and in *E. pseudokernerii* the anthers are usually then undehisced; however, at least the anterior loculi usually dehisce later in the first day. The anthers are just concealed by the upper lip of the corolla, when it is viewed from the side, but later they protrude slightly. The flowers normally last for four

days but some lasted for six; the corolla continued to expand during most of this period (not merely until the anthers dehisce as stated for all species by Pugsley (1930)).

Three samples of *E. pseudokernerii*, a large-flowered one of *E. anglica*, and one of *E. brevipila*, all behaved in much the same way. They seemed to fall between Wettstein's large-flowered and medium-flowered types in behaviour, since the stigma very occasionally came down to where the pollen could fall onto it, and sometimes (usually in *E. brevipila*) the anthers had already dehisced when the flower opened. A second, smaller-flowered, population of *E. anglica*, together with *E. confusa* and *E. nemorosa*, was similar to Wettstein's medium-sized type, for the style curved strongly after the beginning of anthesis so that the stigma was below the anthers or touching their lower front edge. The anthers dehisce just before the flowers open. In *E. scottica* the stigmas were not found below the anthers, but had doubtless been in this position because there was pollen on them when the flowers opened. It was found in *E. micrantha* also that dehiscence of the anthers took place well before the flowers opened. These last two species were therefore in Wettstein's third class. Occasionally, anther-dehiscence took place in *E. nemorosa* and *E. micrantha* long before, instead of immediately before, the flowers opened. This may have been caused by water shortage or hot weather.

In addition to Wettstein's and Pugsley's accounts of floral development in *Euphrasia*, a full account was given by Müller (1883) who mentioned that the pollen is dry and powdery, and that it falls from all the anthers when the spines, which are on the back anthers, are touched. His account of the style elongating after the flower opens in *E. micrantha* is probably mistaken. Schulz (quoted by Knuth 1909) recognized seven flower-forms, but some of these are probably based on the variability of behaviour that I have observed. While some authors state that the largest-flowered Eyebrights cannot be selfed, others suggest that they are self-pollinated to some extent. On one occasion I knocked a young flower of *E. pseudokernerii*, and this brought pollen onto the stigma, so disturbances other than by insects may cause self-pollination, even if the stigma appears to be out of the line of free fall of the pollen.

The ground colour of the corolla is either white or lilac to purple. The lilac colouring is usually slightly stronger in the upper lip and it intensifies slightly with age. Flowers with a white lower lip may thus have a pale lilac upper lip, and flowers which are initially white may become pale lilac. Lilac colouration develops more strongly in cool weather than in warm. Both lips of the corolla usually have some of the longitudinal veins coloured dark violet, forming guide-marks converging towards the throat; the extent and intensity of this coloured veining varies. Near the base of the lower lip is a yellow spot, and there is another just inside the tube on the lower side. The intensity of these marks is also variable. Some pollen always falls from the anthers and most of it usually falls onto the yellow spots. The nectary is at the base of the ovary on the lower side. It is often difficult to find nectar in the flowers, but it sometimes collects in a drop some distance away from the base of the corolla tube, presumably owing to some degree of resistance to wetting by the base of the tube. According to Schulz (see Knuth 1909), the nectary is well-developed in the larger-flowered species and less well-developed or absent in the smaller-flowered species.

The main insect visitors to *Euphrasia* flowers are hover-flies (Diptera: Syrphidae) and bees (Hymenoptera: Apidae)—chiefly *Bombus* (bumble-bees). This is true both in Europe (Daumann 1932, Knuth 1909, Müller 1883, Wettstein 1896) and in Britain (Drabble 1927, Scott-Elliot 1896, Willis & Burkill 1903). Diptera and Hymenoptera of other families have also been recorded, as well as Lepidoptera (Drabble, Knuth, Scott-Elliot, *l.c.*).

My observations on the behaviour of insects visiting the flowers have been made chiefly in glasshouses, where insect visits are quite frequent. However, the greatest insect activity at the flowers of *Euphrasia* that I have seen occurred in 1953 when I had a plot in the garden at Leicester containing over three hundred extremely luxuriant and profusely flowering specimens of *Euphrasia*. This patch of plants became a considerable attraction for insects, which could be seen continually active at the flowers in warm weather. Here eight species of Syrphidae were taken and species of *Bombus*, *Apis* and *Halictus* (all Apidae)

were seen visiting the flowers. I have only rarely seen *Euphrasia* visited by insects in nature, having taken a total of five specimens, and seen about the same number again which I have not caught. The visitors that were identified were *Bombus*, *Halictus*, *Empis* (Diptera: Empididae) and Syrphidae. The flowers visited ranged from the small ones of *E. micrantha* to the large ones of *E. pseudokerneri*. The bee visitors appear to probe for nectar, and sometimes pollen collects on the thorax. Females doubtless gather this into their pollen carrying apparatus, but the males of solitary bees probably have no use for the pollen. Syrphidae probe for nectar, and in doing so put their head and thorax into the throat of the corolla. When feeding on pollen they straddle the lower lip and their proboscis takes up pollen that has fallen into the throat of the corolla from the anthers and any loose pollen from the stigma and anthers. Thus, the insect's head probably comes into frequent contact with the anthers and stigma. It seems possible that the function of the yellow spots is to heighten the visual effect of the patch of pollen which is usually present. Judging from the behaviour of Syrphid visitors, the pollen is at least as much of an attraction to them as the nectar.

THE OCCURRENCE OF HYBRIDS AS EVIDENCE OF CROSS-POLLINATION

In addition to finding wild hybrids, I have obtained spontaneous hybrids from seeds collected from cultivated plants. Two instances are of interest.

It has already been described how the flowers of *Euphrasia* (mainly *E. nemorosa*) grown in the garden at Leicester in 1953 became an attraction to insects. Six populations of *Euphrasia* were grown, well intermingled. Three populations were closely similar, and three others all easily distinguished by eye from the rest and from each other. The one which was most distinct was E151A, and it therefore appeared that it would be easy to pick out hybrids in the progeny of this form. Seed was collected from most of the plants of this population. At the time of collecting, its flowers were greatly outnumbered by those of other populations. The following year the progeny were grown at Cambridge by the same method as the parents; 79 bituminized paper pots, each with one *Euphrasia*, were planted out. The final score was 14 plants of the maternal type and 42 hybrids. That is, 75 per cent. of the survivors were hybrids. The maternal type, which showed heavy mortality and late establishment in 1953, showed late establishment and lack of vigour in 1954, and probably suffered heavier mortality than the hybrids as a consequence. The proportion of hybrids in the seed-sample was, therefore, doubtless less than 75 per cent. Eighty-seven seedlings, including replacements, were planted out, so that if all those that died were of the maternal type the proportion of hybrids was 48 per cent. Therefore, the true figure was not less than 48 per cent. and not more than 75 per cent.

However, the following year about 200 more seeds of the original sample germinated. Eighty-two seedlings were still alive on 4 June 1955, and 30 were then potted up and grown in the greenhouse. In this culture, nine plants of the maternal type and only four hybrids lived long enough to be identified. The ratio of the two types among survivors was thus reversed. If, as seems likely even from this small sample, the ratio of maternal to hybrid types was really changed, a possible explanation is that hybrid types germinated more readily than the maternal in the first year. While this experiment cannot give a reliable estimate of the proportion of hybrids in the seed produced by the plants of E151A grown in 1953, it does show that there was some hybridization between individuals, and that insect-pollination was quite effective. *E. nemorosa* is a fairly small-flowered species, and it probably generally behaves like Wettstein's intermediate flower type.

In the second instance, a quantity of open-pollinated seed of the small-flowered *E. micrantha* (E185A), collected in 1953, was sown on 17 February 1954. Apparently because of the lateness of the sowing, only two seeds germinated in that year, but both plants were grown to maturity, and both proved to be hybrids of *E. micrantha*. In 1955 about 49 more seeds germinated, and 18 of these were potted up. Only four grew well enough to be identified and none was a hybrid. This result again suggests that the hybrid types may germinate more readily than the maternal. In view of the floral behaviour of *E. micrantha*, it was

rather surprising to find two hybrids in this fairly small seed-sample. Presumably, pollen brought to a flower just after it has opened has a fair chance of effecting fertilization, even when the anthers have already dehisced.

Wild hybrids may belong to the F_1 generation, to the first back-cross generation, or to succeeding generations. The occurrence of wild hybrids is thus less informative than that of spontaneous hybrids in cultivation, because only in the latter can the F_1 generation be recognized with certainty; the occurrence of wild hybrids does, however, show that cross-fertilization occurs in nature. In a survey of my herbarium collection covering the years 1951–1958, I found that I had met with 11 dense populations of hybrids between species alike in chromosome number extending over considerable areas, and 16 well defined colonies of relatively small size. In addition, I found 22 *Euphrasia* populations containing more than one species of the same chromosome number and containing a very few hybrids. (In Cornwall I have several times found plants apparently intermediate between *E. nemorosa* and *E. confusa* unaccompanied by typical plants of either of these species; these have been excluded from the totals). Ecological conditions appear to have a very marked effect on the occurrence of hybrids. For example, although *E. salisburgensis* produces highly sterile progeny when crossed with tetraploid species belonging to Subsection *Ciliatae*, a large gathering of a hybrid, apparently fertile, between *E. salisburgensis* var. *hibernica* and *E. nemorosa*, was obtained from Lough Bunny, County Clare, by Professor Tutin in 1951. One can only suppose that the hybrids are highly favoured ecologically in this locality and that they eventually become established with a reasonable degree of fertility. Similar assumptions have been made with regard to forms of diploid species showing introgression from tetraploids (Yeo 1956). A contrary example concerns *E. micrantha* and *E. confusa*. These two were growing in contact on a moor north of Minions, E. Cornwall, where there was a vegetational pattern consisting of areas of *Erica cinerea*, *Calluna vulgaris* and *Ulex gallii*, divided up by grassy areas; *E. confusa* grew in the grassy areas, and *E. micrantha* grew around the *Erica* and *Calluna* plants; no hybrids could be found here, but some were found a little way away growing with the parents on the top of a disused railway embankment; the hybrids formed a small group of uniform plants where the vegetation ended in stony ground. The scarcity of hybrids here appears to have been caused by habitat conditions.

The regular occurrence of wild hybrids demonstrates that cross-pollination is normally possible for *Euphrasias* in Great Britain. It seems reasonable to infer, therefore, that there is in nature an appreciable gene-flow over short distances in most *Euphrasia* populations, including those of small-flowered species.

DISCUSSION

It is well known that the genus *Euphrasia*, at least in Europe, is one of considerable taxonomic difficulty (see, for example, Pugsley 1930, Joergensen 1919). It consists of numerous poorly defined microspecies, many of which interbreed freely where they meet. These microspecies may be very wide-ranging (e.g. *E. tatarica* and *E. hirtella* range from the Pyrenees to eastern Asia), of moderate range (e.g. *E. rostkoviana* and *E. micrantha* of central and northern Europe, including the British Isles) or of very restricted range, down to areas as small as an English county (e.g. *E. cambrica*, from Caernarvonshire). Taxonomic difficulty is increased by the occurrence of aberrant forms of particular species (which could be the result of past introgression), forms assignable to hybrid parentage, though at present unaccompanied by the parent species, and occasional very local but distinctive forms which are most probably hybrid segregants but are difficult to assign to any stated parentage, and too restricted to be worth naming.

The results given in the present paper show that there is normal sexual reproduction in *Euphrasia* and that sterility barriers are formed by polyploidy and by homoploid hybrid sterility. However, there are only two levels of 'ploidy' and gene exchange is possible even between these (Yeo 1956), while many homoploid species are separated by no sterility barrier. More often than not, therefore, any two species are highly interfertile. The amount

of out-crossing to which the different species are adapted is variable, but out-crossing is sufficiently common to make hybrids frequent, even between small-flowered species. On the other hand, the majority of seeds probably result from self-fertilization, at least in all but the largest-flowered species, so that the products of hybridization can probably quickly acquire uniformity. I have on a number of occasions seen quite uniform gatherings in which there was strong evidence of hybrid origin, and my experimental evidence shows that five generations is enough to produce two lines of hybrids derived from one cross, which differ much less among themselves than between each other.

All the microspecies have definite ecological and geographical characteristics, and many show obvious adaptations to major habitat differences (e.g. hay-meadows *versus* sheep grazings). Many species are separated geographically, but in most parts of Europe where the genus occurs at all, more than one species is to be found.

The factors of internal sterility barriers, geographical isolation, and possibly floral biology, contribute to the maintenance of the distinctness of species, but where they do not operate, and hybridization occurs, other factors must come into play, for the species can be found again and again in approximately the same form over most of their range. These other factors must be the selective influence of the habitat and genetic linkage. Anderson (1949) showed that when characters are polygenically controlled there is a strong tendency for the characters of one or other parent to remain associated in the F_2 hybrid and later generations (a phenomenon called genetic cohesion), and that there is a tendency for hybrids of later generations to comprise increasing proportions of individuals resembling one or other parent. These tendencies would be enormously reinforced by back-crossing.

It is necessary to consider the impact of present knowledge of the group on its taxonomic treatment. It seems to me that this knowledge requires either that the taxa recognized currently as species should remain at that rank, or that they should be reduced to the level of subspecies. From a practical point of view, it seems much preferable to continue treating them as species. Not all species are of the same standing, and it would seem that the *Euphrasiae* can justifiably be retained in this category, though they may represent its lowest limit.

In genecological terms, the *Euphrasia* species would be ranked as ecotypes in the sense of Clausen and his school, but higher than the ecotypes of Turesson. There is no doubt that the commoner and more successful *Euphrasia* species include ecotypic variants. It seems inevitable that any species which consists of numerous more or less disconnected local populations (which is the case in the *Euphrasiae*) will include every possible degree and type of ecotypic differentiation.

It will be seen from the appendix that the diploid species (Series *Hirtellae* only) are fewer in number than the tetraploids and are less wide-ranging, their northern limit in Britain being Argyll and Perthshire. In addition, diploids in general are much less abundant than tetraploids; where one finds diploids one almost invariably finds tetraploids also, while the reverse is very often *not* the case. *Euphrasia* thus conforms to the widespread pattern in vascular plants, in which the diploids are generally less diversified and narrower in their tolerance than polyploids.

APPENDIX: THE ECOLOGY OF *Euphrasia*

The following is a brief summary of the ecology and distribution of the more important British *Euphrasiae*, arranged in systematic order. The habit gives an indication of the height of herbage to which the species is adapted.

Series *Latifoliae*

1. *scottica*. Wet flushes in mountain areas in N. and W.; habit tall.
2. *micrantha*. Callunetum, absent E. Anglia, probably extinct S.E. England; habit tall to dwarf.
3. *frigida*. Alpine grassland, streams, ledges; habit dwarf to medium.
4. *foulaensis*. Maritime, northern; habit dwarf.
5. *campbelliae*. Maritime, Outer Hebrides; habit dwarf.

Series Nemorosae

6. *rotundifolia* and *marshallii*. As 4.
7. *curta*. Open habitats (dunes, rock outcrops, river shingle), middle-northern and north-western; habit dwarf to short.
8. *cambrica*. Alpine, N. Wales only; habit dwarf.
9. *occidentalis*. Maritime, southern to middle-northern; habit dwarf to short.
10. *nemorosa*. Roadsides, pastures, woods, dunes, southern, maritime in the north; habit tall to short.
11. *confusa*. Pastures, usually closely grazed, coastal to montane, mainly western and northern; habit dwarf to medium.
12. *pseudokernerii*. Grazed chalk and oolitic grassland, south-eastern; habit short to medium.

Series Brevipilae

13. *borealis* (vars. *zetlandica* Pugsl. and *speciosa* Pugsl. only). Pastures, meadows (?), Orkney, Shetland; habit medium to tall.
14. *brevipila*. Meadows, pastures, mainly western and (especially) northern; habit tall to dwarf.

Series Hirtellae

15. *rostkoviana*. Meadows, pastures, western and middle-northern; habit tall to medium.
16. *montana*. Meadows, middle-northern; habit tall.
17. *vigurii*. *Ulex* heaths, south-western; habit tall to medium.
18. *anglica*. Pastures, often closely grazed, England (except the north), Wales, Ireland; habit short to dwarf, sometimes medium.
19. *rivularis*. Alpine rivulets and flushes, middle-northern; habit dwarf.

Subsection Augustifoliae

20. *salisburgensis*. Grazed turf, lowland, W. Ireland; habit dwarf.

Nos. 4, 5, 6, 8, 11, 12, 13, 17, 18 and 19 are endemic to the British Isles, or nearly so. It is quite common for two species of *Euphrasia* to grow in mixed or closely adjoining populations. The wide-ranging *E. nemorosa* may easily come into contact with as many as nine other species, while more restricted species, such as *E. pseudokernerii* and *E. foulaensis*, may be in contact with three or four others.

Note: An interesting feature of the British *Euphrasiae* is the occurrence of two widespread endemics specially adapted to grazing (*E. confusa* and *E. anglica*), which do not seem to have their counterparts on the Continent of Europe. This is probably related to the prevalence of all-the-year-round sheep-grazing and the strength of rabbit pressure, both factors of very recent origin.

ORIGIN OF MATERIAL

Unless otherwise stated all *Euphrasia* plants grown are from the British Isles. Herbarium specimens of the original gatherings, if they exist, are to be found in my own collection, or in the Cambridge University Herbarium (CGE). Many duplicates are at the University of Leicester. All cultivated specimens are in my own herbarium.

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STUDIES IN *RANUNCULUS* SUBGENUS *BATRACHIUM* (DC.)
A. GRAY. III. *RANUNCULUS HEDERACEUS* L. AND
R. OMIOPHYLLUS TEN.

By C. D. K. COOK

Hartley Botanical Laboratories, The University, Liverpool

ABSTRACT

An account is given of *Ranunculus hederaceus* and *R. omiophyllus* including information on distribution, ecology, floral biology, hybridization, variation and karyotype analysis. Formal descriptions with full synonymies and typifications are also included. Both species are morphologically and ecologically very similar and can exist as diploids or tetraploids. They are largely sympatric throughout their geographical ranges and, occasionally, grow intermingled. They show complete hybrid inviability at the diploid level and hybrid sterility at the tetraploid level but at the same time can be regarded as belonging to a single potential common gene-pool (hologamodeme) as they form fertile hybrids with *R. tripartitus* and *R. baudotii*. In spite of a high degree of inbreeding and numerous isolated populations no genotypic differentiation has been detected in either *R. hederaceus* or *R. omiophyllus*.

INTRODUCTION

R. hederaceus and *R. omiophyllus* are the only species of *Ranunculus* subgenus *Batrachium* that lack throughout their life the ability to produce divided leaves with capillary segments (Cook 1963) and are essentially terrestrial plants of wet places. Salisbury (1934) reviewed these two species and concluded, mainly on the basis of their geography, ecology and meristic variation, that they both originated from a common stock and that because *R. omiophyllus* occupied more specialized habitats than *R. hederaceus* and showed less marked evidence of trimery it was of more recent origin. Salisbury's studies were carried out exclusively on British material collected in the field. During the investigation reported here I have endeavoured to study these species throughout their geographical ranges and have cultivated plants under different conditions, carried out breeding experiments and incorporated cytological observations with the result that some of Salisbury's conclusions need reconsideration.

DISTRIBUTION*

R. hederaceus occurs in Europe and N. America. In Europe it shows an atlantic distribution but is widespread in inland districts of Britain (Fig. 1a). In North America it is confined to Newfoundland and the Chesapeake Bay region (Fig. 1b). It has been recorded from Dalmatia, Italy, Sicily, Iceland, Greenland and north-west America (Salisbury 1934) but I have not been able to trace herbarium material to support these records. It is likely that the Italian and Sicilian records are due to misidentifications of *R. omiophyllus*.

The status of *R. hederaceus* in North America is problematical. It was first recorded from Carolina by Bosc (Bosc & Baudrillard 1821). Gray (1886), Fernald (1929), Drew (1936) and Benson (1948) considered it to be native while Macoun (1891) and Morris (1900) regarded it as introduced. Morris wrote 'patches . . . (Patuxent River) badly cut up by the passage of teams over a temporary farm road,' while Fernald wrote : 'apparently indigenous in Newfoundland especially since it shares natural and undisturbed habitats with or near other European types'. In Europe it is usually found in disturbed habitats. There seems little doubt that it was introduced in Carolina. Walker did not record it in 1788 in *Flora Caroliniana* : it was recorded by Bosc in 1821 and reported extinct by Elliot

*Material from the following herbaria has been examined : CGE, COI, C, E, K, LE, LIVU, LU, BM, M, NAP, W.

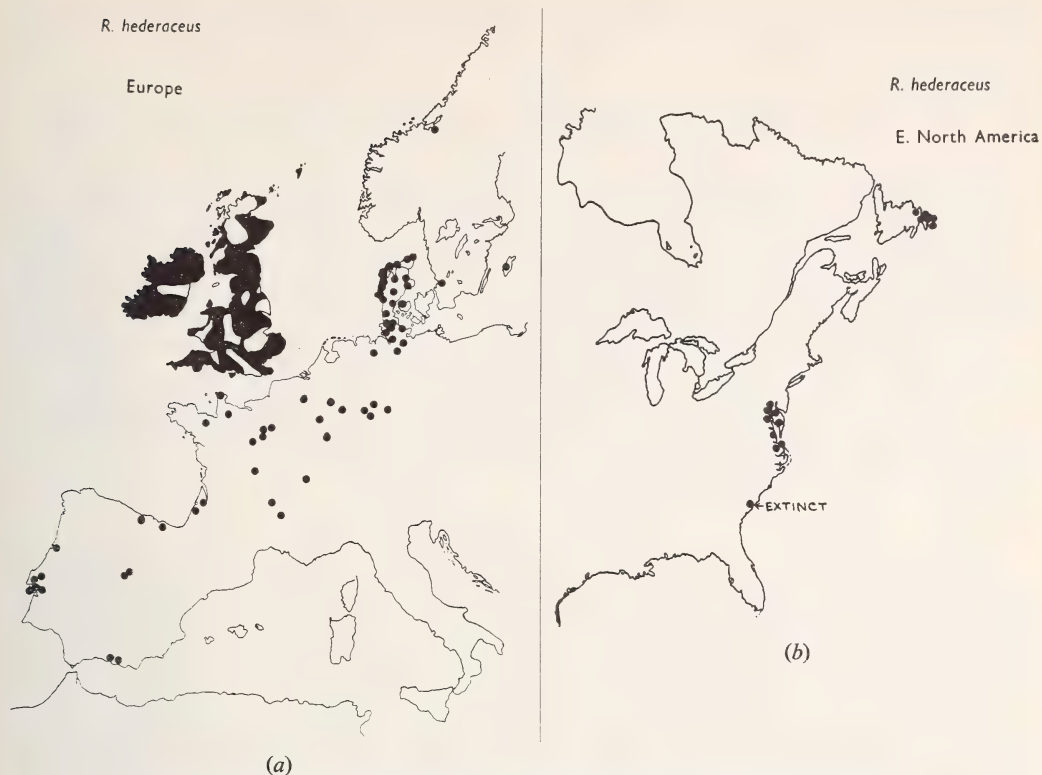


Fig. 1. Distribution of *R. hederaceus* (a) in Europe, and (b) in North America.



Fig. 2. Distribution of *R. omiophyllus*.

in 1824. The general distribution in North America would suggest that it was introduced, but there are two fern species, *Schizaea pusilla* Pursh and *Woodwardia areolata* (L.) Moore which share almost the same distribution in North America and which are certainly not European introductions.

Faegri (1960) considered *R. hederaceus* to have been introduced in Norway where it is confined to a small coastal area near Trondheim.

R. omiophyllus is confined to Europe and North Africa (Fig. 2). In Europe it shows a distinct Atlantic distribution from North France to Portugal but is also present in mountainous districts in South Italy and Sicily. In Britain the limits of distribution follow extremely closely the August 3in isohyet. In North Africa it is confined to the coastal mountains of Algeria. According to Moggi (1963) most species common to Atlantic Europe and South Italy migrated along the Apennine Mountains and are not found in North Africa. *Genista anglica* L. and *R. omiophyllus* are, perhaps, the only two Atlantic south Italian species that are absent from the Apennines but present in North Africa.

Morris (1837) described a plant called *R. aquatilis* L. var. *homophyllus* from Sardinia. The description is inadequate and as I have seen no herbarium specimens some doubt about this record must remain.

FLORAL BIOLOGY

The flowering times of *R. hederaceus* and *R. omiophyllus* show a considerable range of variation. When cultivated in cool but frost-free greenhouses at Cambridge, München and Liverpool Botanical Gardens, occasional flowers were formed throughout the year but most flowers were produced between February and November. Both species are fairly sensitive to constant high temperature and if cultivated in a greenhouse with a continuous temperature of 21° C or more they soon die. In nature *R. hederaceus* has been seen in flower and fruit in March 1958 in South Cornwall while in East Scotland in the same year flowering was just starting in May. In Norway and in the higher parts of the Sierra Nevada in Spain flowering begins as late as August. *R. omiophyllus* is equally variable and plants have been seen in flower in North Wales in November and February, in the Madonie Mountains of Sicily flowering commences during April. In cultivation flowering does not cease abruptly at any particular time of the year. In nature, however, flowering is usually stopped by the plants being smothered by later-growing species such as *R. sceleratus* L., *Peplis portula* L. and *Montia fontana* L. or by the habitat drying out or freezing.

Pollination and fertilization have been described elsewhere (Cook 1963)—see also p. 252. After fertilization the pedicel bends downwards forcing the developing fruits into the substratum. The achenes are probably dispersed in mud, carried by animals or machines. Occasionally they are liberated in water and then they may be dispersed by water currents or by surface contact with larger animals.

Salisbury (1934) reported both species to be winter annuals but this appears to be an over-simplification. If cultivated in waterlogged soil and not subjected to inter-specific competition they behave as perennials and survive for at least six years. In winter, both species form small tight cushions which are very resistant to desiccation, freezing and shade, but in summer they develop a spreading habit and are very susceptible to desiccation and shade. When cultivated in mud with *Peplis portula* both species behave as winter annuals. Seed germination is very irregular when the achenes are kept wet, but if the achenes are dried and then rewetted nearly complete germination takes place. Both species in nature may behave as spring or winter annuals or as perennials depending on the local water regime and competing species.

POLYPLOIDY AND CHROMOSOME MORPHOLOGY

I have already reported (Cook 1962) a chromosome count of $2n = 16$ for a plant of *R. omiophyllus* from Sicily and $2n = 32$ for a plant from Dartmoor, Devon, also *R. hederaceus* with $2n = 16$ from plants collected from six populations. During the summer of

1963 and 1964 the same number has been obtained from four more populations of *R. hederaceus*,* viz.:

Jackson's Pond, Childwall, Liverpool, Lancashire.

Bwlch-y-Rhiw, 4 m east of Aberdaron, Caernarvonshire.

Ditch 1 m south-east of Penrhos Lligwy, Anglesey.

Wet flush near Porthmynawyd, Pembroke.

An artificial autotetraploid of *R. hederaceus* has been induced using aqueous colchicine solution. The method used consisted of maintaining a droplet of 0.04 per cent. colchicine solution between the cotyledon leaves of a young seedling and allowing the young apex to grow through the droplet. To maintain humidity the plants were kept in a sealed tank partly filled with water. The treatment lasted four or five days depending on the growth of the apex. The 0.04 per cent. colchicine had a profound effect on all seedlings—the rate of growth was slowed down and any new leaves produced were markedly deformed and succulent. Only one polyploid was obtained from 150 treated seedlings.

It has been found when diploid and tetraploid plants of *R. hederaceus* and *R. omiophyllus* of the same age are cultivated side by side there are a few morphological differences between them, see Table 1. This table was compiled from measurements made on single plants of each species at both diploid and tetraploid levels. The plants in this experiment were cultivated side by side in a cool greenhouse at the Botanical Gardens at München, Germany and gathered in June 1961. Five flowering shoots from each plant were taken. Stomatal length was measured on 25 stomata from one mature leaf from each shoot and the mean and standard deviation (*s.d.*) calculated. Three anthers from one flower from each shoot were heated in 45 per cent. propionic orcein solution. Pollen diameter was measured on 50 well formed grains from each flower. Apparent male fertility was calculated as an absolute percentage of well formed grains. Female fertility was calculated as a percentage of well-formed achenes in mature heads. Stamen number and carpel number is given for each flower examined. From Table 1 it can be seen that there are considerable differences between the diploid and the tetraploid.

TABLE 1

	<i>R. hederaceus</i>		<i>R. omiophyllus</i>	
	<i>diploid</i>	<i>autotetraploid</i>	<i>diploid</i>	<i>tetraploid</i>
Stomatal length (mm)	0.0275	0.0358	0.0267	0.0361
s.d.	0.0017	0.0028	0.0015	0.0021
Pollen diameter (μ)	27.3	33.3	26.9	30.9
s.d.	1.6	2.5	0.5	1.8
Apparent male fertility (%)	99	85	99	96
Female fertility (%)	80	69	74	75
Stamen number	7 8 9 10 10	6 9 9 10 11	8 8 8 10 10	8 9 9 10 10
Carpel number	20 24 24 26 32	24 27 28 28 36	28 30 31 41 42	30 34 34 37 43

If, however, these plants are cultivated in different conditions or sampled at different times, the above characters are modified and no clear separation can be made between diploid and tetraploid. For example, Fig. 3 shows pollen grain diameters of diploid and autotetraploid *R. hederaceus*. I, II and III represents ramets of a clone of diploid *R. hederaceus* (collected from Ponsongath, The Lizard, Cornwall by C. D. K. Cook, 30th March 1958) while IV and V represent the autotetraploid derived from seeds from this clone. All were cultivated at Liverpool University Botanic Garden and gathered on the same day

*Herbarium specimens have been deposited in the herbarium at the Hartley Botanical Laboratories, Liverpool (LIVU).

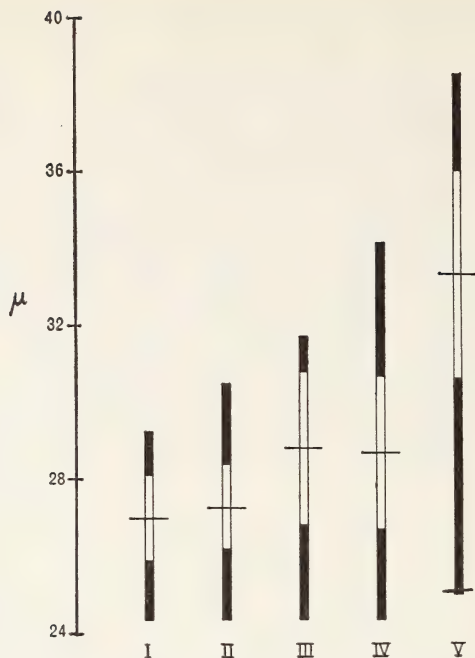


Fig. 3. Pollen diameters of *R. hederaceus* (central line represents the mean, unshaded area the standard deviation and the black area the total range). I, II and III represent ramets of a single clone of 16 *R. hederaceus* (Lizard) and IV and V represent the autotetraploid derived from this clone. I and IV were cultivated terrestrially, side by side outdoors, II and V were cultivated terrestrially, side by side in an unheated greenhouse and III was cultivated in 5 cm. of water outdoors. All plants were grown at Liverpool University Botanic Gardens and gathered on 16th May 1962.

(16th May 1962). I and IV were cultivated terrestrially, side by side outdoors ; III was cultivated in 5 cm of water outdoors, unfortunately the autotetraploid did not survive in 5 cm of water in this experiment.

It can be seen that plants II and V show a marked difference, I and IV show less difference while III and IV are nearly the same. In this experiment the mean pollen diameter of the aquatically cultivated diploid was slightly greater than that of the terrestrially cultivated tetraploid. A similar situation is found in *R. omiophyllus*. In both species stomatal length is extremely variable and when plants are placed under water the stomatal length in successive leaves may increase or decrease but the environmental factors that induce these changes are not understood. The mere fact that pollen grain diameter and stomatal length are plastic and under environmental control precludes the recognition of the level of polyploidy from herbarium material. Sokolovskaya (1962) has found that pollen diameter is not a good indicator of polyploidy in *Saxifraga*, and Schwanitz (1952) demonstrated that both stomatal size and pollen diameter can be altered by changes in the environment and that this variation may obscure differences due to polyploidy.

The other differential characters such as male and female fertility and numbers of stamens and carpels vary considerably as a result of small environmental changes. Nevertheless, living plants of the autotetraploid of *R. hederaceus* can usually be distinguished from the diploids as they are more shiny, somewhat succulent, slower growing with a more compact habit and show a marked tendency to become fasciated. Flowering normally starts about two weeks later than the diploid and continues about two months after the diploid. There is no evidence that the autotetraploid occurs wild in nature. Diploid and tetraploid plants of *R. omiophyllus* are extremely similar and no separation can be made on gross morphological grounds. A similar situation has been described by Solbrig (1964) ; he was unable to distinguish diploids from tetraploids of *Gutierrezia sarothrae* after a

detailed study of their ecology, geography and 11 morphological characters from 53 wild populations.

The karyotypes of diploid *R. hederaceus* and *R. omiophyllus* are similar (Fig. 4) and no convincing difference has been found. The autotetraploid of *R. hederaceus*, as expected, simply has the diploid set represented twice (Fig. 4) with the exception that there is only one pair of satellited chromosomes. The chromosomes that carry the satellites are the smallest in the karyotype and have a sub-terminal centromere. These chromosomes have been seen in all species of *Batrachium* so far investigated (Cook 1962) but except for autotetraploid *R. hederaceus* and its hybrids never more than two satellited chromosomes have been seen. It is possible that the satellites act as nucleolar organizers (they are much larger at prophase than at metaphase) and with time the extra satellites may be lost; this loss of satellites has been described by Navashin (1934).

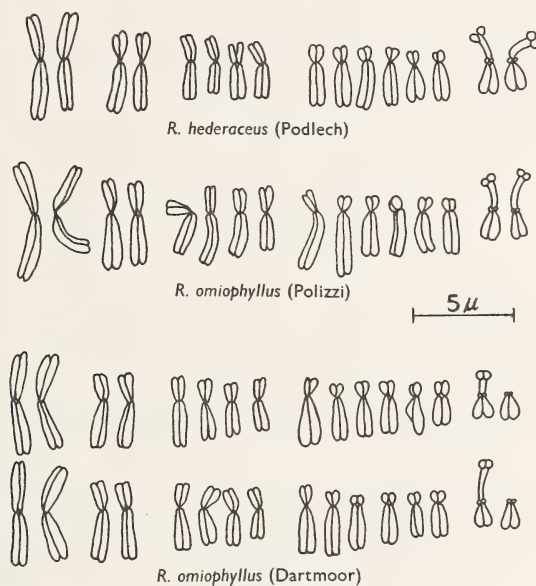


Fig. 4. Karyotypes of diploid *R. hederaceus* and *R. omiophyllus* and tetraploid *R. omiophyllus*.

VARIATION

Plants from the following populations have been maintained in cultivation.

R. hederaceus

1. Near Port Logan, Galloway, Wigtownshire. O. R. Staples, 9 August 1956.
2. Sellindge, near Hythe, Kent. O. R. Staples, 28 August 1956.
3. Ponsongath, The Lizard, Cornwall. C. D. K. Cook, 30 March 1958.
4. Near Mora, prov. Alto Alentejo, Portugal. B. V. Rainha, 12 June 1958, sent by A. R. Pinto da Silva.
5. Eifel, Wirftal, Stadtkyll, Prüm, Germany. D. Podlech, 25 May 1961.
6. Bwlch-y-Rhiw, near Aberdaron, Caernarvonshire. C. D. K. Cook, 14 May 1962.
7. Wet flush near Porthmynawyd, Pembroke. J. J. B. Gill, April 1964.

R. omiophyllus

8. Wet flush just below Wistman's Wood, Two Bridges, Dartmoor, Devon. C. D. K. Cook, 4 May 1958.
9. Small spring about 6 km north of Polizzi Generosa, Madonie Mountains, Sicily. C. D. K. Cook, 21 April 1961.

Plants from collection numbers 1, 2, 3, 4, and 8 were cultivated in the Cambridge Botanic Garden, Cambridge between 1956 and 1960; 2, 3, 4, 5, 8, and 9 were cultivated in the Botanic Gardens, München, Germany between 1960 and 1961; 3, 4, 5, 6, 7, 8, and 9 in the Liverpool University Botanic Gardens, Ness, Cheshire from 1961 to 1965. Crosses between 3, 4 and 5 have been made (see page 253) and batches of 25 seedlings from selfed 3, 4 and 5 have been raised. All these cultivated plants have been compared and no genotypic variation has been detected. No suggestion of possible genotypic variation has been seen from herbarium material examined (see page 2-6).

Glück (1924, 1936) recognized one variety, *R. hederaceus* var. *coenosus* (Gussone) Cosson (*R. coenosus* Gussone) which is referable to *R. omiophyllus* Tenore. Under *R. hederaceus* sensu stricto Glück described six formae (*natans* Glück, *amphibius* Glück, *latifolius* Glück, *terrestris* Glück, *pumilus* Glück, and *reniformis* Glück). Under *R. omiophyllus* Glück described three formae (*natans* Glück, *amphibius* Glück and *terrestris* Glück) and plants matching the descriptions of each of these formae have been induced from ramets of a single clone. The plastic variation pattern of this species closely matches that found in *R. hederaceus* and may be due to homologous variation.

To a great extent Glück based his formae on more or less arbitrarily chosen size categories, and his descriptions, tables and illustrations (Glück 1924, p. 580-591, plaet) V give a very good indication of the plasticity of these species. Cultivation experiments suggest that these formae are no more than phenodemes (Gilmour & Gregor 1939). Plants matching the descriptions of each of Glück's formae have been induced from ramets of a single clone. However the behaviour of both species is not always predictable and merely cultivating plants terrestrially does not necessarily cause them to resemble forma *terrestris*. Each phenodeme results from the interaction of many environmental factors. The water regime is very important but so are light intensity, photo-period, competition, substrate conditions, age of plant etc.

Leaf shape and size are particularly plastic. In *R. hederaceus*, for example, a terrestrially cultivated plant in summer will usually be compact with leaves 4-8 mm long and 3-10 mm wide, while a plant of the same age at the same time cultivated in 5 cm of water will be spreading and normally have leaves 17-25 mm long and 25-35 mm wide. When a plant is growing quickly in favourable conditions the leaves are usually three-lobed with the lobes widest at the base. If the plant is grown in less suitable conditions, such as in deep water, shade or dry soil, the leaves become distinctly five-lobed and the sinus may become deeper making the base of the lobe narrower, or the sinus may disappear producing a typically reniform leaf. It is interesting to note that the synthesized autotetraploid (see page 249) nearly always has five lobes with a very much reduced sinus.

In spite of the extreme phenotypic plasticity in size and leaf-shape the recognition of these species is not difficult since highly modified leaf-shapes are only manifest on mature or over-mature leaves while the immature leaves always show the characteristic form of each species.

HYBRIDIZATION

R. hederaceus and *R. omiophyllus* are protogynous but pollination usually takes place before the flower buds open. The carpels are usually ready to receive pollen from three to six days before the flower opens, but the timing is difficult to judge as opening depends largely on the weather. The lower (outer) anthers dehisce about 24 hrs before the flower opens but at this stage pollen rarely gets beyond the outer carpels. Later when the flower has opened the filaments elongate, shedding pollen on the inner carpels. In spite of there being an opportunity for outbreeding there are no reports of any naturally occurring hybrids between these species.

Occasionally, flowers are produced underwater. When this happens a gas bubble is formed within the closed bud allowing pollination to take place. If a newly opened flower is repeatedly wetted there is a low degree of pollination.

The flowers produce visible quantities of nectar and have a sweet-smelling scent somewhat like *Crataegus monogyna* Jacq. In spite of this no nectar or pollen-taking insects have been seen visiting the flowers. Some chalcids, psychodids, chironomids, *Corixa* sp. and females of *Scopeuma stercorarium* L. have been collected from the flowers. In order to cross these plants it is necessary to emasculate the flowers while they are in bud. This is normally done under a microscope as it is very easy to burst an anther or damage the carpels. Polythene tubing sealed with cotton wool is used to prevent foreign pollen reaching the stigmas. Initially, while the flower is erect the polythene tubing is held in position by wire but later after pollination, when the pedicel starts bending the supporting wire is removed because if prevented from bending the pedicel breaks.

Pollen of *R. bulbosus* L., *R. sceleratus* L., *R. ophioglossifolius* Vill. and *Papaver somniferum* L. was placed on the stigmas of *R. hederaceus* to test for pseudogamy in the restricted sense of Gustafsson (1946). The pollen of these species germinated but soon died and no pseudogamy was detected. Embryological investigations were carried out on emasculated flowers but failed to reveal any agamosperous process. It is probable that faulty technique and not apomixis was to blame for the few maternal plants obtained in F_1 inter-specific hybrid progenies. *R. hederaceus* and *R. omiophyllus* are self-compatible. From hybridization experiments it was found that diploid *R. hederaceus* could be used only as a maternal parent when crossed with other species. To study this crosses between male *R. hederaceus* and female *R. tripartitus* were examined embryologically. The growth of the pollen tube appeared normal and apparently some fertilization took place as the endosperm started normal development but the embryo did not divide and remained dormant.

The following is a list of successful crosses involving *R. hederaceus* and *R. omiophyllus*. The origin of the material used is shown in a separate list after the hybrids. Herbarium material of these hybrids is deposited in the herbarium of the Hartley Botanical Laboratories, Liverpool (LIVU). The female parent is cited first. The somatic chromosome number of the parent is given before the name (for details of chromosome numbers see Cook, 1962). In most cases the hybrid was obtained after the first attempt but in all cases after not more than three attempts.

1. 16, *R. hederaceus* (Podlech) $\times$ 16, *hederaceus* (Lizard).
2. 16, *R. hederaceus* (Lizard) $\times$ 16, *hederaceus* (Podlech).
3. 16, *R. hederaceus* (Lizard) $\times$ 16, *hederaceus* (Portugal).
4. 16, *R. hederaceus* (Lizard) $\times$ 32, *omiophyllus* (Dartmoor).
5. 16, *R. hederaceus* (Lizard) $\times$ 48, *tripartitus* (Lizard).
6. 16, *R. hederaceus* (Lizard) $\times$ *peltatus* (Coimbra).
7. 32, *R. hederaceus* (Aut. Lizard) $\times$ 16, *hederaceus* (Lizard).
8. 32, *R. hederaceus* (Aut. Lizard) $\times$ 32, *omiophyllus* (Dartmoor).
9. 32, *R. hederaceus* (Aut. Lizard) $\times$ 48, *tripartitus* (Lizard).
10. 32, *R. hederaceus* (Aut. Lizard) $\times$ 32, *trichophyllus* (Wicken).
11. 32, *R. omiophyllus* (Dartmoor) $\times$ 32, *hederaceus* (Aut. Lizard).
12. 32, *R. omiophyllus* (Dartmoor) $\times$ 48, *tripartitus* (Lizard).
13. 48, *R. tripartitus* (Lizard) $\times$ 32, *omiophyllus* (Dartmoor).
14. 32, *R. baudotii* (Brading) $\times$ 32, *hederaceus* (Aut. Lizard).
15. 32, *R. baudotii* (Brading) $\times$ 32, *omiophyllus* (Dartmoor).

The following is a list of unsuccessful crosses. The number of attempts made is shown after each cross.

- 16, *R. hederaceus* (Lizard) $\times$ 32, *hederaceus* (Aut. Lizard) (2).
- 16, *R. hederaceus* (Lizard) $\times$ 16, *omiophyllus* (Polizzi) (10).
- 16, *R. hederaceus* (Lizard) $\times$ 16, *oleuleucos* (Maarn) (4).
- 16, *R. hederaceus* (Lizard) $\times$ 32, *baudotii* (Brading) (2).
- 16, *R. hederaceus* (Lizard) $\times$ 16, *circinatus* (Wicken) (7).
- 16, *R. hederaceus* (Lizard) $\times$ 16, *fluitans* (Quorndon) (3).
- 16, *R. hederaceus* (Lizard) $\times$ 32, *fluitans* (Suffolk) (2).

- 32, *R. hederaceus* (Aut. Lizard) $\times$ 16, *omiophyllus* (Polizzi) (5).
 32, *R. hederaceus* (Aut. Lizard) $\times$ 16, *ololeucos* (Maarn) (2).
 32, *R. hederaceus* (Aut. Lizard) $\times$ 16, *circinatus* (Wicken) (2).
 32, *R. hederaceus* (Aut. Lizard) $\times$ 32, *fluitans* (Suffolk) (2).
 16, *R. omiophyllus* (Polizzi) $\times$ 16, *hederaceus* (Lizard) (10).
 16, *R. omiophyllus* (Polizzi) $\times$ 32, *hederaceus* (Aut. Lizard) (2).
 16, *R. omiophyllus* (Polizzi) $\times$ 32, *omiophyllus* (Dartmoor) (3).
 16, *R. omiophyllus* (Polizzi) $\times$ 16, *ololeucos* (Maarn) (2).
 32, *R. omiophyllus* (Dartmoor) $\times$ 16, *hederaceus* (Lizard) (8).
 32, *R. omiophyllus* (Dartmoor) $\times$ 16, *omiophyllus* (Polizzi) (2).
 32, *R. omiophyllus* (Dartmoor) $\times$ *peltatus* (Coimbra) (2).
 32, *R. omiophyllus* (Dartmoor) $\times$ 48, *aquatilis* (Stretham) (1).
 32, *R. omiophyllus* (Dartmoor) $\times$ 32, *trichophyllus* (Wicken) (2).
 32, *R. omiophyllus* (Dartmoor) $\times$ 32, *fluitans* (Suffolk) (1).
 16, *R. ololeucos* (Maarn) $\times$ 16, *hederaceus* (Lizard) (3).
 16, *R. ololeucos* (Maarn) $\times$ 32, *hederaceus* (Aut. Lizard) (1).
 16, *R. ololeucos* (Maarn) $\times$ 16, *omiophyllus* (Polizzi) (4).
 48, *R. tripartitus* (Lizard) $\times$ 16, *hederaceus* (Lizard) (12).
 48, *R. tripartitus* (Lizard) $\times$ 32, *hederaceus* (Aut. Lizard) (2).

The following is a list of the origins of the material used in the crossing experiments.

48, *R. aquatilis* (Stretham). Roadside ditch about 2 km south of Stretham, Cambridgeshire. C. D. K. Cook, 20 September 1956.

16, *R. baudotii* (Brading). On the saltmarsh at Brading, Isle of Wight. C. D. K. Cook, 20 May 1958.

16, *R. circinatus* (Wicken). In the Lode at Wicken Fen, Cambridgeshire. C. D. K. Cook, 2 June 1959.

16, *R. fluitans* (Quorndon). In the Markeaton Brook, Quorndon, Derbyshire. C. D. K. Cook, 11 June 1957.

32, *R. fluitans* (Suffolk). In the River Lark at Temple Bridge, Tuddenham, Suffolk. C. D. K. Cook, 19 June 1958.

16, *R. hederaceus* (Lizard). By a wet farm-track at Ponsongath, The Lizard, Cornwall. C. D. K. Cook, 30 March 1958.

16, *R. hederaceus* (Portugal). Collected wild near Mora. prov. Alto Alentejo, Portugal by B. V. Rainha, 12 June 1958, sent by A. R. Pinto da Silva.

16, *R. hederaceus* (Podlech). In a ditch at Eifel, Wirftal about 1 km south of Stadtykl, Prüm, Germany. D. Podlech, 25 May 1961.

32, *R. hederaceus* (Aut. Lizard). An autotetraploid induced from seeds of 16, *hederaceus* (Lizard) in September 1958, at Cambridge Botanic Garden.

16, *R. ololeucos* (Maarn). In a ditch at Maarn, 15 km east of Utrecht, Holland. C. D. K. Cook and T. W. J. Gadella, 1 April 1960.

16, *R. omiophyllus* (Polizzi). Small spring about 6 km north of Polizzi Generosa, Madonie Mountains, Sicily. C. D. K. Cook, 21 April 1961.

32, *R. omiophyllus* (Dartmoor). Wet flush just below Wistman's Wood, Two Bridges, Dartmoor, Devon. C. D. K. Cook, 4 May 1958.

R. peltatus (Coimbra). Seed sent from the Botanic Gardens of the University of Coimbra, Portugal. Received March 1957 but wild origin unknown.

32, *R. trichophyllus* (Wicken). In the ditch around the bird sanctuary in Adventurers' Fen, Wicken, Cambridgeshire. C. D. K. Cook, 20 September 1956.

48, *R. tripartitus* (Lizard). In a pool by the air-raid shelter, Kynance, The Lizard, Cornwall. C. D. K. Cook, 21 March 1957.

Hybrids 1, 2 and 3 are between plants of *R. hederaceus* collected from Britain, Germany and Portugal. All hybrid plants were fully fertile and indistinguishable from the parents.

Hybrid 7 is the result of a cross between maternal tetraploid and paternal diploid *R. hederaceus*; the reciprocal cross has been attempted twice without success. Stebbins (1958) pointed out that in crosses involving diploids and autotetraploids the diploid usually is the poorer maternal parent. This hybrid is triploid ($2n = 24$) and highly sterile, and has produced no fertile achenes. In summer it closely resembles the diploid parent and in winter the tetraploid parent. All attempts at inducing a hexaploid from this triploid have, so far, failed.

Hybrid 4 (diploid *R. hederaceus* $\times$ tetraploid *omiophyllus*) is a highly sterile triploid ($2n = 24$). Apart from a little more vigour this hybrid is indistinguishable from *R. omiophyllus* on all gross morphological characters. Using the technique described on p. 249 it has an apparent pollen-fertility of 4 per cent. but no fertile achenes have been produced. The reciprocal cross has been attempted eight times but no offspring have been obtained.

Hybrid 7 (autotetraploid *R. hederaceus* $\times$ tetraploid *omiophyllus*) and hybrid 11, the reciprocal cross, are highly sterile tetraploids ($2n = 32$) which are morphologically indistinguishable from the triploid hybrid described above. Both these tetraploid hybrids have an apparent pollen fertility of about 15 per cent. but neither have produced mature achenes. This apparently fertile pollen stains well and looks perfectly formed but when used for backcrossing to either parent it will not germinate. Reciprocal backcrosses have been made and parent pollen will germinate on the hybrid stigmas but no fertile achenes have been formed.

The nature of this hybrid sterility appears to be genic rather than chromosomal. From studies of mitosis there are no visible differences between the karyotypes of *R. hederaceus* and *R. omiophyllus* (Fig. 4). In the tetraploid hybrids there is some univalent formation (Fig. 5a) which is not found in diploid *R. hederaceus* (Fig. 5b). Although the

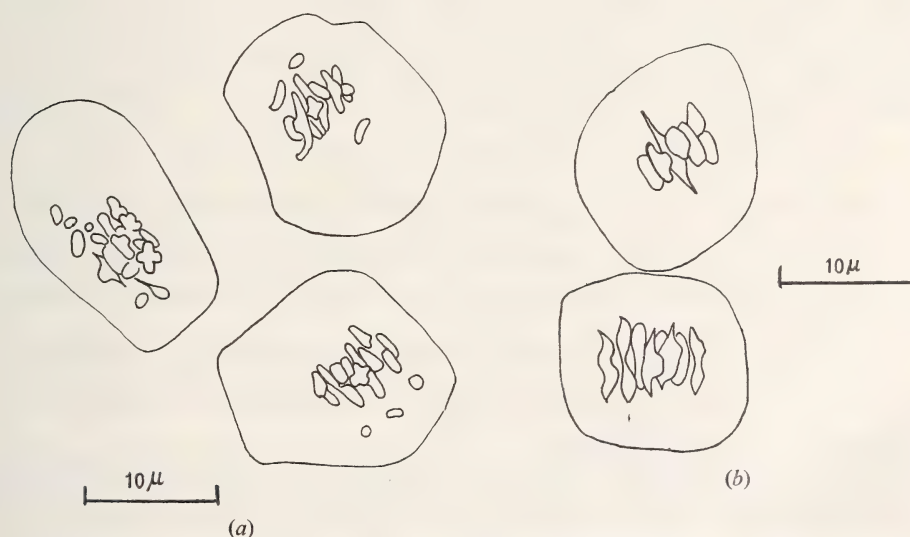


Fig. 5. Preparations of pollen-mother cells to show meiotic metaphase in (a) 32 *R. hederaceus* (Aut. Lizard) $\times$ 32 *omiophyllus* (Dartmoor) and, (b) 16 *R. hederaceus*.

meiotic preparations are not satisfactory there is no great chromosomal unbalance and hybrids between tetraploid *R. hederaceus* and *R. baudotii* show similar meiotic figures and apparent pollen-fertility but produce fertile achenes which germinate and give rise to F_2 progeny which show segregation. Similar situations are found in *Nicotiana* (Lammerts 1931) and *Geum* (Gajewski 1957). In spite of repeated attempts no allopolyploids have been induced from these hybrids, so it is not possible to rule out chromosomal sterility; but as both diploid *R. hederaceus* and tetraploid *R. omiophyllus* will form fertile hybrids with *R. tripartitus* it looks as if the sterility may be genic, especially as the F_2 progeny from these

hybrids show segregation in the degree of fertility. It may appear that an important stage in this sterility is in the formation of the pollen tube, but backcrosses using parental pollen have also been inviable, so that the sterility between *R. hederaceus* and *R. omiophyllus* is present on both the maternal and paternal sides.

DISCUSSION

R. hederaceus and *R. omiophyllus* are largely sympatric, morphologically very alike, and share a similar ecological niche, occasionally being found growing together. Salisbury (1934) reported that *R. omiophyllus* was invariably associated with peaty waters while *R. hederaceus* was more tolerant of waters well supplied with mineral salts, but he had, however, seen both species growing intermingled. In Britain, his generalization may be correct, but in the Madonie Mountains of Sicily *R. omiophyllus* was found growing in eutrophic conditions around cattle troughs on calcareous substrata, the kind of conditions, in fact, where one expects to find *R. hederaceus* in Britain. It may be that where these two species are not competing they exhibit wider ecological amplitudes.

In cultivation, British material of each species grows well on calcareous and non-calcareous soils and no interspecific differences in vigour have been detected. Similarly Sicilian and British material of *R. omiophyllus* do not show any differences in vigour when cultivated side by side under different conditions. In spite of a high degree of inbreeding and the presence of many isolated populations of these species it is remarkable that no local genotypic differentiation has been detected. This is especially noteworthy as they are related species that may compete with each other in one area or may compete with different species in different areas.

R. hederaceus and *R. omiophyllus* show complete hybrid inviability at the diploid level and hybrid sterility at the tetraploid level, but at the same time can be regarded as belonging to a single potential gene pool (hologamodeme) as diploid *R. hederaceus* and tetraploid *R. omiophyllus* will form fertile hybrids with *R. tripartitus*, while tetraploid *R. hederaceus* and tetraploid *R. omiophyllus* will form fertile hybrids with *R. baudotii*. The genetic isolating mechanism is apparently genic and operates between *R. hederaceus* and *R. omiophyllus* alone; one can visualize it as being the result of a comparatively simple mutation. If this is the case then it is possible that sympatric speciation, not dependent on polyploidy, has taken place. Putative records of *R. omiophyllus* and *R. hederaceus* from inter- and post-glacial times are given by Godwin (1956), but after re-examination of some fossil material I find it impossible to distinguish between these species from their quaternary remains so, unfortunately, no acceptable information can be reported about their geographical ranges in the past.

It is possible that *R. hederaceus* and *R. omiophyllus* differentiated allopatrically but if this were the case it seems unlikely that a simple genic sterility mechanism would be present in areas where the species are allopatric and that this mechanism would affect these two species alone within the whole subgenus.

Perhaps of more immediate interest is the phenomenon of two closely related species living in the same area. Harper *et al* (1961) in a review on this subject point out that much interest has been concentrated on the mechanisms whereby productive isolation is achieved and fixed but that this is only part of the process leading to systematic divergence.

R. hederaceus and *R. omiophyllus* are morphologically very similar, only differing in quantitative characters such as the degree of fusion of the stipules to the petiole, depth of sinus between leaf-lobes, ratio of petal length to sepal length and relative position of style. These two species have more attributes in common than they do with any other species of the subgenus *Batrachium*; they also show homologous phenotypic variation patterns which are seen in other aquatic species of the subgenus. I can find no evidence to suggest that these two species have not differentiated fairly recently (in terms of *Batrachium* evolution) from some common stock. It is hoped to discuss the position of these two species in the evolutionary pattern of *Ranunculus* subgenus *Batrachium* in a later paper but the leaf morphogenesis with extreme proleptic growth of stipules (Cook 1963) and presence of

stomata on the upper leaf-surface suggests that these species have had an aquatic ancestor.

Aquatic plants that are partially emergent are subjected to an extreme disruption in space as the lower parts may be submerged in water while the upper are in air. Bradshaw (1965) points out that any disruption that approaches the size of an individual plant will form a selection pressure favouring phenotypic plasticity. It is a safe generalization to say that emergent aquatics do show a considerable amount of phenotypic plasticity in many characteristics; Glück (1923, 1924 and 1936), for example, gives many examples. An aquatic ancestry may well explain how, or perhaps where, *R. hederaceus* and *R. omiophyllus* acquired their considerable degree of plasticity, but once acquired, phenotypic responses will require special selection pressures to restrict them before selection favouring different genotypes can take place.

Peplis portula and *Montia fontana* frequently occupy the same habitat and have essentially the same life-form and ecology as *R. hederaceus* and *R. omiophyllus* but show very different phenotypic response patterns (Glück 1923). The genera *Peplis* and *Montia* contain no submerged aquatic species nor have they any living aquatic relatives so it is unlikely that they have evolved from aquatic ancestors. This difference in phenotypic response may provide further evidence that *R. hederaceus* and *R. omiophyllus* have retained their phenotypic plasticity from aquatic ancestors.

In conclusion, *R. hederaceus* and *R. omiophyllus* are a pair of related species that appear to occupy the same ecological niche. They are genetically isolated and differ in quantitative morphological features. Because they grow together it is impossible to suggest any adaptive advantage for any of the differential morphological characteristics. It is unlikely that any of these morphological differences are due to genetic drift as both species are found in numerous spacially isolated populations and they show a very high degree of inbreeding. My own view is that these two species represent two distinct homozygous strains that have survived from a polymorphic species-group that evolved from some aquatic species of *Ranunculus* subgenus *Batrachium* by loss of capillary leaves, and that these two species owe their success today to plastic responses carried over from their aquatic ancestors.

FORMAL DESCRIPTIONS

RANUNCULUS HEDERACEUS L., Sp. Pl. 556 (1753).

R. hederaceus Salisb., Prod. Stirp. 373 (1796);

Batrachium hederaceum (L.) S. F. Gray, Nat. Arr. Brit. Pl. 2, 721 (1821);

R. hydrocharis B, *homoioophyllus* var. *hederaceus* (L.) Spenner, Fl. Frib. 3, 1008 (1829);

R. hydrocharis Spenner, 'form'* *hederaceus* (Salisb.) Hiern, J. Bot. Lond. 9, 67 (1871);

R. asarifolius Diard, exsicc. fide Rouy & Fouc., Fl. Fr. 60 (1893).

Typification

Benson (1954) designated the specimen on sheet number 74(Savage 1945) in the Linnaean Herbarium, Linnaean Society, London (LINN) the lectotype of *R. hederaceus*. I have examined this specimen and can find no reason to doubt Benson's designation.

Description

Prostrate annual or perennial. Leaves opposite or alternate; stipules adnate to petiole for more than half their length, apex acute; petiole 2–4 times as long as the lamina; lamina 4–25 mm long, 3–35 mm wide, reniform to subcordate with 3 or 5 lobes; lobes broadest at the base; margin entire or crenulate. Sepals (1.0—) 2–2.5 (—3.0) mm long, spreading. Petals (1.25—) 2.5–3.5 (—4.25) mm long,† ovate, not continuous; nectary pits lunate. Stamens (4—) 7–10 (—11). Carpels (9—) 18–24 (—42), glabrous; style lateral. Receptacle glabrous.

*Hiern's 'forms' or 'ultimate forms' as he calls them on p. 44 *loc. cit.* have no definite taxonomic rank.

†Petal length and sepal length are positively correlated.

RANUNCULUS OMIOPHYLLUS Ten., Fl. Nap. 4, 338 (1830).

R. coenosus Guss., Suppl. Fl. Sic. Prod., 187 (1832);

?*R. aquatilis* L. var. *homophyllus* Sensus Moris, Fl. Sard. 1, 26 (1837).

R. lenormandii F. Schultz, Bot. Zeit. 20, 726 (1837);

R. reniforme Desportes, Fl. Sarthe and Mayenne 3 (1838);

R. hederaceus L. var. *grandiflorus* Bab., Man. Brit. Bot. 5 (1843);

Batrachium lenormandii (F. Schultz) F. Schultz, Arch. Fl. Fr. & Allem. 70 (1844);

B. coenosum (Guss.) Nym., Bot. Notis. 100 (1852);

R. hydrocharis Spenner, 'form' *homoeophyllus* (Ten.), 'form' *lenormandii* (F. Schultz) Hiern, J. Bot. Lond. 9, 66 (1871);

R. mauritanicus Pommel, Nouv. Mat. Fl. Atl. 249 (1874);

R. hederaceus L. subsp. *coenosus* (Guss.) Arcangeli, Comp. Fl. Ital. 8 (1882);

R. hederaceus L. proles *homoeophyllus* (Ten.) Rouy & Fouc. Fl. Fr. 60 (1893);

R. hederaceus L. var. *homoeophyllus* (Ten.) Fiori & Paoletti, Fl. Anal. Ital. 1, 500 (1898);

B. omiophyllum (Ten.) C. D. K. Cook, Mitt. Bot. Staatss. München, 3, 600 (1960).

Typification

Written below Tenore's original description (*loc. cit.* p. 339) appears 'Nasce ne' fossi fangosi della Basilicata e della Calabria : a Balvano, Cassano, Corigliano.' In Tenore's own herbarium at Naples (NAP) the most complete specimen is one collected from Balvano; it is affixed to a label bearing *R. omiophyllus* in Tenore's own handwriting. I designate this specimen the lectotype of *R. omiophyllus*.

Description

Prostrate annual or perennial. Leaves opposite or alternate; stipules adnate to petiole for half or less their length, apex obtuse; petiole 3–6 times as long as lamina; lamina 2–26 mm. long, 3–32 mm. wide; reniform to sub-orbicular with 3 or 5 lobes; lobes narrowest at base; margin crenate. Sepals (1.75—) 2.5–3 (—3.75) mm. long, reflexed. Petals (3.75—) 5–6 (—7.00) mm. long, ovate not contiguous; nectary pits lunate. Stamens (5—) 7–10 (—13). Carpels (15—) 20–50 (—67), glabrous; style terminal. Receptacle glabrous.

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STUDIES ON WELSH ORCHIDS.

III. THE COEXISTENCE OF SOME OF THE TETRAPLOID SPECIES OF MARSH ORCHIDS.

By R. H. ROBERTS

ABSTRACT

Studies of mixed populations of some of the tetraploid marsh orchids have shown that in some Welsh localities there are barriers to gene-exchange between the coexisting species.

There is conclusive evidence of a complete sterility barrier between *Dactylorhiza traunsteineri* and *D. purpurella* at four different localities. In a mixed population of *D. majalis* and *D. purpurella* the two species remain distinct, and the evidence suggests that little if any gene-flow has occurred between them. Elsewhere it appears that some introgression may have taken place between *D. praetermissa* and *D. purpurella*, but even there the two species have not become completely merged.

It is suggested that barriers to interbreeding may not be equally effective between all of the species. Possibly they may not everywhere be as complete even between the same two species.

INTRODUCTION

The taxonomic problems of the *Dactylorchids* in the British Isles have received a great deal of attention over the last fifty years. On occasion they have even been the subject of sharp controversy. A comparison of the treatment of this group by Bentham & Hooker (Ed. 7, 1924) with those of Clapham in the first and second editions of the *Flora of the British Isles* (Clapham, Tutin & Warburg 1952, 1962) gives some indication of the very considerable changes which have been made—many of them within the last twenty years.

The difficulties of this group have been due partly to the critical nature of the forms within it, as well as to the fact that the species themselves display a bewildering variability. This is to be found not only between one population and another, but within the populations themselves. It is only by the recent application of biometric and cytological techniques—mainly by J. Heslop Harrison—that a fuller understanding of the British forms of this genus has come about.

The genus *Dactylorchis* was divided by Vermeulen (1947) into three main sections, but only one of these, the section *Maculatae* (Parl.) Vermln., occurs in the British Isles. This has been further divided by Heslop Harrison (1954) into three sub-sections: *Incarnatae* Vermln., *Eumaculatae* Vermln., and *Majales* (Pugsley) H. Harr. f. Of these the most difficult taxonomically is the last. The variation within the sub-section *Majales* is often extremely localized. It is therefore not surprising that systematists have held widely differing opinions as to the number of species involved, or where the boundaries separating them should be drawn.

In Britain the interest aroused by the description of two new species: *D. praetermissa* by Druce (1914) and *D. purpurella* by T. & T. A. Stephenson (1920), was further increased by Pugsley's announcement of the discovery of two additional new forms in Ireland (Pugsley 1936), and resulted in a period of active field work. While this added considerably to our knowledge of these plants, the orthodox methods of the herbarium taxonomist proved inadequate to deal with the enormous variation found among the forms of the sub-section *Majales* in the field. The result was the making of several new 'species', among which *Orchis pardalina*, *O. kerryensis*, *O. occidentalis*, *O. traunsteinerioides* and *O. francis-drucei* will be recalled.

In the British Isles four main entities are at present recognized in this sub-section:

Dactylorhiza majalis (Reichb.) P. F. Hunt & Summerh.*

D. traunsteineri (Saut.) Soó

D. praetermissa (Druce) Soó

D. purpurella (T. & T. A. Stephenson) Soó

These are treated as species though their relationships with one another are not yet fully understood (Heslop Harrison 1954; Clapham 1962). The occurrence of populations morphologically intermediate between some of them has led to the assumption that they are not separated by inherent sterility barriers, but depend for their continued existence as separate entities on geographical and ecological factors (Clapham 1962). In certain localities there is said to be evidence of complete interfertility, as, for example, in a mixed population of *D. traunsteineri* and *D. praetermissa* in Norfolk (Heslop Harrison 1954), and in some localities in the north of England where *D. traunsteineri* is stated to have been 'hybridized out of existence' by *D. purpurella* (J. W. Heslop Harrison & J. A. Richardson 1953). If this is the case, then it would be reasonable to treat all four entities as sub-species of an aggregate species *D. majalis*—a treatment which Clapham (1962) has already gone some way towards adopting. The possession by all of them of the same chromosome number ($2n = 80$) would also appear to have encouraged the acceptance of such a view.

On the contrary, at several localities in Wales two of these species coexist in close association, but appear to remain specifically distinct: *D. traunsteineri* with *D. purpurella* at five separate places in Anglesey and Caernarvonshire, *D. majalis* with *D. purpurella* at one locality in Anglesey (Roberts 1961b), and *D. praetermissa* with *D. purpurella* at a Merionethshire locality (Benoit & Richards 1963). These observations were not in accord with the complete interfertility of the various species, and biometric studies were made in an attempt to clarify some aspects of this problem.

METHODS

Several of the morphological characters which are used to differentiate the species were studied by the usual biometric methods. The mean values for each sample were then plotted along five axes, and the points were joined to form a polygon, combining the data from each species population into a single visual expression. Comparison of the polygons then shows at a glance how the various populations resemble or differ from one another.

RESULTS

D. traunsteineri and *D. purpurella*

D. traunsteineri and *D. purpurella* are found growing intermixed or in closely adjacent habitats at four separate places in Anglesey (v.c. 52) and at one in Caernarvonshire (v.c. 49). At two of the Anglesey localities both species occur in such close proximity as to afford every opportunity for cross-pollination to have taken place. They also grow in sufficiently large numbers to make a biometric study worth while; and, moreover, the boundaries of the selected populations coincide closely with the limits of the sampling areas.

The vegetative characters studied were mainly those which have been used to separate these two species, namely, the total number of leaves, the number of non-sheathing leaves, and the ratio of leaf length to leaf width. The flower characters chosen were the length and width of the labellum, the product of these two being used as an approximate index of labellum size. Since in many populations of *D. traunsteineri* the number of flowers in the inflorescence is remarkably low, a comparison of this character in the two species was also made.

In order to eliminate the possibility that the sample data might not be sufficiently representative of these populations, sampling was repeated during a second season, but no

*This name is taken here in a wider sense than that of Hunt and Summerhayes (1965), to include *Orchis kerryensis* Wilmott, *O. occidentalis* Pugsf. and *Dactylorhiza majalis* subsp. *cambrensis* R. H. Roberts, *Watsonia* 5, 37–42 (1961). This last plant now becomes *Dactylorhiza majalis* (Reichb.) P. F. Hunt and Summerh. subsp. *cambrensis* (R. H. Roberts) R. H. Roberts *comb. nov.*

significant differences were found between the two lots of data so obtained. The results can therefore be regarded with some confidence.

From the sample data (Tables 1 and 2) the large and highly significant differences in these characters between the two species are clearly evident, despite their close association

TABLE 1. Sample data for vegetative characters of *D. traunsteineri* and *D. purpurella* from two mixed populations.

	<i>N</i>	Total number of leaves		No. of non-sheathing leaves		Leaf length (cm)		Leaf width (cm)		Mean length Mean width
		mean	s.e.m.	mean		mean	s.e.m.	mean	s.e.m.	
PENTRAETH										
<i>D. traunsteineri</i>	50	3.7	.08	0.6		8.4	.22	1.0	.03	8.4
<i>D. purpurella</i>	54	6.1	.13	1.5		9.1	.23	1.6	.05	5.7
CORS ERDDREINIOG										
<i>D. traunsteineri</i>	101	3.9	.06	0.7		10.4	.21	1.0	.02	10.4
<i>D. purpurella</i>	50	6.0	.14	1.3		9.9	.25	1.9	.06	5.2

TABLE 2. Sample data for labellum dimensions, labellum-size index, and number of flowers in the inflorescence from two mixed populations.

	<i>N</i>	Labellum length (cm)		Labellum width (cm)		Labellum-size index	No. of flowers in inflorescence
		mean	s.e.m.	mean	s.e.m.		mean
PENTRAETH							
<i>D. traunsteineri</i>	40	.79	.014	1.02	.018	.81	7.5
<i>D. purpurella</i>	55	.70	.006	.88	.011	.62	20.6
CORS ERDDREINIOG							
<i>D. traunsteineri</i>	72	.89	.015	1.10	.017	.98	9.7
<i>D. purpurella</i>	35	.71	.009	.93	.014	.66	23.0

within these two areas. Histograms (Fig. 1) for leaf number, number of non-sheathing leaves, and number of flowers in the inflorescence for the two species at these localities are shown as examples of how distinct the biometric data prove them to be.

Polygons derived from the sample means are shown (Fig. 2) together with those for a population of each of the two species growing in the absence of the other: one from a colony of *D. traunsteineri* (Hellfield, M.-W. Yorks., v.c. 64) in a locality where *D. purpurella* has not been found (Roberts & Gilbert 1963), and the other from a colony of *D. purpurella* (near Bangor, Caerns., v.c. 49) in which *D. traunsteineri* does not occur. The essential similarities of the three populations of *D. traunsteineri* are evident, as are those of the three populations of *D. purpurella*. On the other hand the conclusion is unavoidable that at the two localities where they coexist there is no suggestion of the contamination of either species by the other. On the contrary, all the data indicate the complete absence of hybridization or of introgression between these two species.

In view of the conclusive evidence afforded by the biometric data, a thorough search was made on several occasions during the flowering seasons in 1962, 1963 and 1964 for plants which could reasonably be suspected of being the F_1 hybrid. Not one such plant was seen, however, in either of these areas, nor at two other places in Anglesey where these species also grow within a few yards of one another. This confirmed previous observations

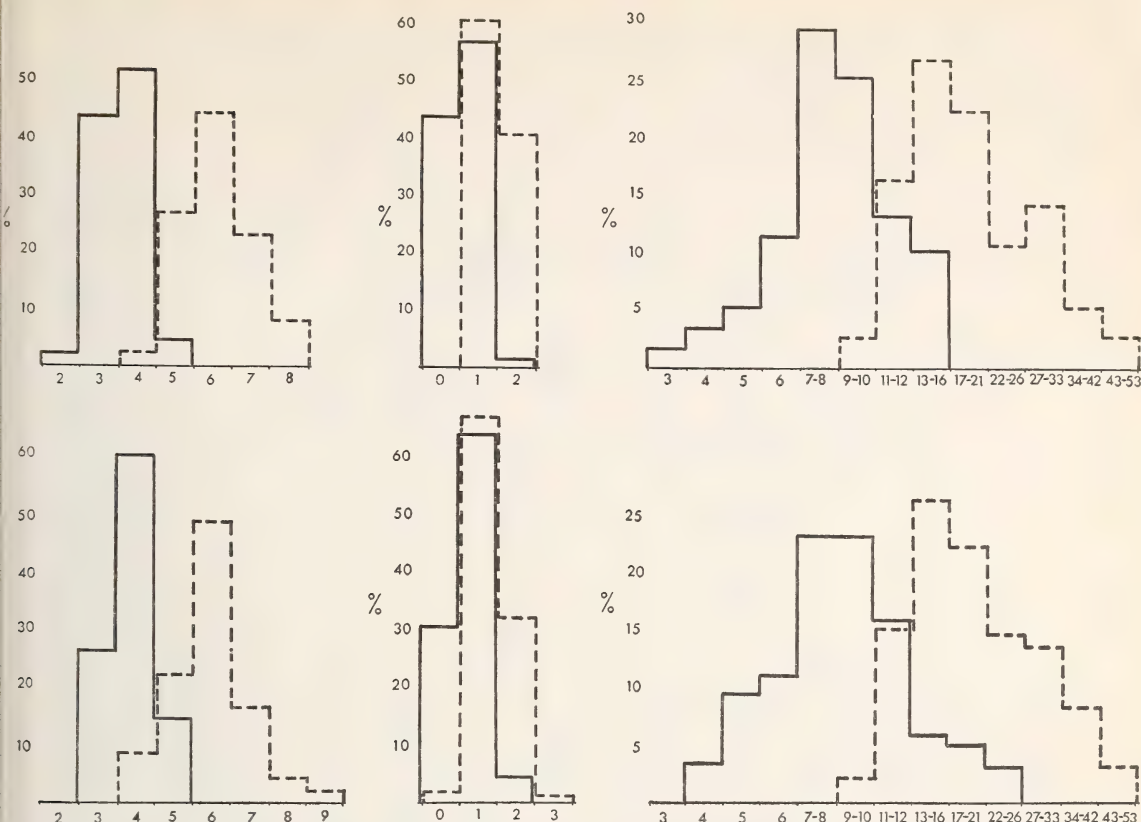


Fig. 1. Histograms of (from left to right) leaf number, number of non-sheathing leaves, and number of flowers per inflorescence in two mixed populations of *D. traunsteineri* (solid lines) and *D. purpurella* (broken lines); top row, Pentraeth; bottom row, Cors Erddreiniog.

when deliberate searches for the F_1 hybrid had also failed (Roberts 1960). A previous record of the putative hybrid (Lacey & Roberts 1958) from Caernarvonshire must now be regarded with doubt, and re-examination of the herbarium specimens on which it was based suggests that they are more probably aberrant forms of *D. traunsteineri*.

One of the characteristics of *D. traunsteineri* in the British Isles is that it is among the earliest of the marsh orchids to come into flower (Heslop Harrison 1953). In Anglesey it has been found to commence flowering as early as 5 May, reaching a peak around the end of May and continuing until the third week of June. Rarely are any flowers to be seen after 20 June. *D. purpurella*, on the other hand, starts to flower usually during the first week of June, reaching a peak around 20 June, and continuing well into the first half of July. Thus, although the peak flowering periods of the two species are separated by about three weeks, there is still a considerable overlap, and it appears that, in these localities at least, these species are isolated by an inherent sterility barrier.

D. majalis and *D. purpurella*

At three places in Wales there are colonies of a heavily leaf-spotted marsh orchid which has been placed as a subspecies under *D. majalis* (Roberts 1961b, 1962). In one locality—near Newborough, Anglesey—it grows intermixed with *D. purpurella*, and observations on this population had indicated that, despite cohabiting, the two forms remained specifically distinct.

With one exception the same characters have been used as for the mixed populations of *D. traunsteineri* and *D. purpurella*. However, the number of flowers in the inflorescence

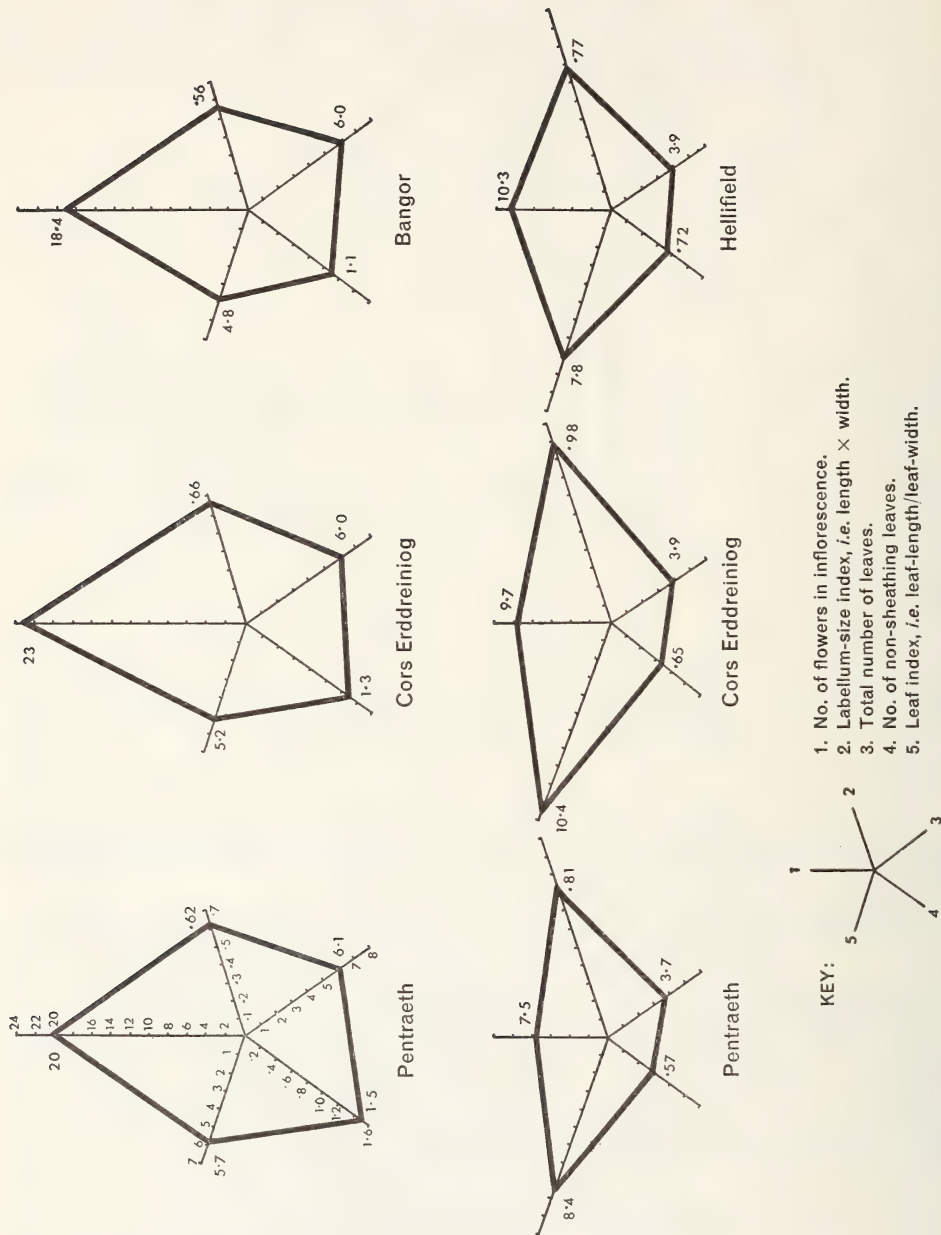


Fig. 2. Polygraphs from two mixed and two 'pure' populations of *D. trauststeineri* (bottom row) and *D. purpurella* (top row). Scales as shown at top left.

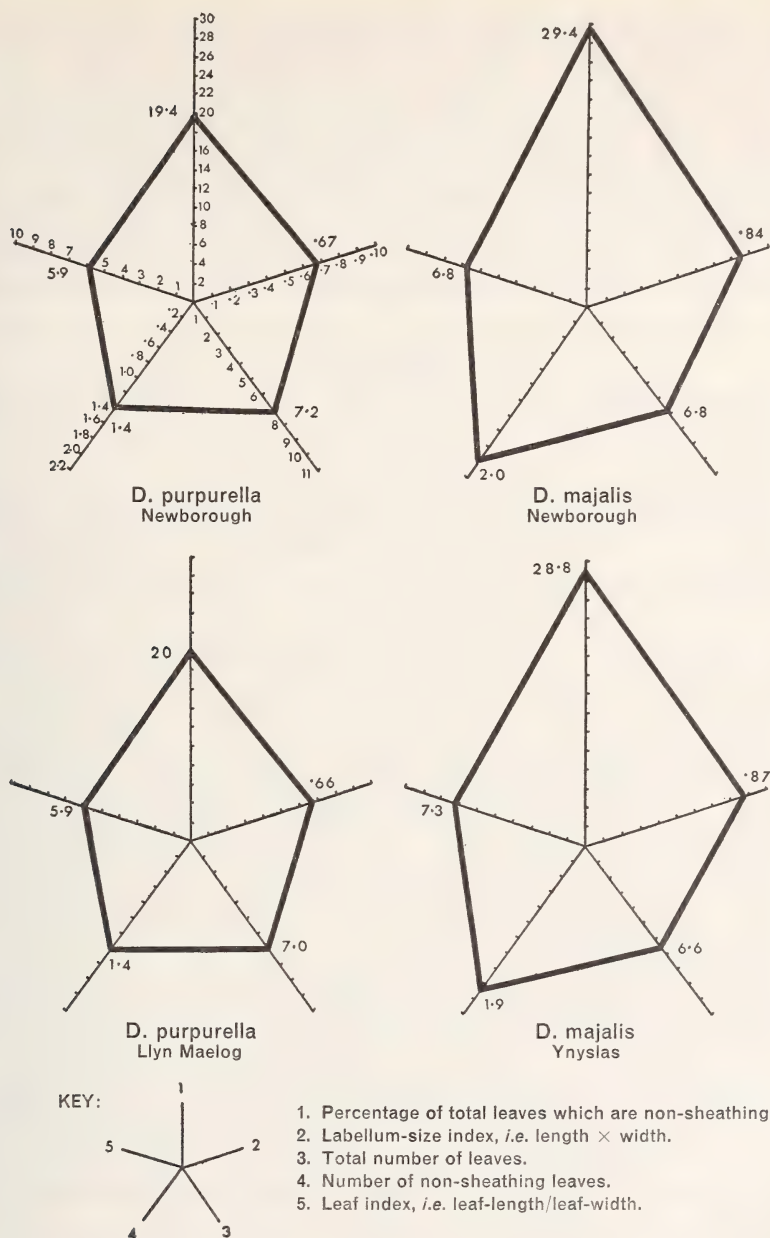


Fig. 3. Polygraphs from one mixed and two 'pure' populations of *D. majalis* and *D. purpurella*. Scales as shown at top left.

is not used to separate *D. majalis* and *D. purpurella*. The percentage of the total number of leaves which are non-sheathing has been used instead as a fifth variable, because these two species had previously been found to differ significantly in this respect.

The polygraphs (Fig. 3) for *D. majalis* and *D. purpurella* in the mixed population, as well as for *D. majalis* growing without *D. purpurella*, at Ynyslas, Cardiganshire, are based on data which have already been published (Roberts 1961a, 1961b). The fourth is from unpublished data for a pure population of *D. purpurella* growing near Llyn Maeiog, Anglesey.

These polygraphs show the considerable differences between the populations of the two species where they coexist. Moreover, the close identity of the *D. majalis* colony in Anglesey with that in Cardiganshire, as well as the similarity of the colony of *D. purpurella* growing with it to another of this species growing in the absence of *D. majalis*, are both apparent. From this it seems reasonable to conclude that there has been little or no modification of either species by the presence of the other in the mixed population.

So far it has not been possible to decide whether F_1 hybrids between these species occur in the Newborough population. On the other hand it is not possible to state categorically that they do not occur, but even if they do, these results suggest that gene-exchange between the two species in either direction is at least extremely restricted, if not completely prevented.

DISCUSSION

In the mixed populations of *D. traunsteineri* and *D. purpurella* which have been studied it has been shown that there is no evidence of hybridization or of introgression between the two species. Although their flowering periods differ, there is sufficient overlap to provide ample opportunity for cross-pollination to take place. Furthermore, it does not seem probable that the insect pollinators are able to discriminate between the flowers of the two species. It is well known that cross-pollination of *D. purpurella* with *D. fuchsii* occurs frequently, as is shown by the presence of their hybrid in most of the places where they grow together. Since the differences between the flowers of these two species are greater than between those of *D. traunsteineri* and *D. purpurella*, it is unlikely that flower specificity on the part of the pollinating insects is the isolating factor in the latter instance. But it must be stressed that there is, as yet, no positive information on this point.

This suggests that there are internal barriers to hybridization, and the absence of F_1 hybrids indicates that the isolating mechanism is effective at an early stage: either the prevention of fertilization through pollen incompatibility, the degeneration of the incompatibly fertilized ovules, the inviability of the F_1 hybrid, or some even more obscure factor.

In the case of the mixed population of *D. majalis* and *D. purpurella* the continued co-existence of the two species without merging seems to show at least that they are not completely interfertile. In this instance, however, it has not been possible to obtain conclusive evidence of whether hybrids are present or not, and there are difficulties in the way of recognizing them if they do occur.

As has been mentioned already, the complete interfertility of the tetraploid marsh orchids has become generally accepted in Britain in recent years. Although the conclusions arrived at here do not agree with that view, it must be emphasized that the scope of the present study is too limited to enable wider generalizations to be drawn from it. The fact that *D. traunsteineri* is incapable of interbreeding with *D. purpurella* in Anglesey does not necessarily imply that it may not be able to do so elsewhere, or with other members of the sub-section *Majales*. Nevertheless, the remarkable uniformity displayed by *D. traunsteineri* in certain morphological characters such as the extremely small number of very narrow leaves, as well as in its specialized ecological preferences, makes one suspect that this species, at any rate, is genetically isolated from the other tetraploid species over most of its British range.

A rather different situation seems to prevail in a mixed population of *D. praetermissa* and *D. purpurella* at Harlech, Merioneth. Limited observations suggest that here a certain amount of hybridization and introgression may have taken place, as has already been indicated by Benoit & Richards (1961). On the other hand Mr. V. S. Summerhayes (personal communication) has failed to find any evidence of hybridization in a mixed population of these two species in a Hampshire locality. The apparent introgression in the Harlech population may, in fact, be due partly to the presence of extreme variants of the very variable population of *D. praetermissa*. But the evidence obtained so far from this population is incomplete, and more sensitive methods than those used here may be required to deal with the problems involved.

It may be that the inter-relationships of the tetraploid species of marsh orchids are more complex than has been suspected, and that barriers to gene-exchange may not be equally strong between all of the species, or even between the same two species in different localities. Even if hybridization occurs when two of the tetraploid species, having evolved in geographical isolation, first come into contact, it is possible that the barriers to interbreeding may subsequently become intensified. In this connection it is pertinent to recall that the isolating mechanisms between some allopatric species are most effective in those areas where the species actually meet.

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Mr. P. M. Benoit for showing me the Harlech population; Mr. P. F. Hunt of Kew, for checking a reference, and Mr. V. S. Summerhayes for allowing me to quote his observations on the Hampshire population.

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BOOK REVIEW

The Vegetation of Scotland. J. H. Burnett, (editor). Pp. xiii + 613 with 96 plates, 61 figures in the text and 65 tables. Oliver & Boyd, Edinburgh. 1964. Price £6. 6s.

'In Scotland there is a wider range of plant habitats than anywhere else in the British Isles.' This modest reminder of the enormous task undertaken in 1958 by the nine co-authors of this work greets the reader on the caption of the frontispiece. In six years they have produced a description of the main types of Scottish vegetation with the exception of the vegetation of the islands, of the rivers, of the mountain lochs above 1,000 feet, of the screes and cliffs and of the pure bryophyte communities of the Atlantic seaboard.

The method of survey used (except for coastal vegetation and the phytoplankton of the lowland lochs) is that described by Poore (1955 etc.). The presentation of results is also mainly inspired by Poore and the Scandinavian school of phytosociology.

Introductory chapters on climate and soil and a concluding one on the ecological history of Scottish vegetation provide illuminating background to the main body of the text. The chapter on soils is particularly satisfying to the non-specialist; the classification used is based mainly on European models (Kubiěna 1953) and is, perhaps, more 'vegetation-orientated' than the other systems being used in these countries. The chapter on climate rightly emphasises the importance of potential water deficit as a factor correlating with the distribution of vegetation and a map is presented giving estimates for this parameter.

The survey, based on over 1,600 stand descriptions, may be accepted as a reasonable first approximation towards an inventory and description of Scottish plant communities. Some types of vegetation have been more thoroughly sampled than others. Spence's chapter on the macrophytic vegetation of the lowland lochs, swamps and fens is perhaps the most thorough (and longest), being based on 382 relevés, many of which are accompanied by analyses of soil and sediments. The chapter on grasslands also includes soil analyses for each of the lowland types described.

While acknowledging the energetic and painstaking work that went into the collection of the data, one may be permitted to criticise the presentation of the results. Relevant studies on each vegetation type, both published and unpublished, are well reported and much of the material has been specially collected for this work. The floristic data for each community type are summarized in a synoptic list printed in tables at the end of each chapter. However, the overall impression one is left with after reading the book is of a wealth of information but of a marked lack of synthesis and unity. A large number of vegetation units have been recognized and named (161 bold-faced headings in the text; some of these have been subdivided to give 183 vegetation types in the synoptic lists). These units vary enormously in status. Some correspond to associations of the Braun-Blanquet system, a few may embody data from two different associations (e.g. table 6, col. 3; table 26), but the majority have the status of sub-associations or of variants,

Now, one of the main aims of a monograph of the vegetation of a region should be to give a readily grasped conceptual scheme based on sound analytic data. Such a scheme can later be further developed but it serves meanwhile an extremely useful didactic purpose in applied and theoretical ecology. At the same time it provides a useful 'conceptual model' for those engaged in research which they may choose to modify, perfect or even reject as further information comes in. In this work, however, the 161 or more vegetation types fall into no perceptible scheme beyond a roughly physiognomic one suggested by the chapter headings and subdivisions.

An example may show that the data were susceptible of a more satisfying treatment. The bog communities distinguished correspond exactly with those of McVean and Ratcliffe (1962) where the full plant lists are to be found. If all relevés from bog vegetation (class *Oxycocco-Sphagneteta*) are culled from McVean and Ratcliffe (one will find them scattered over six tables) and if they are combined with the Scottish relevés of Osvald (1949) and then analysed according to the methods of Braun-Blanquet, three very clearly defined associations will be found to emerge, each belonging to a separate alliance in the B.-B. system. The two associations on deeper peat and possibly also one 'wet heath' association will be found to be sub-divisible into the frequently found pattern of three sub-associations. Had the material from other vegetation types been subjected to similar treatment, no doubt comparable results could have been achieved.

True, the editor shrugs off responsibility for such a task with the quip that it may be left 'to those phytosociological taxonomists to whom such a pastime is rewarding'. It is to be hoped that the original field records have been preserved in a readily available form to allow such phytosociologists to indulge in their pastime.

However, this rather partisan criticism should not be allowed to detract from the solid value of the work. Typographical errors are surprisingly few (*Ranunculus lingua* was omitted in the table containing

the *R. lingua*–*Cicuta virosa* variant of a *Phragmites* sociation). A special word of praise is due to the plates—well chosen and excellently printed. Especially fascinating are the aerial views of raised and blanket bogs and the pairs of photographs of lochs taken in 1905 and in 1960 from approximately the same spot.

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FURTHER OBSERVATIONS ON *TRIFOLIUM OCCIDENTALE*

By D. E. COOMBE and P. MORISSET

The Botany School, University of Cambridge

ABSTRACT

Trifolium occidentale, previously known with certainty only from W. Cornwall and the Channel Islands, is widespread along the exposed rocky and sandy coasts of Brittany and the Cotentin peninsula in N.W. France where it is morphologically, cytologically and ecologically identical with or closely similar to typical British plants. Chromosome counts from French material confirm the number $2n = 16$.

INTRODUCTION

Trifolium occidentale (Coombe 1961) is related to *T. repens* but morphologically, genetically, cytologically and ecologically distinct from it. By 1961 *T. occidentale* was known to occur in W. Cornwall and the Channel Islands and its existence along the coasts of W. and N.W. France seemed likely. A specimen in the Herbarium at Kew suggested that it might also occur in N.E. Spain. Its chromosome number was found to be $2n = 16$ in three clones from W. Cornwall, in two from Guernsey and two from Jersey, whereas $2n = 32$ in wild plants of *T. repens*.

DISTRIBUTION

On 1 May 1962, *T. occidentale* was found by H. des Abbayes (Rennes) on maritime sand dunes at Le Cabellou, Concarneau, on the S. coast of Finistère; the specimen (now in CGE) is identical with the type from W. Cornwall. This is the first localized record for France. H. des Abbayes also noted the plant on the Iles Glénans off Concarneau, but failed to find it around Dinard (Ille-et-Vilaine). Subsequently R. Tüxen (Stolzenau-Weser) found *T. occidentale* in Finistère at Beuzec-Cap-Sizun (14 km W. of Douarnenez) on 7 June 1962, and on maritime sand dunes at Santec (5 km W.S.W. of Roscoff) on 9 June 1962. In the same month J. M. Géhu (Lille and Besançon) found *T. occidentale* on the coast of the northern part of the Cotentin Peninsula (Manche) at the Pointe de Barfleur (26 km E.N.E. of Cherbourg), on the dunes at Vauville (15 km W. of Cherbourg) and at the Cap de Carteret (near Barneville). Later in 1962 and 1963 J. M. Géhu (accompanied on occasion by A. Dizerbo (Brest), P. Jovet (Paris) and R. Franquet (Nancy)) added a large number of localities in Finistère, a lesser number in Manche and Côtes-du-Nord, and one locality in Morbihan.

Géhu (1962) describes the coastal habitats (sand-dunes and cliffs) and communities in which *T. occidentale* was known at that time in N.W. France; Géhu (1963*b*) gives a more detailed distribution map, full lists of localities, and further ecological notes. Neither he nor P. Jovet have been able to find it in the Pays Basque or around Biarritz, or along the W. coast of France south of Lorient (including Belle Ile), or along the Golfe de St. Malo between the Iles Bréhat and Granville; nor has Géhu found it on numerous visits to the coasts of the Pays de Caux and the Pas-de-Calais (Géhu 1962; see also Géhu 1963*a*, 1964 for further observations on associated species*).

In the British Isles *T. occidentale* has still not been found outside W. Cornwall and the Channel Islands; localities which somewhat extend its known range since 1961 are Alderney (Crabby Bay, 19 April 1962, Miss M. McCallum Webster) and Towan Head, Newquay, W. Cornwall (3 June 1964, J. H. Chandler, confirmed in the field by D.E.C.

**T. occidentale* occurs at Marazion Station (W. Cornwall) together with *Cynodon dactylon* (cf. Quadrat 1(a) from Guernsey in Coombe, 1961).

on 9 April 1965). Other new records in W. Cornwall merely close the gaps between published localities: Lamorna Cove, Treen, Gwennap Head, Cape Cornwall, Pendeen Watch (D.E.C., 1961–62); Zennor Head, Portherras Cove (Mrs. J. Paton 1962); St. Levan (D.E.C., 1966); Tresco (abundant near the Blockhouse, both on dune sand and on granite, D.E.C., 1966).

Fig. 1 shows all localities of *T. occidentale* known by 5 May 1966; each dot in the British Isles represents at least one record in a 10 km square of the National Grid (as defined by Perring & Walters 1962); records in France are based on Géhu (1963) and exclude the unconfirmed locality at San Sebastien in N.E. Spain (Coombe 1961).

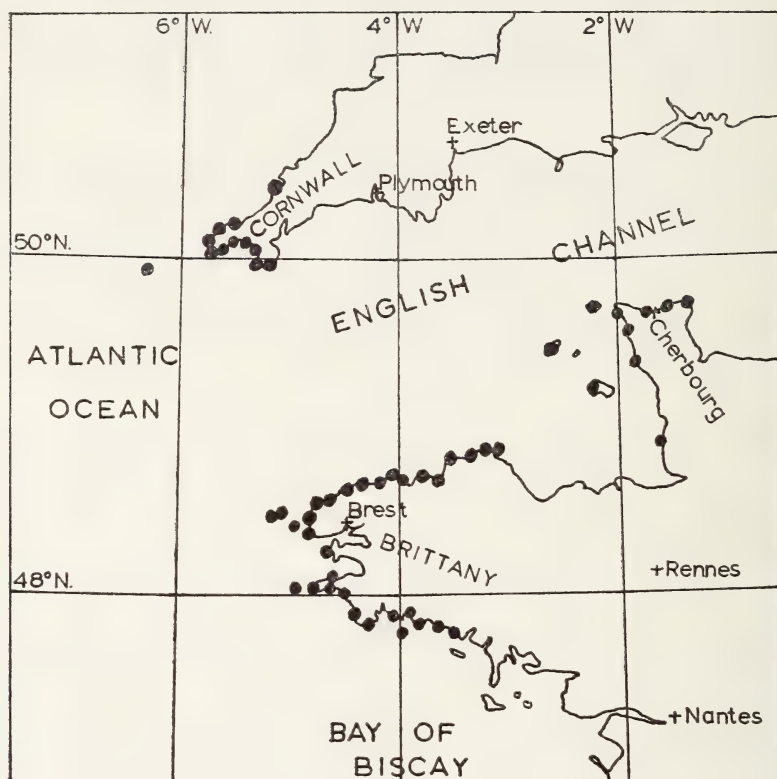


Fig. 1. Distribution of *Trifolium occidentale*.

MORPHOLOGY OF FRENCH PLANTS

In 1965 M. Kerguélen (Laboratoire de Recherches sur les Plantes Fourragères, Rouen, S.M.) distributed wild-collected seed of *T. occidentale* from three localities in Finistère: Lampaul-Ploudalmézeau (24 km N.W. of Brest); Guissény (28 km E.N.E. of Brest); and Pointe de Trévignon near Trégunc (36 km W.N.W. of Lorient). Some of the seed from each of these localities was sown in June 1965 in a cool glass-house at the Cambridge University Botanic Garden where the plants flowered freely from March to June 1966. These plants are identical with typical *T. occidentale* in all characters described by Coombe (1961) with one exception: the calyx-teeth of some of the plants from Trégunc are somewhat recurved at anthesis instead of being straight or even convergent as in all other plants. Otherwise the calyx-teeth are typical in their ovate-lanceolate or broadly triangular shape and in usually having one or two denticulations, particularly on the upper margins of the two uppermost teeth. As these denticulations are not illustrated in Coombe (1961, p. 86), the calyx-teeth of a plant from Trégunc are shown in Fig. 2.

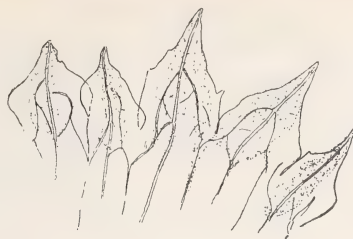


Fig. 2. The calyx-teeth of a plant of *Trifolium occidentale* from Trégunc. Stippled areas: chlorenchyma. Scale: $\times 10$.

CYTOLOGY*

The somatic chromosome number of *T. occidentale* from Brittany was determined using the following method with root-tip meristems from mature plants at the flowering stage, grown at the Cambridge University Botanic Garden: pre-treatment in a saturated aqueous solution of monobromonaphthalene for two hours at room temperature, fixation in acetic-alcohol (1 : 3), clearing of cytoplasm in a mixture (1 : 1) of concentrated HCl and ether for 10 minutes at room temperature, maceration in N HCl for five minutes at 60° C, staining in alcoholic carmine, and squashing in 45 per cent. acetic acid (Snow 1963). Three individuals were studied, one from each of the following localities in Finistère: Lampaul-Ploudalmézeau; Guissény; Pointe de Trévignon (near Trégunc).

Chromosome number

The three individuals of *T. occidentale* studied all have $2n = 16$ (Fig. 3) like those seven plants from W. Cornwall and the Channel Isles previously studied by M. J. E. Coode and M. J. Swift (in Coombe 1961). Wild *T. repens* on the other hand always has $2n = 32$ (references in Löve & Löve 1961). Atwood & Hill (1940) believe that the numbers $n = c. 12$ and $n = 14$ reported for *T. repens* are erroneous. Erith (1924) interpreted figures of meiosis

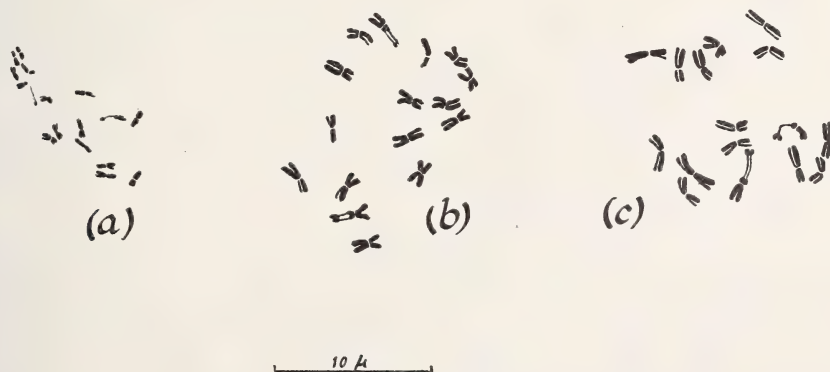


Fig. 3. Root meristem chromosomes of *Trifolium occidentale*; camera lucida drawings, all at the same scale. Plants from Brittany: (a) Trégunc; (b) Lampaul-Ploudalmézeau; (c) Guissény.

in macrosporocytes of *T. repens* as showing $n = 8$ but, as pointed out by Wexelsen (1928), her drawings clearly show that her material had $n = 16$. The only counts of $2n = 16$ in the group of perennial species closely related to *T. repens* are those of *T. thalii* Schreber (Löve & Löve 1961) and *T. occidentale*.

*By P. Morisset (now at Jardin botanique de Montréal, Montréal 36, Canada)

Chromosome morphology

In *T. occidentale* there are seven pairs of chromosomes with the centromere more or less in the median region ($\pm$ metacentric) and without a secondary constriction. The eighth pair is a pair of satellited chromosomes with an intercalary secondary constriction at about the middle of one arm. The satellites are therefore rather large. The length of the secondary constriction can vary from 0.5 to 5 μ within individuals; sometimes it even differs in the two satellited chromosomes of the same mitotic cell (Fig. 3(a)). Such variation in the length of the secondary constriction has been reported in other genera (e.g. *Polygonatum*; Therman-Suomaleinen 1949); it is probably due partly to differences in the action of the pre-treatment, partly to stretching brought about in squashing the cells.

Another point worth notice is that the individual from Trégunc has chromosomes much smaller (Fig. 3(a)) than those of the other two plants studied. In this plant the length of the chromosomes (excluding the pair of satellited chromosomes) varies from 1 to 1.5 μ ; in the other two from 2 to 3 μ . This is a genuine difference and not an artefact brought about by differing pre-treatment: in the plants from Lampaul-Ploudalmézeau and Guissény with generally larger chromosomes occasional cells have very contracted chromosomes of about the same length as those of the Trégunc plant, but such contracted chromosomes have much thicker arms than those in the Trégunc plant. Genotypically controlled intra-specific differences in chromosome size have been known for some time (Thomas 1936); we are probably dealing with the same phenomenon. Indeed, Wexelsen (1928) observed similar differences in *T. repens* and found in the F_1 plants from a cross between 'var. giganteum' (large chromosomes) and 'var. sylvestre' (small chromosomes) a chromosome size intermediate between that of the parents. Wexelsen also found a positive correlation between chromosome size and leaf size in his material; no such difference appears to exist in our material of *T. occidentale*, but as mentioned on p. 272 the calyx-teeth of some plants from Trégunc differ (at least in cultivation) from any other so far seen in being recurved and not more or less convergent at anthesis.

DISCUSSION

As expected *T. occidentale* is widespread along the coasts of N.W. France where it occurs in habitats very similar to those already described in Cornwall and the Channel Islands. Géhu (1963b, p. 207) remarks that it is especially characteristic of cliffs exposed to salt spray (*Armerion maritimae*) and of fixed dunes (*Koelerion albescentis*); it occurs more rarely in maritime heaths (*Ulicion gallii*) and related communities (*Sedion anglici*); it is absent from sheltered rocky coasts where vegetation influenced by spray is reduced or absent and where scrub (*Prunetalia*) or woodland (*Quercetalia robori-petraeae* or *Fagetalia*) come right down to the water's edge (as in many rias); and that it is also absent from saltmarshes (*Juncetalia maritimae*).

The record for N.E. Spain remains unconfirmed, and if, as Géhu suggests, *T. occidentale* has the character of a 'eu-atlantic' species, it would be unlikely to occur in the hotter, more extreme climate of the Gulf of Gascony. Nevertheless, it would be interesting to look for *T. occidentale* along the north coast of Spain, particularly in Galicia where plants of *T. repens* have been recorded with villous stems, petioles and peduncles (Merino 1909).

Although *T. occidentale* is superficially similar to *T. repens*, the data presented here confirm that the two species are readily distinguished in the field and are cytologically, ecologically and geographically distinct.

ACKNOWLEDGMENTS

We are grateful to the French, German and British botanists mentioned in the text for generously sending specimens and field notes, but particularly to Monsieur J. M. Géhu for his continued interest and courtesy, and to Monsieur M. Kerguélen for organizing the distribution of seed from wild plants from Brittany.

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NOTES ON *MYOSOTIS SCORPIOIDES* AGG.

By D. WELCH

Natural Environment Research Council, The Nature Conservancy, Moor House Field Station, Garrigill, Alston, Cumberland

ABSTRACT

The distinguishing characters of the British aquatic *Myosotis* species are summarized. Comparison of herbarium material suggests that *M. brevifolia* C. E. Salmon is not specifically distinct from the Iberian *M. stolonifera* Gay, which has the same chromosome number ($2n = 24$).

There has recently been a reawakening of interest in the water forget-me-nots. *Myosotis scorpioides* L. (*M. palustris* (L.) Hill), the single species of Linnaeus, was divided into several species and many varieties, some of which were called species, during the nineteenth century. However, in the sixth edition of Bentham and Hooker's British Flora (1892) it was said that *M. scorpioides*, *M. secunda* A. Murr. (*M. repens* auct.) and *M. caespitosa* K. F. Schultz ran so much into another as not to be distinguishable with certainty even as varieties. Later these three became generally accepted as good species, each containing varieties and forms, as described by Wade (1930 and 1933). A distinct water forget-me-not was reported from the Cross Fell area of the north Pennines by Salmon (1926). It was named *M. brevifolia* C. E. Salmon, and is accorded specific rank by Tutin (1952, 1962), though its relations with European forget-me-nots have not been resolved. The fifth British species in the group is the South European *M. sicula* Guss., which was discovered in Jersey in 1922.

Recently European workers have been looking at the genus cytologically (Merxmüller & Grau 1963). Benoit (1958) has described *M. scorpioides* $\times$ *caespitosa*, the first hybrid reported in the group, and Welch (1961) has pointed out certain errors in the description of the species which may be responsible for their widespread misidentification.

In order to ascertain the status of *M. brevifolia* and the best criteria for distinguishing this species, the author has, between 1961 and 1965, examined and measured water forget-me-nots from many different populations. *M. sicula* was not considered. The numbers of plants examined were: *scorpioides* 44, *caespitosa* 44, *secunda* 31, *brevifolia* 25, and in addition certain of the measurements have also been made on herbarium specimens, 12 of *secunda* and 3 of *brevifolia*. The data obtained support the existing taxonomy, each species having its own unique combination of characters, though individual characters may be shared. Variation in several of the characters measured is shown in Fig. 1.

Certain differences from Tutin's descriptions are apparent. Some plants of *M. scorpioides* were bracteate, some of *M. caespitosa* had corollas with diameters greater than 4 mm, and some of *M. secunda* had fruiting pedicels less than three times the length of the calyx. Also in *M. caespitosa* the calyx teeth never exceeded two-fifths of the length of the calyx.

The most useful characters for distinguishing the British water forget-me-nots are the cyme bracteation, the style length, the calyx division and the fruit pedicel length. Corolla diameter has some value, since only in *M. scorpioides* does the diameter exceed 7 mm, but in old cymes the flowers become smaller, resulting in overlap between the species.

M. scorpioides is best recognized by a combination of long style length, ebracteate cymes, and a calyx divided to only $\frac{1}{3}$ of its length. *M. caespitosa* is distinct in its hairs being always adpressed—all other plants examined except four of *M. brevifolia* had some spreading hairs—and in having a short style. *M. secunda* is distinguished from the other species by its long fruit pedicels and deeply divided calyx with acute teeth. The spreading hairs and bright blue flowers confirm its separation from *M. caespitosa* and *M. brevifolia* respectively. *M. brevifolia* may be recognized by the pale colour of its grey or blue flowers, and by the rounded teeth of its deeply divided calyx. The figures in Butcher & Strudwick

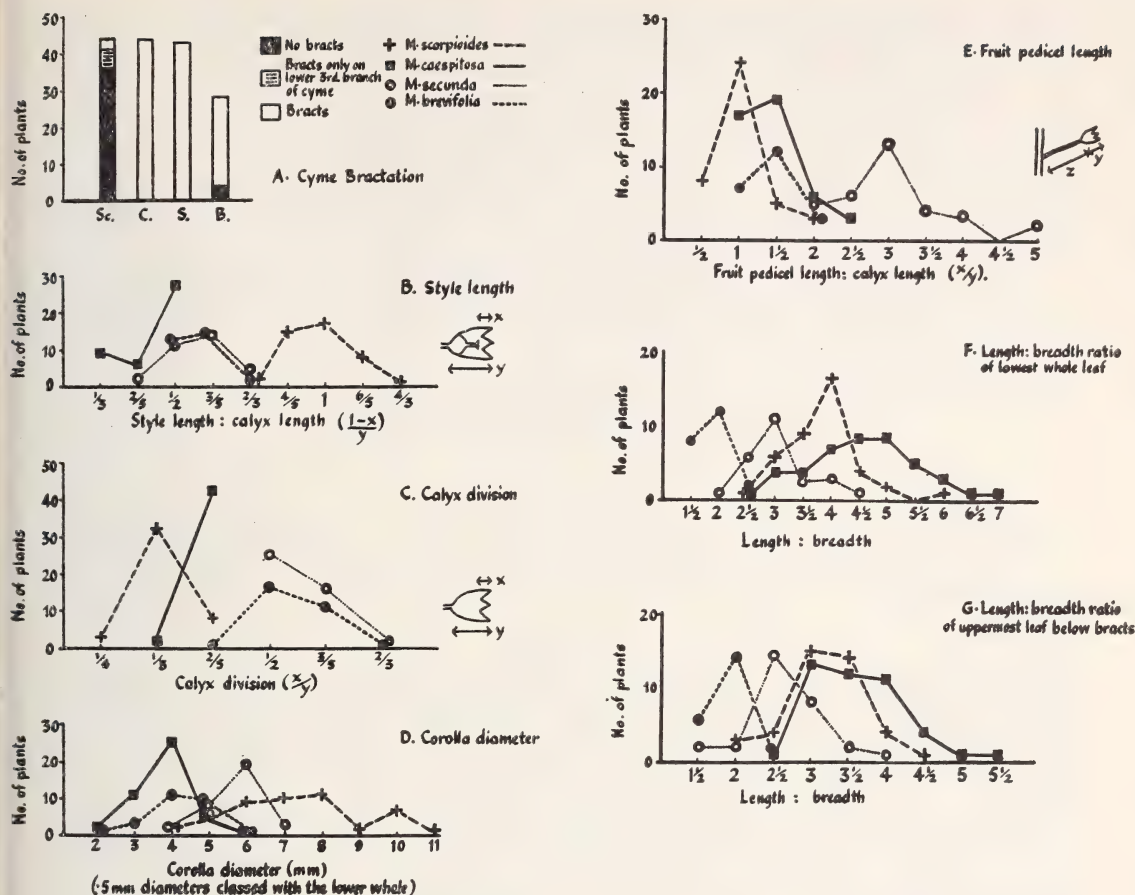


Fig. 1. Biometrics of four *Myosotis* species. Because of distortion, herbarium specimens have been excluded in F and G, and very largely in D.

(1930) illustrate well the calyces of this species and *M. secunda*. The short wide leaves are also a useful character, but the dark bluish-green colour said to be diagnostic by Tutin is not seen in all plants. In the Cross Fell area at least, many are small, grow in flushes, have the usual yellow-green *Myosotis* colour, and die down quickly after flowering in July.

The four species vary also in their ecological requirements. *M. scorpioides* is the usual lowland forget-me-not, often being abundant in ponds and marshes, and by river and stream sides. It does not usually ascend above 800 ft, but I have found it at 1,200 ft by Malham Tarn, and Tutin gives an altitudinal limit of 1,600 ft in Perth. *M. caespitosa* is much less common over most of lowland Britain occurring chiefly on cattle-churned mud and clay and also by brackish ditches. It is commoner in hilly districts, though I have not seen it above 1,400 ft.

M. secunda is the upland species, liking acid conditions with some flushing. It is only locally common, being absent from many apparently suitable habitats, but in parts of western Britain it descends to sea-level. *M. brevifolia* is a calcicole species, growing in upland and mountain flushes, and by tiny rills. It is rare and confined to the Lake District, the north and central Pennines, the North York Moors and the Southern Uplands.

The recent Continental investigations into the cytology of the water forget-me-nots prompt a re-examination of the relations of the British forms. Tutin suggests that *M. brevifolia* is endemic, but as Salmon (1926) points out, *M. stolonifera* Gay, found in the

hill areas of Spain and Portugal, is very similar. It is therefore of considerable interest that *M. brevifolia*, of which some of the material examined was obtained by me from Salmon's type locality, and *M. stolonifera* have been found to have the same chromosome number, $2n = 24$ (Grau 1965). Salmon's reasons for separating the two species were given in the following passage 'The closest ally of *M. brevifolia* would seem to be *M. stolonifera* Gay, small stunted examples of the former having much the same facies. A closer examination shows that Gay's dwarf plant possesses far smaller leaves on the stolons, more spatulate stem-leaves, shorter fruiting pedicels, more acute calyx-segments, etc.; well-grown examples of *M. brevifolia* are abundantly distinct.'

A total of 6 herbarium specimens of *M. stolonifera* have been examined, both for the parameters given in Fig. 1, and the characteristics thought to differentiate the species from *M. brevifolia*. The results are set out in Table I. It is clear that, of Salmon's four

TABLE 1. Observations and measurements on individual plants of *Myosotis stolonifera* and a comparison of their means and totals with those of *M. brevifolia*.

Plant number	1	2	3	4	5	6	Means and Totals	
							<i>M. stolonifera</i>	<i>M. brevifolia</i>
Height of stem (cm)	10	22	20	12	25	30	20	—
Bracteaion	c	c	c	c	c	c	6c	24c 4e
Calyx division	$\frac{3}{5}$	$\frac{3}{5}$	$\frac{3}{5}$	$\frac{3}{5}$	$\frac{3}{5}$	$\frac{3}{5}$	$\frac{3}{5}$	$\frac{4}{7}$
Diameter of corolla (mm)	4	5	6	—	—	—	5	4 $\frac{1}{2}$
Fruit pedicel length	1 $\frac{3}{4}$	1 $\frac{1}{2}$	3	2	1 $\frac{1}{2}$	2	2	1 $\frac{1}{2}$
L : b of lowest leaf	3	3	3	2 $\frac{1}{2}$	4	3 $\frac{1}{2}$	3	2
L : b of uppermost leaf	3	3 $\frac{1}{2}$	3	4	4	3	3 $\frac{1}{2}$	2
Stolon leaf length (mm)	5	6	10	—	—	11	8	—
Hairiness	a	s	s	s	a	s	4s 2a	24s 4a
Shape of calyx lobes	r	r	t	t	t	r	3r 3t	20r 8t

c = bracts on cyme

a = all hairs adpressed

r = lobes of calyx rounded but acuminate

e = ebractate

s = some hairs spreading

t = lobes of calyx subacute

reasons for separating the two species, only one, the calyx segment shape, and that doubtfully, can be used to differentiate plants called *M. stolonifera* by Iberian botanists from the British *M. brevifolia*. The stem leaves of the herbarium specimens, even allowing for some lateral shrinkage, were not more spatulate than those of *M. brevifolia*, and the fruit pedicels were not shorter. Furthermore, *M. stolonifera* can hardly be described as dwarf in comparison to *M. brevifolia*, for which Tutin gives a height of 12–20 cm, and the stolon leaves attain a considerable size, being at least as large as those of *M. brevifolia*.

In leaf shape and fruit pedicel length the Iberian material approaches *M. secunda*, and three twentieth-century floras of Portugal (Coutinho 1913, Coutinho 1939 and Sampaio 1946) reduced *M. stolonifera* to a variety of *M. welwitschii* Boiss. et Reut. This species, as here described, is very similar morphologically to *M. secunda*, with a complementary geographical range, and though the two are treated as separate, for example in the British Museum herbarium, the material collected in Portugal by British botanists is named *M. secunda*! However, Grau (1965) has found the British *M. secunda* and most of the Iberian material to be $2n = 48$, but some material from the Lisbon area and Morocco is diploid and morphologically distinct, having taller stems, narrower leaves, no stolons and corollas up to 10 cm in diameter. As this resembles Welwitsch's type specimen, she proposes that the diploid forms should be called *M. welwitschii*, and the tetraploid *M. secunda*. Furthermore, she suggests that *M. secunda* is an amphidiploid with *M. stolonifera*. In a few minor respects Grau's descriptions of *M. secunda* differ from the measurements given

above, as does her drawing of the calyx of *M. stolonifera* from that of typical *M. brevifolia*. However, it seems safe to conclude that *M. brevifolia* belongs to *M. stolonifera*, a good diploid species, and that *M. secunda* is widespread in Iberia. Whether its diploid forms are sufficiently distinct and constant to be given specific recognition and whether they have a wider distribution, possibly being present in Britain, has still to be determined.

Polyploidy has also been found in the *M. scorpioides*-*caespitosa* subgroup, and it may be that the varieties described in the nineteenth century can be fitted to the different ecotypes. The base number is $n = 11$, and diploid and tetraploid forms of *M. caespitosa* and diploid and hexaploid forms of *M. scorpioides* have been found so far (Merxmüller & Grau 1963). Perhaps local distribution of the cytotypes is the reason why the hybrid first reported by Benoit in 1958 has so far been found only in Hertfordshire, Warwickshire and Merionethshire, though the parents often grow together.

Thus it is clear that the water forget-me-nots offer plenty of further scope for taxonomic investigation. It would also be worthwhile to search for *M. brevifolia* in the base-rich mountain areas of the Scottish Highlands and Ireland.

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THE TAXONOMY AND NOMENCLATURE OF THE RADIATE VARIANTS OF *SENECIO VULGARIS* L.

By D. E. ALLEN

ABSTRACT

The radiate variants of *Senecio vulgaris* L. fall into two distinct groups, one found apparently exclusively in natural maritime habitats, the other almost entirely in inland, artificial ones. If these are recognized as two varieties, the correct names are respectively var. *denticulatus* (O. F. Muell.) Hyland. and var. *hibernicus* Syme. Alternatively, a single taxon may be recognized, at formal level, for all radiate variants irrespective of other characters in which they differ. The correct name would then be f. *radiatus* Hegi.

Plants of *Senecio vulgaris* L. with conspicuous ray florets have been known in the British Isles and other parts of Europe for many years, almost universally as 'var. *radiatus* Koch'. This name, however, is not only antedated but—if one possible taxonomic view is accepted—commonly misapplied.

The problem of establishing the correct name in this instance is complicated by the fact that, as several authors have pointed out at different times in the past, there is not, on a strict view, just a single radiate variant to be considered, but several. Some workers have advanced the opinion that all these variants as well as other eradiate biotypes that can be distinguished within this species, deserve to be given names. Others, while not going to this extreme, have at least acknowledged the existence of two groups of radiate forms differing sufficiently in other external characters and in distribution to make the recognition of two separate taxa defensible. Still others, more particularly in recent years, have held that the species contains altogether too many minor genetic variants for taxonomic distinctions to be worth attempting, although admitting that for practical purposes a single collective name for all the radiate forms would be convenient, even if devoid of precise genetical meaning. Of these three views, the second and third seem to have the most to commend them. Both would appear to be tenable in the light of existing knowledge, and which of the two is followed can only be a matter of personal inclination.

For those who prefer to distinguish two taxa the correct names, at varietal level, appear to be var. *denticulatus* (O. F. Muell.) Hyland. and var. *hibernicus* Syme. The synonymy of each is given below.

- S. VULGARIS* var. *DENTICULATUS* (O. F. Muell.) Hyland., *Nordens Växter* **1**, 132 (1955).
S. denticulatus O. F. Muell., *Fl. Dan.* (1780), **5**, pt. 14, t. 791; Nolte, *Nov. Fl. Holsat.* (1826), 71.
S. sylvaticus var. *denticulatus* (O. F. Muell.) Wahlenb., *Fl. Suec.*, **1**, 521 (1826).
S. lividus var. *denticulatus* (O. F. Muell.) DC., *Prodr.* **6**, 343 (1837).
S. vulgaris var. *radiatus* Koch, *Syn. Fl. Germ.* ed. 1, 386 (1837), *non auct. mult.*
S. vulgaris var. *dunensis* Knuth, *Fl. Nordfries. Ins.* 79 (1895).
S. lanuginosus Trow, *Rep. Bot. E. C.* 380; *non Spreng. Syst.* (1909), **3**, 565 (1828).
S. vulgaris var. *lanuginosus* Druce, *Rep. Botl. Soc. Exch. Club Br. Isl.*, 382 (1909).
S. vulgaris var. *lanifer* Wilmott, *Rep. Botl. Soc. Exch. Club Br. Isl.*, **12**, 663 (1946).

Under this name are grouped radiate variants occurring in natural maritime habitats, such as dunes, cliffs and sandy fields near the sea, on the coasts of west and south-west Britain (V.c. 2, 3, 52, 58, 59, 71), the Channel Isles, Normandy, the East and North Frisian Islands, western and northern Jutland, Lolland, Bornholm, and the south and east coasts of Sweden. Similar plants possibly also occur in Iceland, but the record (Ostenfeld &

Gröntved 1934) is not specific enough for certainty. No records have been traced for Ireland.

In general these maritime plants are simple or weakly branched, with 1–8 capitula, arachnoid-hairy (in cultivation this can sometimes become so pronounced as to form a conspicuous whitish felt), with spatulate, sinuate-dentate or laciniate, amplexicaul leaves and usually small and often strongly revolute ray florets. One of several workers to have grown Channel Isles specimens of this variety from seed, Trow (1912) found they adhered strictly to type through four generations. His attempts to produce an eradiate counterpart by selective breeding were not certainly successful (in marked contrast to his experience with var. *hibernicus*), but wild populations apparently of this type have been reported in coastal habitats at Pevensy, Sussex (Wilmott 1925, 1949), and on Bornholm (Lange 1851).

These maritime plants appear to constitute a distinct ecological race, which in view of its wide geographical range conceivably even merits subspecific rank, as suggested by Trimen (1871). Possibly the eradiate forms of the species now such ubiquitous weeds of cultivated land originally arose from populations of this type occupying natural maritime habitats. If this was the case, presumably the eradiate character was favoured by selection—or the maritime populations have become predominantly radiate at a more recent period.

S. VULGARIS var. *HIBERNICUS* Syme.

S. vulgaris var. *radiatus* Döll, *Rhein. Fl.*, 469 (1843); Ritschl, *Fl. Grossh. Posen*, 118 (1850); non Koch (1837).

S. vulgaris var. *hibernicus* Syme, *Rep. Botl. Soc. Exch. Club Br. Isl.* 27 (1875).

S. vulgaris var. *radiatus* Rouy, *Fl. Fr.* 8, 343 (1903).

S. erectus var. *radiatus* Trow, *Trans. Cardiff Nat. Soc., Suppl.* 92 (1909); *Rep. Botl. Soc. Exch. Club Br. Isl.* 380 (1909).

It is quite certain that Koch intended the maritime race by his var. *radiatus*, for he cites *S. denticulatus* as a synonym. A few years later, however, other German authors first described radiate plants from definitely inland localities—unfortunately employing the same varietal epithet as Koch. It fell to Syme to show that these inland plants are in general markedly different from those occurring by the sea, being only slightly hairy, much more branched, and having more deeply-cut leaves and usually larger, spreading ray florets.

These inland rayed variants are so conspicuous that it is difficult to believe earlier botanists would have failed to mention them, had they known of them. This fact and the relatively late date at which they were first described suggest that until at least the middle of the last century they were either very rare mutants or stray alien immigrants, possibly from more plentifully radiate populations in south Europe or further east. By 1875 they had evidently begun to appear in greater quantity in the vicinity of ports, such as Cork (whence Syme's choice of the epithet *hibernicus*) and, perhaps somewhat later, Cardiff and Avonmouth. Since then they have appeared as a weed in several botanical gardens, as at Cambridge and Copenhagen, doubtless as a result of seed being distributed for genetical purposes; and in recent years have greatly extended their range to waste ground in several fresh parts of Britain, notably in the central Midlands and the west of England.

By growing the Cork plants from seed Syme was the first to prove that these radiate variants are not the hybrid with *S. squalidus* L., which is sometimes confused with them but differs in its high degree of sterility. Trow (1912) succeeded in finding a radiate form of only one of his microspecies, '*S. erectus*'. When these two were crossed, intermediate plants with very short rays resulted. More recently a radiate form of another of Trow's microspecies, '*S. multicaulis*', has been detected (D. P. Young, pers. comm.), and there are possibly other forms in Britain in addition to these.

If var. *hibernicus* is preferred at formal rank, a new combination will be necessary. On the other hand, those wishing to recognise only a single taxon at formal level to cover all radiate variants within the species may still employ the epithet *radiatus* despite the fact that this is illegitimate at varietal level. The correct name in that event would appear to be

S. vulgaris f. *radiatus* Hegi, *Ill. Fl. Mitteleur.*, 6, 2, 788 (1929), though an earlier author using this name in an aggregate sense may well come to light on further search.

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ON THE IDENTITY OF THE IRISH POPULATIONS OF *SISYRINCHIUM*

By RUTH INGRAM

Department of Botany, Queen's College, Dundee
University of St. Andrews

ABSTRACT

The taxonomic status of the Irish populations of *Sisyrinchium* is discussed in the light of a morphological and cytological study of the genus in Ireland and the eastern states of the United States of America. It is concluded that the Irish populations should be referred to *S. bermudiana* L., since they are indistinguishable from this species in the United States. The phytogeographical implications of these results are considered.

INTRODUCTION

The genus *Sisyrinchium* (Iridaceae) contains four sections, *Bermudiana*, *Echthronema*, *Eriphlema* and *Nuno*, but all the species which will be considered in this paper belong to the section *Bermudiana*. This section consists of predominantly blue-flowered species, collectively known in the United States and Canada as the 'blue-eyed grasses'. Members of the genus are widespread in North America, though it is difficult to assess the actual number of species present because the nomenclature, particularly that of species of the interior and of the south and west coast regions, requires thorough investigation and revision. Species belonging to section *Bermudiana* also occur in South America, but inadequate documentation makes it difficult to gauge their extent there.

Outside America, species of the section *Bermudiana* have been recorded from Greenland and most of the North European countries. A member of this genus occurs in the Carpathian mountains and apparently gives every indication of being native there (Lauterborn 1929), though elsewhere on the continent of Europe the genus is thought to be an introduction.

In the British Isles, *Sisyrinchium* was first recorded from Ireland in 1845 by the Rev. J. Lynam, who found it near Woodford in Co. Galway (Praeger 1934). Further records later in the nineteenth century showed that it occurred in most counties of Western Ireland from Donegal to Cork. Praeger considered it an unlikely introduction in Ireland because so many of the recorded localities for it were remote from habitation, and he quotes Scully and Barrington as being of the same opinion. An eastern station for *Sisyrinchium* in Ireland is recorded in Co. Antrim (Praeger 1934), but as I have not examined plants from this locality, they are not included in the following discussion of the identity of the Irish plants. In England, members of the genus have been recorded from many localities, particularly in the south, but it seems likely that most if not all of these plants are garden escapes, and they will not be considered further.

One species has also been recorded from Greenland. The ecology and possible immigration history of this plant is discussed in considerable detail by Böcher (1948) who reaches the conclusion that it is almost certainly not an introduction by man.

MORPHOLOGY OF THE RELEVANT AMERICAN SPECIES

The investigation now to be described was an attempt to define clearly the cytological and taxonomic status of the Irish populations in relation to the American species of the genus. This necessitated a first-hand study of the genus both in Ireland and the United States. In previous discussion of the problem from various angles there has been a tendency to assume that the European garden plant, the Irish plant and the Greenland plant all belonged to the same taxon or to closely related taxa (Böcher 1948, Hegi 1939, Heslop-Harrison 1952), but this work has shown that more than one species is involved. The difficulty is that in this genus quite small morphological differences separate taxa with large biological

and cytological differences. This was clearly demonstrated by a study of those species which occur in the Atlantic States of North America (Ingram 1964). On the assumption that European plants would bear a fairly close resemblance to their North American relatives, particular attention was paid to those species bearing at least a superficial resemblance to plants obtained from Ireland and from gardens in England and Europe. Three species are particularly important in this context;

- (1) *S. bermudiana* L. (*S. angustifolium* Mill. *sensu* Fernald, *S. gramineum* Lam. *pro parte*, *S. anceps* Cav. *pro parte*, *S. graminoides* Bick.)
(Synonymy discussed by Shinnars 1957).
- (2) *S. montanum* Greene var. *crebrum* Fernald (*S. angustifolium* Mill. *sensu* Bick.)
(Synonymy discussed by Fernald 1946).
- (3) *S. mucronatum* Michx.

Detailed descriptions of these species are to be found in Fernald (1950). Other species occurring in the Atlantic States which are morphologically very different from the European plants, such as *S. capillare* Bick. and *S. arenicola* Bick., will not be considered.

Table 1 is a comparison of the Irish population with the three American species

TABLE 1

	<i>Sisyrinchium</i> (Irish)	<i>S. bermudiana</i> L. (American)	<i>S. montanum</i> Greene var. <i>crebrum</i> Fern.	<i>S. mucronatum</i> Michx.
Range	Western areas of Ireland	Widespread in eastern North America	Eastern North America from Newfoundland south to Pennsylvania	Eastern North America from Maine south to North Carolina
Habit	Spreading	Lax to spreading in Virginia and N. Carolina. More upright to the east and north	Stiff and upright	Stiff and upright
Stem morphology	Usually branched	Usually branched	Usually simple	Always simple
Spathe bracts	Outer bract only slightly exceeding inner	Outer bract only slightly exceeding inner	Outer bract $1\frac{1}{2}$ to 2 $\times$ length of inner	Outer bract 2 to 3 $\times$ length of inner
Flower colour	Light blue	Light blue	Violet blue	Light blue in Virginia and N. Carolina. Violet blue in New England
Reproductive morphology	Filament tube shorter than or equal to style	Filament tube shorter than or equal to style	Filament tube always equal to style	Filament tube always shorter than style
Capsule colour	Dark when ripe	Dark when ripe	Dark when ripe often purple tinged	Straw coloured
Habitat	Damp meadows, lake shores and river banks	Ubiquitous in N. Carolina, Tennessee and Virginia, but damper places only in New England	Open, dry situations	Meadow land and scrub

it most closely resembles, from a morphological point of view. The table is only intended to emphasize those features found to be reliable in identification, and those which could lead to confusion. The character which could lead to the greatest confusion is stem morphology. In *S. bermudiana* the stem is usually branched, but if the plant is grazed in the spring, and then allowed to develop flowers later in the season, there is a tendency to produce unbranched stems, which can lead to confusion with *S. montanum* var. *crebrum*. Conversely, *S. montanum* var. *crebrum* occasionally produces branched stems, though it is not known what environmental stimulus leads to this.

CYTOLOGY OF THE AMERICAN SPECIES

All the chromosome counts recorded here were made from pollen mother cell squashes. Root-tip counts were abandoned early in the investigation because some of the root-tip squash preparations revealed inconsistencies even within a single preparation. For example, two mitotic plates from a root-tip of *S. montanum* var. *crebrum* gave counts of $2n = 95$ and $2n = 86$. The true chromosome number for this plant was $2n = 96$, as a preparation of meiosis in pollen mother cells clearly showed (Fig. 1). No variation from cell to cell

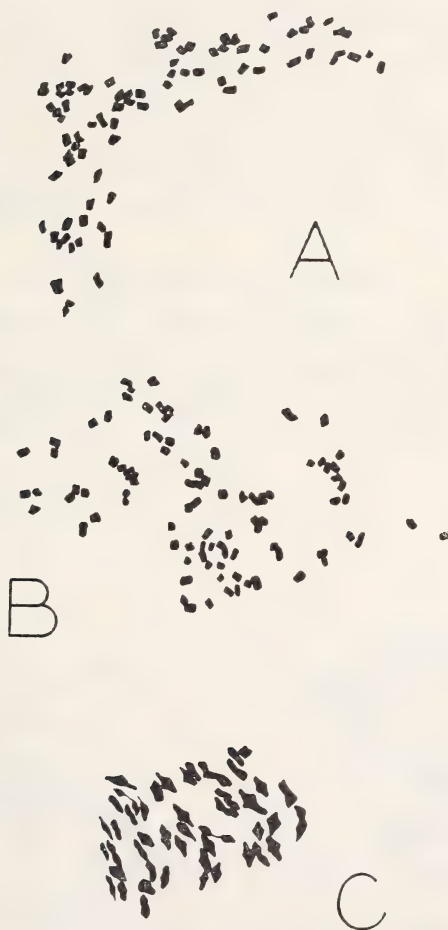


Fig. 1. Drawings to illustrate the unreliability of root-tip preparations in *Sisyrinchium* $\times 500$.

A. Mitotic plate from a root-tip of *S. montanum* var. *crebrum*, $2n = 95$.

B. Mitotic plate from the same root-tip, $2n = 86$.

C. Metaphase of meiosis in the same plant, $2n = 96$.

was seen in any pollen mother cell squash. When it became obvious that aneuploid races were important in the species *S. bermudiana*, it was considered impossible to use root-tip squashes. It is difficult to say whether the mitotic variability is real, or whether it is an artefact due to very small chromosomes overlying one another.

Root-tip material was stained by the Feulgen technique after pre-treatment in paradichlorobenzene and fixation in acetic alcohol. Pollen mother cell material was fixed in acetic alcohol, and stained with aceto-carmin. Preparations were made permanent by the quick-freeze method described by Conger & Fairchild (1953). The speed of this method reduced cytoplasmic staining, and led to a reduced loss of material from the slide.

All counts for American populations in this paper are based on at least three preparations from three different plants.

S. bermudiana L. (Fig. 2).

$2n = 82$ Chapel Hill, North Carolina.

$2n = 84$ Tolland State Forest, Massachusetts.

$2n = 88$ Clinch River Valley, Tennessee.

$2n = 88$ Campus of Lynchburg University, Virginia.

$2n = 90$ Near Wartburg, Morgan Co., Tennessee.

$2n = 90$ Near Chickahominy River Bridge, Charles City Co., Virginia.

$2n = 90$ Near Courtland, Suffolk Co., Virginia.

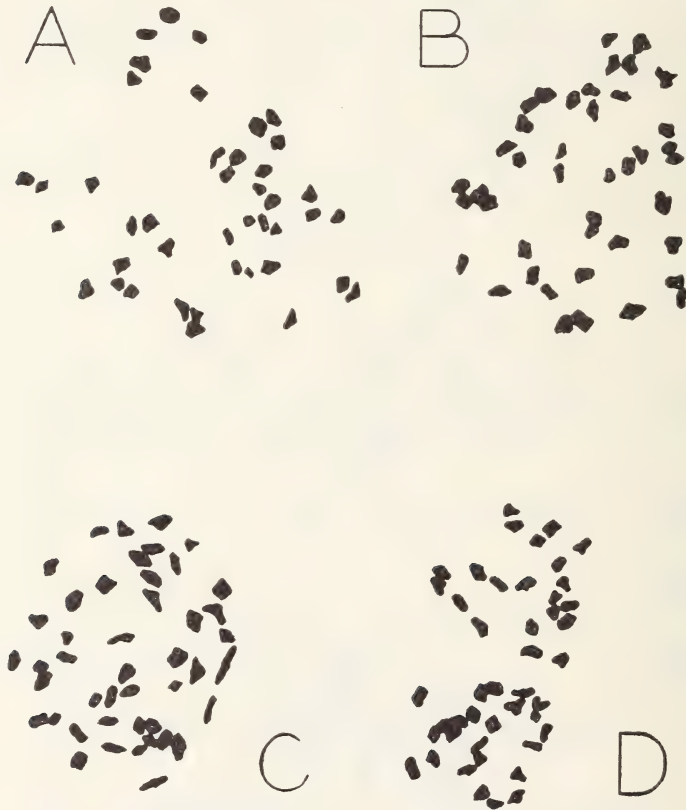


Fig. 2. Diakinesis in aneuploid populations of *S. bermudiana* L. $\times 500$.

A. Tolland State Forest, Massachusetts. $2n = 84$.

B. Clinch River Valley, Tennessee. $2n = 88$.

C. Near Wartburg, Morgan Co., Tennessee. $2n = 90$.

D. Chickahominy River Bridge, Charles City Co., Virginia. $2n = 90$.

No populations of this species having $2n = 96$ were recorded in the course of this investigation, but a count from Louisiana by Oliver & Lewis (1962) gave this number. It would therefore seem reasonable to assume that the counts recorded form an aneuploid series derived from the dodecaploid number $2n = 96$. The variation in chromosome number could not be correlated with observed morphological variability.

S. montanum Greene var. *crebrum* Fernald.

$2n = 96$ Springfield Reservoir, Massachusetts.

$2n = 96$ Near Bondville, Vermont.

$2n = 96$ South of Lake Catherine, Vermont.

Bowden (1945) also reported $2n = 96$ for this species.

S. mucronatum Michx.

$2n = 32$ Chapel Hill, North Carolina.

$2n = 30$ East of Chyde, Haywood Co., N. Carolina.

$2n = 32$ Magruder, Virginia.

$2n = 32$ Campus of Lynchburg University, Virginia.

It was unfortunately impossible to obtain counts from more northerly plants, but Oliver & Lewis (1962) record $2n = 32$ for material of this species from Canada.

Hybridization between *S. mucronatum* and the other two species proved impossible. No seeds were ever produced. Hybridization between the two dodecaploid species was possible, however, and hybrids were formed which were completely sterile, usually producing aborted capsules, and never yielding any seed. Meiosis in these hybrids was highly irregular, giving a maximum of 14 bivalents. This could be taken to indicate that the two species had only about one third of their chromosomes in common.

In spite of these wide cytological differences, there is a superficial morphological resemblance between these three species. Obviously, this does not indicate a close relationship.

SISYRINCHIUM IN IRELAND

Morphologically, plants from various parts of Ireland are very uniform when grown under similar conditions in an experimental greenhouse. It would seem therefore that the apparent variability in branching shown in herbarium specimens, and commented on by Northfield (1961), is caused by varying conditions of grazing and land use. Cytologically too, they show no variation, as the following counts indicate (Fig. 3).

$2n = 88$ Cloonee Loughs, Co. Kerry.

$2n = 88$ Caragh Lough, Co. Kerry.

$2n = 88$ Woodford River, Co. Galway.

$2n = 88$ Killybegs, Co. Donegal.

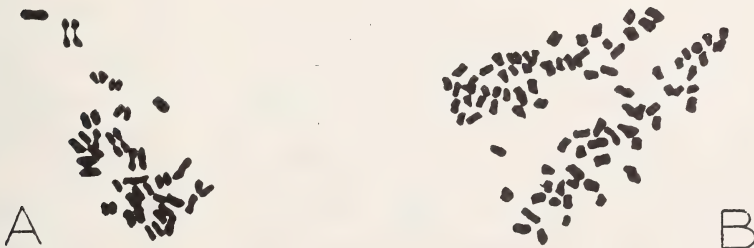


Fig. 3. *S. bermudiana* L. Irish populations. $2n = 88$. $\times 670$.

A. Metaphase.

B. Early anaphase, Woodford River, Co. Galway.

These counts were each based on two preparations of two plants, and confirm the count made by Northfield (1961), though they conflict with that of Löve & Löve (1958), who record $2n = 64$ as the number for the Cloonee Loughs population.

The morphological comparison of the Irish and the American species is summarized in Table 1. It is obvious that the Irish population is hardly if at all distinguishable from the American species *S. bermudiana* L., and the results of the present investigation do not justify the proposal by Löve & Löve (1958) that the Irish plant should be designated as a new species, *S. hibernicum*. Cytologically too, the Irish plant fits into the aneuploid series exhibited by the American species. The Irish plant must therefore be referred to the species *S. bermudiana* L.

SISYRINCHIUM IN GREENLAND

It is interesting to note that *S. bermudiana* L. is not the species described by Böcher (1948) as occurring in Greenland. Böcher refers to the Greenland species as *S. montanum* Greene, which is a species characteristic of the extreme north of the American continent. The plant illustrated by Böcher is simple stemmed, and is described as having light blue flowers. The chromosome number of this plant is $2n = 32$ (Böcher & Larsen 1950). Whatever may be its true taxonomic position, it is obviously not the same as the Irish species, nor is it *S. montanum* var. *crebrum*.

SISYRINCHIUM IN EUROPE

The status and extent of *Sisyrinchium* in Europe is a topic beyond the scope of this work, but it may be pointed out that the plant illustrated by Hegi (1939, Fig. 631) is a simple stemmed species, closely resembling *S. montanum* var. *crebrum*. Moreover, this seems to be the species most commonly cultivated as a garden plant in Europe. Certainly, observation of garden material in the British Isles has shown that although a great variety of specific names are in use, in fact most of the garden material can be referred to the taxon *S. montanum* var. *crebrum*. Although the names *S. bermudiana* or *S. bermudianum* are frequently used, I have never seen *S. bermudiana* L. (*sensu stricto*) cultivated, and no material referable to this taxon has been received from any British or continental Botanic Garden. Indeed this species has little horticultural merit, so perhaps its absence is not surprising.

THE STATUS OF SISYRINCHIUM BERMUDIANA IN IRELAND

The question of whether *Sisyrinchium* is native in Ireland, or whether it has been recently introduced, is one that was mentioned in the introduction. Although the present investigation does not justify the drawing of any firm conclusion on this question, the following points have some relevance.

(1) Morphologically and cytologically the Irish and American populations of *S. bermudiana* are indistinguishable, although only one chromosome type is present in Ireland, whereas a wide aneuploid series is present in America. This would be compatible with the theory that *S. bermudiana* in Ireland originated with the introduction of a single biotype.

No breeding difficulties would arise if this were the case, as the species is self-compatible, and is fairly often self-pollinated. However, the possibility that the Irish population represents an extreme reduction of a previously wider distribution cannot be ruled out.

(2) *S. bermudiana* is unlikely to have arisen as a garden escape in Ireland, as it often occurs well away from habitation, and is not likely to have been cultivated anyway.

(3) If *Sisyrinchium* was introduced by birds, Greenland is unlikely to have been a 'half way house' for the species, as suggested by Heslop-Harrison (1952), since the Greenland plant is a different species from the Irish one, which has never been recorded there.

(4) Evidence which will be presented in a later paper indicates that the Irish plants are unlikely to be a recent introduction, because the Irish and American populations of *S. bermudiana* show cryptic genetic differences which it is difficult to imagine are of recent development.

On a balance of probabilities, it may provisionally be suggested that the Irish population originated directly though not very recently from the American population of *S. bermudiana*.

ACKNOWLEDGMENTS

I wish to thank Dr. J. L. Crosby for his supervision of this work and his constructive criticism of this manuscript. I am grateful also to the technical staff of the Botany Department, Durham University, and to all those in America who made my visit there worthwhile. The work was carried out whilst in receipt of a N.A.T.O. studentship, which was held in the Botany Department of Durham University.

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CLEISTOGAMY IN *SPARTINA*

By J. C. E. HUBBARD

The Nature Conservancy, Furzebrook, Wareham, Dorset

ABSTRACT

Cleistogamous spikes enclosed in the leaf sheaths below the terminal inflorescence have been observed in the forms of *Spartina* × *townsendii* (*sensu lato*) at many localities in southern England; their structure and position are briefly described. Seed has been found in such spikes in only a few isolated cases.

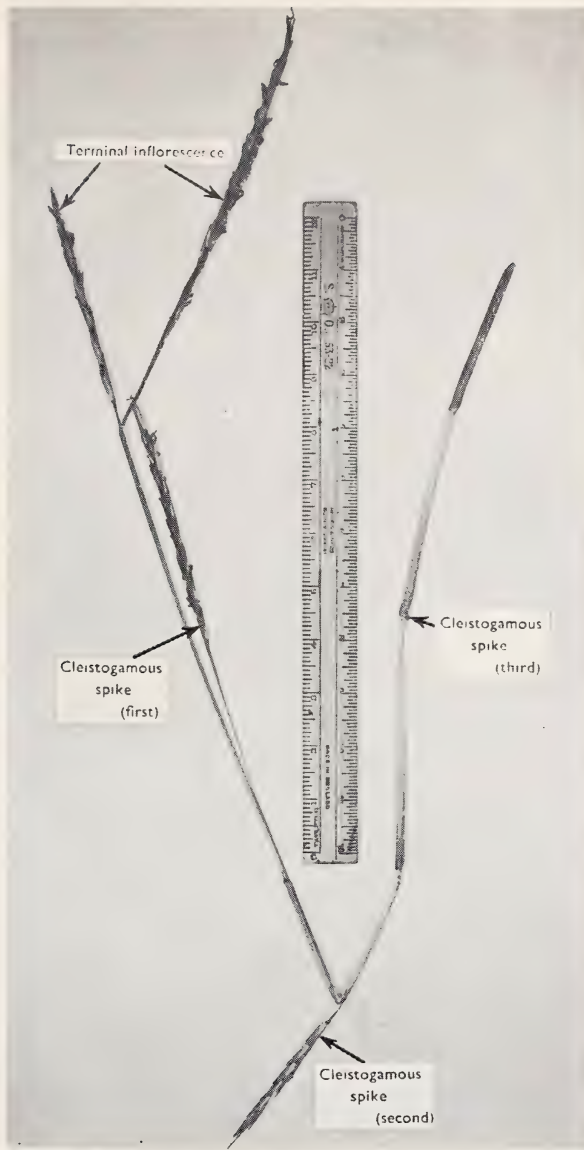
It is first necessary to clarify the nomenclature of *Spartina townsendii* (*sensu lato*) to be used in this account. Following the recent cytological investigation by Marchant (1963, 1964) and in accordance with Hubbard (1965) the following names are used: *Spartina* × *townsendii* ($2n = 62$), *Spartina* X ($2n = 120$ or more), *Spartina* $2n = 90$ and *Spartina* $2n = 76$.

In August 1963 several unusual specimens of *Spartina* X were collected from marshland adjoining the north-west of Brownsea Island, Poole Harbour, Dorset. They possessed a single cleistogamous spike arising immediately above the upper node and enclosed by the leaf sheath. The spike was independent of the terminal inflorescence and 25 cm below it. On revisiting the area in July 1964 many examples were found and a search along the shoreline marshes of the harbour revealed this phenomenon to be a common occurrence. Subsequently numerous cleistogamous specimens were discovered in every locality visited between Poole and Pagham on the south coast and at Bridgwater Bay and Sand Bay in the Severn Estuary (22 localities).

In addition, inflorescences of *Spartina* × *townsendii* bearing cleistogamous spikes were found at twelve of the localities visited, including Hythe in Southampton Water and Sand Bay in the Severn Estuary. The cleistogamous condition also occurred in *Spartina* $2n = 76$ and *Spartina* $2n = 90$ but was not found in populations of *Spartina alterniflora* Lois. and *Spartina glabra* Muhl. from Southampton Water or *Spartina maritima* (Curt.) Fernald from Hayling Island.

The cleistogamous spike of *Spartina* X and *Spartina* × *townsendii* is structurally similar to the spikes comprising the terminal inflorescence although the portion of the axis below the lowest spikelet may become greatly extended. There appears to be no reduction or modification in the floral structure of the spikelets. In every specimen examined, the upper internode was grooved from panicle to node on the face adjacent to a cleistogamous spike, but cylindrical and more easily broken when the spike was absent. The development of the spike was usually out of phase with that of the terminal inflorescence and it was possible to find a range of developmental stages from 0.1 cm in length to fully-formed ones.

The position of the cleistogamous spike relative to the terminal inflorescence varies according to the expansion of both the internode and the axis below the spike, making a range of positions possible. The spike may therefore be 30 cm below the terminal inflorescence and entirely enclosed by the leaf sheath or occasionally it may emerge and appear to be part of the inflorescence. In the latter case cleistogamous spikes may sometimes be found at the lower nodes and up to three additional spikes have been discovered on a large specimen (Plate 13). Cleistogamy occurs more frequently with increase in size and it is especially evident in the larger plants of *Spartina* X at Bridgwater Bay where it is possible to find terminal inflorescences containing up to twenty-two spikes. Herbarium specimens of *Spartina* X, bearing the characteristic groove on the internode below the terminal inflorescence, have been seen in the herbaria of the Royal Botanical Gardens, Kew (K), the British Museum (BM) and in the private collection of Mr. N. D. Simpson.



Specimen of *Spartina X* from Poole Harbour (August 1964). The leaves have been removed to show cleistogamous spikes arising from 3 internodes. The axis of the 2nd spike is fused to the adjacent internode which is damaged at its base. The 3rd spike has failed to develop and is less than 2 mm in length.

An abnormality often associated with the presence of a cleistogamous spike is the fusion of its axis to the internode of the terminal inflorescence and in extreme cases the culm is fractured. During elongation of the internode in *Spartina* $\times$ *townsendii* the extremely thin axis of the cleistogamous spike is frequently broken just above the node and the severed spike is carried up with the terminal inflorescence. Retention of moisture by the leaf sheath may lead to rotting of the mature spike. Specimens have been collected from Bridgwater Bay and Poole Harbour in which two culms bearing separate leaf sheaths have arisen from the upper node.

Although hundreds of specimens were examined during 1964, only in a few isolated cases was seed collected from cleistogamous spikes of *Spartina* X and *Spartina* $2n = 76$.

I wish to thank Miss J. Perkins and Miss G. Shannon for their assistance in collecting and processing the specimens.

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TAXONOMIC AND NOMENCLATURAL NOTES ON THE BRITISH FLORA

The following notes have been prepared to validate new names and combinations of taxa to appear in the forthcoming *Critical Supplement* to the *Atlas of the British Flora*. At the same time some taxonomical notes on taxa not dealt with in the current British literature have been included. Each of the notes should be attributed to the authors whose names appear at the end of each account, unless it is otherwise stated in the text. I am extremely grateful to those authors who have so kindly contributed, and especially to J. E. Dandy for help with the nomenclature. I am also indebted to H. Gilbert Carter for help with the latin descriptions and to W. T. Stearn for checking them.

P. D. SELL

ATHYRIUM DISTENTIFOLIUM Tausch ex Opiz, *Tent. Fl. Crypt. Boem.* **1**, 14 (1820).

var. *flexile* (Newm.) Jermy, comb. nov.

Basionym: *Pseudathyrium flexile* Newm., *Phytol.* **4**, 974 (1853).

Athyrium alpestre var. *flexile* (Newm.) Milde, *Fil. Eur.*, 53 (1867).

Athyrium flexile (Newm.) Druce, *Brit. Pl. List*, ed. 2, 137 (1928).

This plant requires further study; it appears to have a wider ecological range than var. *distentifolium* and is likely to be more common than at present thought. The much-branched rhizome gives rise to narrow fronds of a delicate texture mostly growing prostrate along the ground, even in sheltered situations. The lower pinnae are characteristically reflexed or drooping.

A. C. JERMY

POLYPODIUM VULGARE L.

subsp. *SERRATULUM* Arcangeli, *Comp. Fl. Ital.*, 809 (1894).

P. vulgare var. *serratum* Willd., *Sp. Pl.* **5** (1), 173 (1810).

P. australe Fée, *Mém. Fam. Foug.* **5**, 236 (1852).

P. serratum (Willd.) Sauter in A. Kerner, *Sched. Fl. Exsicc. Austr.-Hung.* **2**, 150 (1882), non Aublet, *Hist. Pl. Guiane*, **2**, 962 (1775).

P. vulgare subsp. *serratum* (Willd.) H. Christ, *Foug. Alp. Marit.* **2** (1900).

subsp. *VULGARE*.

P. vulgare L., *Sp. Pl.*, 1085 (1753).

subsp. *PRIONODES* Rothm., *Mitt. Thur. Bot. Ver.*, **38**, 106 (1929).

P. interjectum Shivas, *J. Linn. Soc. (Bot.)* **58**, 28 (1961).

In Clapham, Tutin & Warburg, *Fl. Brit. Isles*, ed. 2, 40 (1962) three species are recognized within the *Polypodium vulgare* aggregate. Elsewhere the three possible hybrids between these species have also been recognized on morphological characters, and inferred from the presence of the parents growing together where the intermediates occur. As the occurrence of such intermediates makes field identification of material impossible with certainty, it seems better to treat them as subspecies. The correct nomenclature is as above.

F. H. PERRING

P. D. SELL

CERASTIUM FONTANUM Baumg., *Enum. Stirp. Transs.* **1**, 425 (1816).

Usually a short-lived perennial, rarely annual herb up to 60 cm high, with short basal non-flowering shoots. Leaves oblanceolate, lanceolate, elliptical or ovate-oblong, subacute, sessile. At least the upper bracts with scarious margins. Petals equalling or somewhat exceeding the sepals. Capsule usually curved. Seeds 0.4–1.3 mm, tuberculate.

subsp. *scoticum* Jalas & Sell, subsp. nov.

Holotype: Little Kilrannock, Forfarshire, 1 August 1872, J. Sadler (CGE).

[*C. triviale* var. *alpinum* auct., non Mert. & Koch (1831), nec *C. vulgatum* **alpinum* Hartm. (1849).]

Planta ut videtur perennis, 3–12 cm alta; ramuli steriles breves, apice parvorosulati, vix vel raro radicanes; caules floriferi adscendentes, internodiis plerumque 1·5–2·5 cm longis, ubique pubescentes vel interdum lineis duabus exceptis et praecipue basin versus fere glabri; pili glanduliferi omnino desunt. Folia caulina sessilia, parva, lanceolata, (6–) 7–8 (–10) mm longa, 2–3 mm lata, plerumque 3–3·5-plo longiora quam latiora, apice obtusa vel subacuta, utrimque sparse pilosa vel subglabra, marginibus pilosis nervis medianisque subtus prominentibus. Bracteae herbaceae vel superiores apicem versus scarioso-marginatae. Inflorescentia confertim (1–) 3 (–5) flora, pedicellis tenuibus calyce subduplo longioribus. Calyx basi truncatus, (4·5–) 5·5 (–6·5) mm longus, sepalis lanceolatis acutis margine scariosis, parce pilosis; basis sepalorum nervo mediano distincte carinata. Petala calyce c. 1·4 plo (usque ad 1·7 plo) longiora. Capsula leviter curvata vel fere recta, calycem vix superans vel usque ad 10 mm longa, dentibus rectis margine revolutis. Semina 0·8–1·0 mm longa, verrucosa, verrucis c. 50 μ altis et 125 μ longis.

Habitat in partibus alpinis montis scotici 'Clova' dicti, c. 970 m supra mare, ubi ut videtur endemica est.

subsp. TRIVIALE (Murb.) Jalas, *Arch. Soc. Zool.-Bot. Fenn. Vanamo* **18** (1), 63 (1963).

C. viscosum L., *Sp. Pl.*, 437 (1753), nom. ambig.

C. vulgatum L., *Amoen. Acad.* **4**, 101 (1759); non *Fl. Suec.*, ed. 2, 158 (1755).

C. holosteoides Fries, *Nov. Fl. Suec.* **4**, 52 (1817).

C. triviale Link, *Enum. Hort. Berol. Alt.* **1**, 433 (1821), nom. superfl. illegit. pro *C. viscosum* L.

C. vulgare subsp. *triviale* Murb., *Bot. Not.* **1898**, 252 (1898).

C. caespitosum subsp. *eucaespitosum* Graebner in Ascherson & Graebner, *Syn. Mitteleur. Fl.* **5** (1), 638 (1918).

C. holosteoides subsp. *glabrescens* (G. F. W. Meyer) Möschl, *Bot. Not.* **1948**, 375 (1948).

C. holosteoides subsp. *pseudoholosteoides* Möschl, *Bot. Not.* **1948**, 364 (1948).

Flowering stems up to 50 cm high, pubescent to nearly glabrous, with or without glandular hairs. Leaves normally 10–25 $\times$ 3–10 mm, hairy. Sepals 3–7 mm long. Petals shorter than to slightly longer than sepals. Capsule up to 12 mm long. Seeds 0·4–0·9 mm, tubercles 15–40 $\times$ 15–40 μ .

Throughout the British Isles. In much of Continental Europe, but often replaced by other subspecies in mountainous districts.

C. fontanum subsp. *scoticum* clearly differs from all the subspecies recognized within *C. fontanum* by Jalas (*Arch. Soc. Zool.-Bot. Fenn. Vanamo* **18** (1), 61–64 (1963); *Fl. Eur.* **1**, 142 (1964)). From subsp. *triviale* (Murb.) Jalas it can be distinguished by its longer petals and larger seeds which have larger tubercles, and by the basal part of the sepals which seem to be more prominently keeled. In its seed and petal characters it is much closer to subsp. *scandicum* Gartner from Fennoscandia, and to subsp. *fontanum* from the Alps and Carpathians, but they are much taller plants with larger sepals and capsules and even larger seeds (up to 1·3 mm). Subsp. *hispanicum* Gartner from the Pyrenees and S. Spain has seeds of the same size, but it also is a taller plant and the tubercles of the seed are flattened and look quite different. In general appearance subsp. *scoticum* somewhat resembles small individuals of *C. alpinum*, but the long, soft, entangled 'alpinum-hairs' are lacking and the flowers are conspicuously smaller in all their parts. In addition to the numerous specimens in herbaria of subsp. *scoticum* from the mountains of the Clova region, specimens collected on coastal rocks at Strathy Point, W. Sutherland on the 30 July 1915 by E. S. Marshall (No. 4076), differ only in having the tubercles of the seeds 70–100 $\mu \times$ 50–100 μ , and are best placed in this subspecies.

Subsp. *triviale* is a most variable plant which tends to form local recognizable races which are geographical and/or ecological. This type of variation, is, no doubt, mainly due

to the predominance of autogamy, and the utmost care is needed before new subordinate taxa are described. Var. *triviale* (*C. holosteoides* sensu Clapham, non Fries) is the common plant of the lowlands both in the British Isles and on the Continent of Europe. In the British Isles var. *holosteoides* (Fries) J alas (*C. holosteoides* Fries; *C. holosteoides* var. *glabrescens* (G. W. F. Meyer) Hylander) seems to be a plant of wet places and riversides of the north. It also occurs in southern Sweden and Denmark and has been recorded from the Alps. A plant collected by W. H. Beeby (No. 404) in wet meadows by the Thames at Putney in 1887 differs only in having obtuse, not acuminate hairs (*C. holosteoides* subsp. *pseudoholosteoides* Möschl). A variable group of rather dwarf plants with medium sized seeds from alpine and coastal localities may perhaps be referred to *C. triviale* var. *serpentinum* Syme. They somewhat resemble var. *serpentinicola* (Domin) J alas and var. *kajanense* (Kot. & Salmi) J alas from Fennoscandia. Plants from a number of widespread localities in wet places in the British Isles which are like var. *triviale*, but have larger flowers and seeds, seem to merit recognition as a distinct variety. *C. triviale* var. *pentandrum* Syme is a curious annual plant that warrants further research. A full account of these varieties will be published at a later date.

J. JALAS

P. D. SELL

ARENARIA SERPYLLIFOLIA L.

subsp. *LEPTOCLADOS* (Reichenb.) Nyman, *Consp.* 115 (1878).

A. serpyllifolia var. *tenuior* Mert. & Koch in Röhling, *Deutschl. Fl.*, ed. 3, 3, 266 (1831).

A. serpyllifolia var. *leptoclados* Reichenb. in Reichenb. & Reichenb. fil., *Icon. Fl. Germ.* 5, 32 (1842).

A. leptoclados (Reichenb.) Guss., *Fl. Sic. Syn.* 2, 824 (1845).

A. serpyllifolia subsp. *tenuior* (Mert. & Koch) Arcangeli, *Comp. Fl. Ital.*, 101 (1882).

Inflorescence lax. Capsule straight-sided, less than 3 mm long and 1.5 mm wide, possible to indent without fracture when mature. Pedicel slender, about 0.3 mm wide, upturned towards the tip, longer than sepals. Ripe seeds $c. 0.4 \times 0.4$ mm. $2n = 20$.

South, west and central Europe extending locally north and east.

subsp. *SERPYLLIFOLIA*

A. serpyllifolia L., *Sp. Pl.*, 423 (1753).

Inflorescence lax. Capsule distinctly swollen at base, exceeding 3 mm long, 1.5–2 mm wide, possible to fracture when pressed at maturity. Pedicels stout, about 0.5 mm wide, straight, longer than sepals. Ripe seeds reniform, 0.5×0.4 mm. $2n = 40$.

Almost throughout Europe.

subsp. *MACROCARPA* (Lloyd) Perring & Sell, stat. nov.

A. serpyllifolia var. *macrocarpa* Lloyd, *Fl. Loire-Inf.*, 42 (1844).

Inflorescence usually very dense. Capsule slightly swollen at base, exceeding 3 mm long and 2 mm wide, possible to fracture at maturity when pressed. Pedicels stout, about 0.5 mm wide, straight, often shorter than sepals. Ripe seeds reniform, exceeding 0.6×0.4 mm.

Dunes on coasts of west Europe.

The above three taxa have been variously treated. Sometimes *A. serpyllifolia* and *A. leptoclados* are regarded as species, with *macrocarpa* as a variety of *serpyllifolia*. Sometimes *leptoclados* is made a subspecies of *serpyllifolia* with *macrocarpa* a variety of subsp. *serpyllifolia*. Sometimes capsule shape is regarded as the most important, sometimes the seed size. When all characters are considered, as in *Fl. Eur.* 1, 121 (1964), the descriptions make it very difficult to place many of the specimens. For this reason we think that the taxa are best regarded as subspecies, with the three main seed types as the primary character and the remaining characters subsidiary. *A. marschlinsii* Koch, *Flora (Regensb.)* 24, 509 (1841), (*A. serpyllifolia* subsp. *marschlinsii* (Koch) Nyman, *Consp.*, 115 (1878)), from above 1,900 m in the Alps, is closely allied to subsp. *leptoclados*, and is probably best placed as a montane subspecies of *A. serpyllifolia*. It differs from subsp. *leptoclados* in being often perennial, with fewer-flowered, dense inflorescences, and narrow scarious margins to the inner sepals.

F. H. PERRING

P. D. SELL

GENISTA TINCTORIA L.

subsp. TINCTORIA

G. tinctoria L., *Sp. Pl.*, 710 (1753).

Plant more or less erect. Leaves 4–6 times as long as broad. Pods glabrous.

subsp. LITTORALIS (Corb.) Rothm., *Feddes Repert.* 67, 5 (1963).*G. tinctoria* var. *prostrata* Bab., *Man. Brit. Bot.*, 70 (1843) (Lectotype: Between Kynance and the Soap rock, Lizard, Cornwall, 23 July 1839 (CGE)).[*G. humifusa* Dickson ex Bab., loc. cit. (1843), nom. in syn.]*G. tinctoria* var. *humifusa* Bab., *Man. Brit. Bot.* ed 2, 73 (1847), nom. superfl. illegit. pro*G. tinctoria* var. *prostrata* Bab.*G. tinctoria* var. *littoralis* Corb., *Nouv. Fl. Normand.*, 144 (1893).Plant prostrate. Leaves 2–4 times as long as broad. Flowers more handsome. Pods hairy on the back of the valves. *Coasts of Cornwall (England), Pembroke (Wales) and Normandy (France).*

The British populations of subsp. *littoralis*, at least, are geographically isolated from those of subsp. *tinctoria*. Prostrate forms with glabrous pods and broad leaves are recorded from the coasts of Cornwall and north Devon and may show hybridization or gradation between the two subspecies. No specimens of subsp. *littoralis* have been seen from Normandy, but Corbière's description seems to fit the British plants and it is a likely habitat and locality for it. The exact distribution of subsp. *tinctoria* is not known, but as several other subspecies have been described in central and east Europe, it may be confined to western Europe.

The nomenclature of subsp. *littoralis* has been somewhat confused in that Druce, *Brit. Pl. List*, ed. 2, 2, 24 (1928), recognized each of the three synonyms given above as distinct varieties. *G. humifusa* Dickson (non L.) seems only to have been used as a name on herbarium sheets and never to have been validly published. Babington when describing var. *prostrata* presumably used a specimen in Herb. Dickson (not seen) and one in his own herbarium at Cambridge which is selected as the lectotype. In the second edition of his *Manual* Babington replaces the epithet *prostrata* with *humifusa*, using exactly the same diagnosis and citing the same manuscript name. Var. *humifusa* is thus a superfluous illegitimate name for var. *prostrata*.

A plant of subsp. *littoralis* collected above Pentreath Beach, Lizard, Cornwall, by L. C. Frost in 1956, and grown in the Botanic Garden at Cambridge, has retained all its characters.

F. H. PERRING

P. D. SELL

ANTHYLLIS VULNERARIA L.

subsp. *corbierei* (Salmon & Travis) Cullen, comb. et stat. nov.*A. maritima* var. *corbierei* Salmon & Travis, *J. Bot., Lond.* 55, 320 (1917).

J. CULLEN

RUBUS ECHINATUS Lindley, *Syn. Brit. Fl.*, 94 (1829) (Holotype: Hale End, no date, Forster in Herb. Lindley no. 43 (CGE)); Focke, *J. Bot., Lond.* 28, 132 (1890); Rogers, *J. Bot., Lond.* 30, 301 (1892); Rogers, *Handb. Brit. Rubi*, 64 (1900); E. S. Marshall, *J. Bot., Lond.* 43, 76 (1905); Rogers & E. F. Linton, *J. Bot., Lond.* 43, 203 (1905); Riddelsdell, *J. Bot., Lond.* 76, 311 (1938); non *R. echinatus* P. J. Muell., *Flora (Regensb.)* 41, 171 (1858).

R. rudis var. *attenuatus* Bab., *Ann. Mag. Nat. Hist.*, ser. 1, 17, 245 (1846) (Lectotype: Twycross, Leicestershire, 1845, A. Bloxham in Herb. C. C. Babington no. 792 (CGE)).

R. fuscoater var. *echinatus* (Lindley) Bab., *Ann. Mag. Nat. Hist.*, ser. 1, 17, 314 (1846).

R. discerptus P. J. Muell., *Pollichia*, 16, 146 (1859); Focke in Ascherson & Graebner, *Syn. Mitteleur. Fl.* 6 (1), 565 (1903); Sudre, *Bull. Soc. Étud. Sci. Angers* 33, 115 (1904); Sudre, *Rubi Eur.* 132 (1908–13); W. C. R. Watson, *Rep. Bot. Exch. Club Brit. Is.* 8, 86 (1929 for 1928); W. C. R. Watson, *Rep. Bot. Exch. Club Brit. Is.* 11, 568 (1938 for 1937); W. C. R. Watson, *Handb. Rubi Brit. Ireland*, 132 (1958).

[*R. rudis* sensu Bab., *Brit. Rubi*, 189 (1869), et auct. angl. plur. ante 1890; non Weihe & Nees in Bluff & Fingerh., *Comp. Fl. Germ.* **1**, 687 (1825).]

Watson (1938, p. 566) states that *R. echinatus* Lindl. = *R. hystrix* Weihe & Nees, basing this judgement on specimens identified for Leighton by Lindley several years after the publication of *R. echinatus*. Watson also states that there is no specimen of *R. echinatus* in Herb. Lindley (CGE). As Riddelsdell (1938, p. 311) points out, there is an excellent specimen of *R. echinatus* in Herb. Lindley, and this must be the holotype of the species. The holotype shows that *R. echinatus* Lindl. = *R. discerptus* P. J. Muell. It is very distinct from both *R. hystrix* and *R. rudis*, the latter being the name given to it by most British botanists before 1890.

Focke (1902, p. 566) rejects *R. echinatus* in favour of *R. discerptus* as he regards *R. echinatus* as a 'nomen seminudum'.

The name *R. echinatus* Lindl. is the oldest legitimate name of the species and must replace the later synonym *R. discerptus* P. J. Muell.

B. A. MILES

Sorbus wilmottiana E. F. Warburg, sp. nov.

[*S. wilmottiana* E. F. Warburg in Clapham, Tutin & Warburg, *Fl. Brit. Is.* ed. 2, 432 (1962), anglice, sine diagn. lat.]

Holotype: Clifton, edge of the greensward at the top of the Avon Gorge cliffs, v.c. 34 W. Glos., 4 October 1958, R. A. Graham, R. M. Harley, D. H. Lewis & E. F. Warburg, 5841 B (OXF).

Arbuscula vel arbor parva. Rami hornotini brunneo-rubri, annotini nigri, glabri; gemmae 5–6 mm longae, subglabrae, apice tantum pilis lanatis instructae. Folia petiolata; lamina elliptica vel obovata, 7–12 cm longa, 1·6–2 (–2·7)-plo longiora quam latiora, apice acuta basi cuneata, duplicato-serrata marginibus per partem quintam basalem folii integris, dentibus acutiusculis plerumque ascendentibus apicaleisque nervos primarios terminantibus vix prominentibus, supra laete viridia nitidiuscula, subtus cinereo-tomentosa, nervis utrinque 6–9 supra vix elevatis; petiolus 1–2 cm longus. Inflorescentia pauciflora, glabra, c. 5 cm longa, 4 cm lata. Fructus subglobosus, 10–13 mm longus, latior quam longior, coccineus, lenticellis paucis magnis praeditus.

This member of the *Sorbus aria* aggregate is named in memory of Alfred James Wilmott (1888–1950).

E. F. WARBURG†

LYTHRUM PORTULA (L.) D. A. Webb, *Feddes Repert.* **74**, 13 (1967).

subsp. **PORTULA**

Peplis portula L. *Sp. Pl.*, 332 (1753).

subsp. **longidentata** (Gay) Sell comb. nov.

P. portula var. *longidentata* Gay, *Notic. Endress*, 38 (1832).

P. portula subsp. *longidentata* (Gay) Nyman, *Consp.*, 252 (1879).

P. fradini Pomel, *Mat. Fl. Atl.*, 156 (1860).

P. longidentata (Gay) Batt. in Batt. & Trabut, *Fl. Alger. (Dicot.)*, 320 (1889).

Subsp. *portula* with the epicalyx segments about 0·5 mm long occurs throughout Europe. Subsp. *longidentata* with the epicalyx segments 1·5–2 mm long is found only in France, Spain, Portugal, Algeria and the Azores. Intermediates occur where the two subspecies meet and in the British Isles there is an east-west cline (cf. D. E. Allen, *Watsonia* **3**, 85–91 (1954)).

P. D. SELL

ERICA PRAEGERI Ostenfeld and E. STUARTII E. F. Linton

The earliest binomial deliberately given to a plant believed to be a hybrid between *E. mackaiana* and *E. tetralix* is *E. × praegeri* Ostenfeld, *New Phytol.* **11**, 120 (1912). Dandy (*List. Brit. Vasc. Pl.*, 85 (1958)) listed this hybrid as *E. × stuartii* E. F. Linton, citing *E. praegeri* Ostenfeld as a later synonym. The name *E. stuartii* was given by Linton

(*Ann. Scot. Nat. Hist.* **1902**, 177 (1902)) to a curious plant collected in Connemara by Stuart in 1890 and never found again, though it has been propagated by cuttings; all stocks of it in cultivation and all herbarium specimens are fragments of the same clone. For long it was regarded as *E. mediterranea* auct. (more correctly *E. hibernica* (Hook. & Arn.) Syme) $\times$ *E. tetralix*, but some years ago (Webb, *Irish Nat. Jour.* **11**, 190 (1954)) I pointed out that there were serious objections to this explanation of it and concluded by saying that 'if I am forced to choose, I prefer to regard it as a very peculiar mutant of *E. mackaiana*'. A little later I came to the conclusion that it was more like a mutant of *E. praegeri*, and I mentioned this to Mr. Dandy. Unfortunately he took this rather casual *obiter dictum* as a firm taxonomic opinion, with the result that this unique plant and the common and familiar hybrid are now regarded as two nothomorphs which must share the name *E. $\times$ stuartii*.

I now wish to retract my opinion to the extent of saying that I do not know what *E. stuartii* is, and that I do not believe that anyone else does either. I think that it has some claim to be regarded as a 'monstrosity', in view of its very curious corolla, in which case it cannot stand as a nomenclatural type. Unfortunately our grandfathers had a much clearer concept of 'monstrosity' than their more sophisticated descents, and a recent attempt to give more precision to the term by defining it as a non-hereditary structural abnormality is not very helpful in the numerous cases of monstrosities or near-monstrosities which are (like *E. stuartii*) completely sterile. But even if this plant is not a monstrosity it is likely, in my opinion, to remain permanently *incertae sedis*. That it is a mutant of *E. $\times$ praegeri* is a plausible guess and no more, for the evidence is conflicting. I do not think that a name whose application represents a rather desperate guess should, even if it is published earlier with a different application, take priority over one whose application was based originally on strong circumstantial evidence and has since been confirmed by experiment. A name whose type is inexplicable can be rejected as a *nomen dubium* (in so far as it designates a taxon of definite rank or a hybrid of specified parentage) just as legitimately as one whose type cannot be ascertained; and I believe that the continued application of the name *E. stuartii* to the hybrid is likely to be a source of permanent confusion. In my opinion the hybrid *E. mackaiana* $\times$ *tetralix* should be called *E. $\times$ praegeri* Ostenfeld.

D. A. WEBB

ANAGALLIS ARVENSIS L.

subsp. ARVENSIS

forma ARVENSIS

A. arvensis L., *Sp. Pl.*, 148 (1753).

A. phoenicea Scop., *Fl. Carn.* ed. 2, **1**, 139 (1772).

A. arvensis subsp. *phoenicea* (Scop.) Vollman, *Ber. Bayer. Bot. Ges.* **9**, 44 (1904).

forma CARNEA (Schränk) Hyland., *Uppsala Univ. Årsskr.* **7**, 256 (1945).

A. coerulea var. *carnea* Schrank, *Baier. Fl.* **1**, 461 (1789).

forma PALLIDA (Hook. fil.) Hyland., *Uppsala Univ. Årsskr.* **7**, 256, (1945).

A. arvensis var. *pallida* Hook. fil., *Stud. Fl. Brit. Islands*, 265 (1870).

forma AZUREA Hyland., *Uppsala Univ. Årsskr.* **7**, 256 (1945).

A. latifolia L., *Sp. Pl.*, 149 (1753).

A. arvensis var. *azurea* Wilmott, *Rep. Bot. Exch. Club Brit. Is.* **14**, 664 (1946).

forma LILACINA Alefeld (quando ?) Hylander, *Uppsala Univ. Årsskr.* **7**, 256 (1945).

A. arvensis var. *lilacina* (Alefeld) Marsden-Jones & Weiss, *Proc. Linn. Soc. Lond.* **150**, 147 (1938).

A. arvensis subsp. *phoenicea* forma *lilacina* (Alefeld) Schinz & R. Keller, *Fl. Schweiz*, ed. 2, **2**, 173 (1905).

subsp. FOEMINA (Mill.) Schinz & Thell. in Schinz & R. Keller, *Fl. Schweiz*, ed. 3, **1**, 419 (1909).

A. foemina Mill., *Gard. Dict.* ed. 8, (1768).

The taxonomy of this species is that recommended by E. M. Marsden-Jones and F. E. Weiss, *Proc. Linn. Soc. London* **150**, 146–155 (1938). The five flower-colour forms of subsp. *arvensis* breed true for colour. Any one of them can be crossed with any of the remainder and the offspring produces fertile seed. Subsp. *foemina* can be crossed with any of the colour forms of subsp. *arvensis*, but only the cross with forma *carnea* produces fertile offspring.

P. D. SELL

CALYSTEGIA SEPIUM (L.) R. Br. subsp. *roseata* Brummitt, subsp. nov.

A subspecies typica corolla rosea, caulibus saepius pubescentibus et foliis apice acutioribus differt; a subsp. *americana* (Sims) Brummitt floribus minoribus (corolla plerumque 19–25 mm longa, staminibus plerumque 19–25 mm longis) differt.

Holotype: Wales, Merionethshire, near Towyn, overlooking Afon Dysynni estuary, Grid Ref. 23/5703, 24 September 1959, *J. A. Ratter, J. Cullen & R. K. Brummitt* 59.815 (LIVU; isotypes in GB, K, NY).

This subspecies is found on the Atlantic coasts of Europe (Norway, Sweden, Netherlands, British Isles, probably also Spain and Portugal, perhaps also France), and the Pacific and perhaps Atlantic coasts of temperate South America, Easter Island, New Zealand and south-eastern Australia.

The type specimen of *C. sepium* subsp. *baltica* Rothmaler in *Feddes Repert.* **67**, 10 (1963), from the Baltic coast of northern Germany, has been examined by the author through the courtesy of the curator of the herbarium of the University of Greifswald. It is best referred to *C. sepium* subsp. *sepium* forma *colorata* (Lange) Dörfler, a pink-flowered variant of the typical subspecies occurring frequently in lowland areas of many parts of Europe.

R. K. BRUMMITT

RHINANTHUS L., *Sp. Pl.*, 603 (1753); *Gen. Pl.*, ed. 2, 263 (1754) (Type: *R. crista-galli* L. nom. ambig. = *R. serotinus* (Schönh.) Oborny).

Alectorolophus Zinn, *Cat. Pl.* 288 (1757), nom. superfl. illegit. pro *Rhinanthus* L.

RHINANTHUS SEROTINUS (Schönh.) Oborny, *Verhandh. Naturforsch. Ver. Brünn.* **22** (2), 435 (1884).

R. crista-galli L., *Sp. Pl.*, 603 (1753), nom. ambig.

R. major Ehrh., *Beitr. Naturk.* **6**, 144 (1791), non L., *Amoen. Acad.* **3**, 53 (1756).

Alectorolophus serotinus Schönh., *Flora (Regensb.)* **15**, 601 (1832).

subsp. *APTERUS* (Fries) Hyland., *Uppsala Univ. Årsskr.* **1945**, 292 (1945).

R. major var. *apterus* Fries, *Nov. Fl. Suec., Mantissa* **3**, 60 (1842).

R. apterus (Fries) Ostenf., *Bot. Not.* **1904**, 83 (1904).

R. major subsp. *apterus* (Fries) Schinz & Thell. in Schinz & R. Keller, *Fl. Schweiz*, ed. 3, **2**, 314 (1914).

R. major subsp. *vernalis* Zinger, *Herb. Fl. Ross.*, no. 2530a.

R. serotinus subsp. *vernalis* (Zinger) Hyland., *Uppsala Univ. Årsskr.* **1945**, 292 (1945).

[*R. borbasii* et *R. polycladus* auct. brit.]

I agree with E. F. Warburg (Clapham, Tutin & E. F. Warburg, *Fl. Brit. Isles*, ed. 2, 699 (1962)) that all British material of this species is referable to subsp. *apterus*.

RHINANTHUS MINOR L.

subsp. *MINOR*

R. minor L., *Amoen. Acad.* **3**, 54 (1756).

R. drummond-Hayi subsp. *salmonii* Soó, *Feddes Rep.* **26**, 182 (1929). (Holotype: rocks foot of Craig Maid, Clova, Forfar v.c. 90, 16 July 1912, C. E. Salmon (BM)).

Usually with only very short flowerless branches, but sometimes with longer suberect flowering branches from the middle and upper part of the stem. Internodes (except the lowest) more or less equal. Leaves of main stem (10–) 20–40 (–50) × (3–) 5–7 mm, usually

oblong and parallel-sided for the greater part of their length. Intercalary leaves 0 (–1) pairs. Calyx hairy only on the margins. Lowest flowers usually from the 6th–9th node. Corolla yellow with a violet (or rarely white) tooth. Flowers May to July.

Grassy places on dry basic soils, common in England, rarer in Scotland where it often grades into subsp. stenophyllus. Throughout Europe extending to Caucasus and W. Siberia; S. Greenland, Newfoundland.

subsp. *calcareus* (Wilmott) E. F. Warburg, comb. et stat. nov.

[*R. minor* subsp. *calcareus* (Wilmott) E. F. Warburg in Clapham, Tutin & E. F. Warburg, *Fl. Brit. Is.*, ed. 2, 700 (1962) sine ref. ad basionymum.]

R. calcareus Wilmott, *J. Bot., Lond.* **78**, 202 (1940) (Holotype: Grassy chalk down above Sutton, W. Sussex v.c. 13, 3 August 1901, E. S. Marshall, no. 2584 (BM)).

Usually with long arcuate-ascending flowering branches from about the middle of the stem. Lower internodes short, upper very long. Leaves of main stems 10–25 × 1.5–3 mm, linear, more or less spreading. Intercalary leaves usually (2–) 3–6 pairs. Calyx hairy only on the margins. Lowest flowers usually from 14th–19th node. Corolla yellow; tooth violet.

Local on chalk and limestone downs from Dorset and Sussex to Gloucester and Northants. ? Endemic. Plants from Ireland which somewhat resemble it are probably best placed in subsp. stenophyllus.

subsp. *STENOPHYLLUS* (Schur) O. Schwarz, *Feddes Repert.* **46**, 56 (1939).

R. minus var. *stenophyllus* Schur, *Enum. Pl. Transs.*, 511 (1866).

R. crista-galli subsp. *stenophyllus* (Schur) Soó, *Feddes Repert.* **26**, 186 (1929).

R. stenophyllus (Schur) Druce, *Ann. Scot. Nat. Hist.* **1901**, 178 (1901); *J. Bot., Lond.* **41**, 360 (1903).

Usually with long arcuate-ascending flowering branches and shorter flowerless branches from the lower and middle part of the stem. Lower internodes usually short, equalling or shorter than the leaves, upper much longer. Leaves of main stems 15–45 × 2–5 (–7) mm, narrowly lanceolate or linear-lanceolate, more or less tapering from near the base. Intercalary leaves (0–) 1–2 (–4) pairs. Calyx hairy only on the margins. Lowest flowers usually from (8th–) 10th–13th (–15th) node. Corolla yellow with violet tooth, sometimes becoming brown. Flowers July to September.

Damp grassland and fens. Common in Scotland, north and west England, Wales and probably Ireland, rare (mainly in fens) in south-east England. Throughout much of Europe particularly in upland regions.

subsp. *MONTICOLA* (Sterneck) O. Schwarz, *Feddes Repert.* **46**, 56 (1939).

R. minor var. *monticola* Lamotte, *Mém. Acad. Clermont.* **22**, 880 et 166 (1881), nom. superfl. illegit. pro *R. minor* var. *angustifolius* Gren. & Godron.

Alectorolophus monticola Sterneck, *Abh. Zool.-Bot. Ges. Wien* **1** (2), 111 (1901).

R. monticola (Sterneck) Druce, *Ann. Scot. Nat. Hist.* **1901**, 178 (1901); *Ann. Scot. Nat. Hist.* **1903**, 171 (1903); *J. Bot., Lond.* **41**, 360 (1903).

R. crista-galli subsp. *monticola* (Sterneck) Soó, *Feddes Repert.* **26**, 187 (1929).

R. spadiceus Wilmott, *J. Bot., Lond.* **78**, 203 (1940). (Holotype: Glen Dee near Braemar, S. Aberdeen v.c. 92, 30 July 1906, E. S. Marshall no. 2947 (BM)).

R. spadiceus subsp. *orcadensis* Wilmott, *J. Bot., Lond.* **78**, 207 (1940) (Holotype: Grassy and healthy pasture, Point of Onston, Stenness, Mainland, Orkney, v.c. 111, 21 July 1922, H. H. Johnston no. 1879 (BM)).

Usually with short or moderate flowerless branches from near the base, sometimes with 1–3 longer flowering branches in addition. Lower internodes usually very short, upper much longer. Leaves of main stems 10–20 (–25) × 2–4 mm, linear-lanceolate, more or less tapering from near the base, tending to be more erect than in subsp. *stenophyllus*. Intercalary leaves usually 1–2 (–3) pairs. Calyx hairy only on the margins. Lowest flowers usually from the (7th–) 8th–11th (–12th) node. Corolla dull yellow becoming treacle brown or treacle-brown throughout, with a violet tooth. Flowers July and August.

Grassy places in mountainous regions from Yorks to Shetland, rare in Ireland. Also in the Alps.

subsp. **lintonii** (Wilmott) Sell, comb. et stat. nov.

R. drummond-Hayi sensu Sterneck, *Abh. Zool.-Bot. Ges. Wien* **1** (2), 115 (1901) quoad descript.; et sensu auct. brit.

R. gardineri Druce, *Rep. Bot. Exch. Club Brit. Is.* **4**, 205 (1915).

R. lintonii Wilmott, *J. Bot., Lond.* **78**, 209 (1940) (Holotype: Glen Fiagh, Forfar, 13 July 1889, E. F. Linton (BM)).

R. lochabrensis Wilmott, *J. Bot., Lond.* **78**, 211 (1904). (Holotype: near Meall Cumhaun, Glen Nevis, Inverness, 19 August 1902, C. E. Salmon (BM)).

R. vachelliae Wilmott, *Watsonia* (1948), **1**, 85 (Holotype: Glen Cannich, near the north-east end of Loch Mullardoch, E. Inverness, v.c. 96, 16 July 1947, E. Vachell (BM)).

Simple or with 1–2 pairs of branches from the lower or middle part of the stem. Internodes more or less equal in length, or the lower shorter. Leaves of main stem (8–) 10–20 (–30) $\times$ 1.5–3 (–4) mm, very narrow linear-lanceolate, more or less tapering from the base. Intercalary leaves 0–3 pairs. Calyx hairy all over. Flowering from the 7th–10th node. Corolla ? yellow or orange-yellow. Flowers July (or August).

Grassy places in Scottish mountains. Apparently originating from hybridization between subspecies borealis, monticola and stenophyllus, but now often occupying a zone (where it is uniform) between borealis (higher up) and monticola and stenophyllus (lower down). ?Endemic.

subsp. **borealis** (Sterneck) Sell, comb. et stat. nov.

R. crista-galli var. *drummond-hayi* F. B. White, *Ann. Scot. Nat. Hist.* **8**, 324 (1886). (Type: Ben Lawers, Breadalbane, F. Buchanan White (BM)).

Alectorolophus borealis Sterneck, *Annu. Cons. Jard. Bot. Genève* **1889**, 25 (1889).

Alectorolophus drummond-hayi (F. B. White) Sterneck, *Abh. Zool.-Bot. Ges. Wien* **1** (2), 115 (1901) quoad basionymum exclud. descript.

R. drummond-hayi (F. B. White) Druce, *Ann. Scot. Nat. Hist.* **1903**, 171 (1903); *J. Bot., Lond.* **41**, 360 (1903).

R. borealis (Sterneck) Druce, *Ann. Scot. Nat. Hist.* **1901**, 178 (1901); *J. Bot., Lond.* **41**, 361 (1903).

R. borealis var. *calvescens* Wilmott, *J. Bot., Lond.* **78**, 209 (1940). (Holotype: Ben Nevis, v.c. 97, July 1903, H. J. Riddelsdell (BM)).

Usually unbranched, but occasionally with short flowerless (very rarely flowering) branches, and then intercalary leaves 0. Internodes more or less equal. Leaves 10–30 $\times$ 3–7 mm, oblong or oblong-linear, more or less parallel-sided. Calyx hairy all over. Lowest flowers from the 5th–7th (–8th) node. Corolla bright yellow with violet or white teeth. Flowers July and August.

Local in grassy places on mountains up to 3,200 ft in Scotland, Caernarvon and Kerry. Also in Alaska, Greenland, Iceland and ?Scandinavia.

Extensive work on *Rhinanthus* has been carried out on the Continent by A. Chabert, *Bull. Herb. Boiss.* **7**, 497–517 (1899), R. V. Soó, *Feddes Repert.* **26**, 179–219 (1929), and J. V. Sterneck, *Abh. Zool.-Bot. Ges. Wien*, **1** (2), 1–150 (1901). E. S. Marshall, *J. Bot., Lond.* **41**, 291–300 (1901) and G. C. Druce, *J. Bot., Lond.* **41**, 359–361 (1903) published the identifications of their material by Sterneck, but not until A. J. Wilmott's paper in *J. Bot., Lond.* **78**, 201–213 (1940) was any serious work published on the British species of the genus. D. J. Hambler, *Watsonia*, **4**, 101–116 (1958) reports on a series of investigations he carried out on the genus *Rhinanthus*, in which he concludes that only two species, *R. minor* and *R. serotinus* (Schönh.) Oborny, distinguished on corolla characters, are found in the British Isles. With this conclusion I agree. Although he points out that populations of *R. minor* are often distinct he gives no infraspecific categories, a situation hardly tolerable to a botanist who has examined the species in the field. The account by E. F. Warburg in Clapham, Tutin & E. F. Warburg, *Fl. Brit. Isles*, ed. 2, 699–701

(1962) is much more realistic, though I do not think that *R. borealis* should be distinguished as a distinct species, and I think that the supposed hybrid, *R. × gardineri*, which produces uniform populations, is better regarded as a separate taxon. Examples comparable to this last plant are seen in *Euphrasia vigursii* Davy (formed from a cross between *E. micrantha* Reichb. and *E. anglica* Pugsl.) and *Montia fontana* subsp. *variabilis* Walters (a variable intermediate between subsp. *fontana* and subsp. *amporitana* Sennen which may be of hybrid origin).

The nomenclature of the group is not difficult once the mass of synonyms have been sorted out. *R. crista-galli* L. is rejected as a nomen ambiguum. Sterneck was the first author to use most of the names of our taxa at the rank of species, but under the generic name *Alectorolophus*. They were transferred to *Rhinanthus* by Druce in *Ann. Scot. Nat. Hist.* (1901 and 1903), and *J. Bot., Lond.* (1903). Wilmott's plants have good descriptions and holotypes. E. F. Warburg supplied the data for subsp. *calcareus* and is responsible for that combination.

P. D. SELL

EUPHRASIA L.

EUPHRASIA MICRANTHA Reichb., *Fl. Germ. Excurs.*, 358 (1831) (Lectotype: In via qui iter vertram Lauram, legi Jul. 1830 [Reich. p.] (W)).

The type specimen is white-flowered.

EUPHRASIA FRIGIDA Pugsley, *J. Linn. Soc. (Bot.)* **48**, 490 (1930) (Lectotype: Ujaragsuit, Godthaabs Fjord, W. Greenland, 13 August 1885, S. Hansen (C)).

[*E. latifolia* auct., non L., *Sp. Pl.*, 604 (1753).]

[*E. arctica* auct. amer., non Lange ex Rostrup, *Bot. Tidsskr.* **1** (4), 47 (1870-71).]

EUPHRASIA TETRAQUETRA (Brébisson) Arrondeau, *Bull. Soc. Polymath. Morbihan* **1862**, 96 (1863).

E. officinalis var. *tetraquetra* Brébisson, *Fl. Normand.* ed. 2, 183 (1849).

E. occidentalis Wettst., *Mon. Gatt. Euphrasia*, 135 (1896).

E. canadensis Towns., *J. Bot., Lond.* **36**, 1 (1898).

The types of none of these names have been traced, but in each case a good original diagnosis was given.

EUPHRASIA NEMOROSA (Pers.) Wallr., *Ann. Bot.*, 82 (1815).

E. officinalis var. *nemorosa* Pers., *Syn. Pl.* **2**, 149 (1807).

As there are no specimens in the Persoon herbarium at Leiden, we have typified the name by Plate 233 in Bulliard, *Herbier de la France*, 4 (1785), which was cited with the original diagnosis.

EUPHRASIA ARCTICA Lange ex Rostrup, *Bot. Tidsskr.* **1** (4), 47 (1870-71) (Lectotype: Sandyford, Stromo, 31 August 1867, E. Rostrup (C)).

[*E. borealis* auct. mult. incl. Wettst. pro parte.]

E. borealis var. *zetlandica* Pugsley. et var. *speciosa* Pugsley, *J. Linn. Soc. (Bot.)* **48**, 516 (1930).

P. D. SELL

P. F. YEO

ODONTITES VERNA (Bellardi) Dumort.

subsp. PUMILA (Nordst.) A. Pedersen, *Bot. Tidsskr.* **58**, 291 (1963).

Odontites serotina forma *pumila* Nordst., *Bot. Not.* **1898**, 220 (1898).

[*Odontites litoralis* sensu F. N. Williams, *Prod. Fl. Brit.*, 316 (1909).]

[*Bartsia odontites* var. *litoralis* auct. brit.]

Plant up to 17 (-21) cm high, often unbranched but sometimes with one or two pairs

of short branches. Internodes short, giving the plant a condensed habit. Leaves lanceolate to ovate-lanceolate and distinctly toothed. Bracts longer than the flowers. Flowers apparently darker red than in other subspecies. Flowers July–August (September).

Grassy places by the sea. N. & W. Scotland (Sutherland, Caithness and Hebrides), Netherlands, Denmark and S. Sweden.

subsp. *VERNA*

Euphrasia verna Bellardi, *Mem. Acad. Sci. Turin*, ser. 1, **1790-91**, 239 (1793).

Odontites verna (Bellardi) Dumort., *Fl. Belg.*, 32 (1827).

Odontites verna subsp. *longifolia* Corbière, *Nouv. Fl. Normand.*, 436 (1894).

Bartsia odontites var. *verna* (Bellardi) Druce, *List Br. Pl.*, 54 (1908).

Bartsia odontites var. *longifolia* (Corbière) Druce, *List Br. Pl.*, 54 (1908).

[*Bartsia odontites* var. *rotundata* auct. brit.]

Plant 10-30 cm high, with branches coming off at an angle of less than 45° and more or less straight. Internodes longer giving the plant a more open habit. Leaves lanceolate, distinctly toothed. Bracts longer than the flowers. Flowers June and July. $2n = 40$.

Cultivated, waste and grassy places. In the British Isles commoner in the north than the south. In Europe as a whole more common in the north and mountainous regions, perhaps absent from some areas in the south.

subsp. *SEROTINA* Corbière, *Nouv. Fl. Normand.*, 437 (1894).

Euphrasia odontites L., *Sp. Pl.*, 604 (1753).

Euphrasia serotina Lam., *Fl. Fr.* **2**, 350 (1778) nom. superfl. illegit. pro *E. odontites* L.

[*Odontites rubra* Gilib., *Fl. Lith.* **1**, 126 (1781) nom. non rite publ.]

Euphrasia rubra Baumg. in Hoffm., *Deutschl. Fl.*, 215 (1791).

Odontites vulgaris Moench, *Meth.*, 439 (1794) nom. nov. pro *Euphrasia odontites* L.

Odontites serotina Dumort., *Fl. Belg.*, 32 (1827), nom. superfl. illegit. pro *Euphrasia odontites* L.

Euphrasia divergens Jord. in F. W. Schultz, *Arch. Fl. Fr. Allem.*, 191 (1851).

Odontites rubra subsp. *serotina* Wettst., *Denkschr. Akad. Wiss. Math.-Nat. Kl. (Wien)* **70**, 321 (1901).

Bartsia odontites var. *serotina* auct. mult. includ. Druce, *List Brit. Pl.*, 54 (1908).

Bartsia odontites var. *divergens* (Jord.) Druce, *Brit. Pl. List*, 54 (1908).

Plant 20–50 cm high, with branches spreading at a wide angle, sometimes nearly at right angles, their tips often upcurved. Internodes long, giving the plant an open habit. Leaves linear-lanceolate, somewhat narrowed at the base, obscurely toothed. Bracts shorter than or equalling the flowers. Flowers July and August. $2n = 20$.

Similar habitats to subsp. *verna*. Common in S. England, rarer farther north and in hilly regions. Common in the lowlands of continental Europe, but rare in the north and sometimes the only subspecies in the south. ? East Europe.

The genus *Odontites* seems to be represented in the British Isles by the above three subspecies. Subsp. *verna* and subsp. *serotina* are said to have different chromosome numbers, but their morphological characters (particularly in the British Isles) overlap so greatly, and there are so many intermediates, that it seems impossible to distinguish them as species. In continental Europe subsp. *verna* seems to be predominantly a northern or montane plant, while subsp. *serotina* is more lowland, with a distribution which goes much farther south. In the south and the north they seem to be much more distinct than in a zone running across central Europe and including the British Isles. Subsp. *pumila* is a dwarf coastal race most nearly allied to subsp. *verna*, with which it intergrades in the Hebrides. Round the Baltic occurs another dwarf coastal race which is usually unbranched, has long lower internodes, much longer than the leaves, and bracts longer than the flowers. It would seem to be most nearly allied to subsp. *pumila*. Its correct name seems to be *O. verna* subsp. *LITORALIS* (Fries) Nyman, *Consp.*, 551 (1881) (*Euphrasia odontites* var. *litoralis* Fries, *Fl. Scan.*, 40 (1835)). G. Marklund (*Acta Soc. Fauna Fl. Fenn.* **72**, 1–18 (1955)) when dealing with the Finnish plants of the genus, has described *O. litoralis* subsp. *fennica*

and *O. litoralis* subsp. *littoralis* var. *baltica*. I have not seen material of these plants, but from their descriptions they seem to be very close to *O. verna* subsp. *litoralis*, and may form connecting links between it and subsp. *verna*. Subsp. *verna*, subsp. *pumila*, subsp. *litoralis* and *O. litoralis* subsp. *fennica* thus form the northern elements of the *O. verna* complex. In the south, subsp. *serotina* is the dominant plant, but in Sicily plants with linear or linear-lanceolate, markedly dentate leaves and yellowish-pink flowers seem to be distinct. I call them *O. verna* subsp. *sicula* (Guss.) Sell, comb. et stat. nov. (*Euphrasia serotina* var. *sicula* Guss., *Fl. Sic. Prodr.* 2, 149 (1828)). In eastern Europe the plants most resemble subsp. *serotina*, but they become increasingly pubescent eastwards and another subspecies may have to be distinguished there.

The large number of small taxa of various ranks, and their combinations in *Euphrasia*, *Bartsia* and *Odontites*, plus a superfluity of names, have made the nomenclature of the group very difficult. I have done my best here to establish the correct names of the British taxa, and to show where synonyms or misapplied names belong, but only an exhaustive study of all the European literature could possibly establish the correct authors of the various combinations.

P. D. SELL

VALERIANELLA LOCUSTA (L.) Betcke

subsp. **dunensis** (D. E. Allen) Sell, stat. nov.

V. locusta var. *dunensis* D. E. Allen, *Watsonia* 5, 45 (1961).

I have discussed this taxon with Allen. He tells me that he uses the rank of subspecies for geographical variation and that of variety for ecological variation. I see no clear difference between geographical, ecological or even altitudinal isolation of populations, all three factors sometimes applying to the same taxon. I have thus elevated Allen's variety to the rank of subspecies.

P. D. SELL

SENECIO VULGARIS L.

subsp. **denticulatus** (O. F. Muell.) Sell, comb. et stat. nov.

S. denticulatus O. F. Muell., *Fl. Dan.* 5 (14), 4 et t. 791 (1780).

This taxon appears to constitute a distinct ecological race, which in view of its wide geographical range seems to me to merit subspecific rank. For a discussion of the radiate forms of *S. vulgaris* see D. E. Allen, *Watsonia* 6, 280-282 (1967).

P. D. SELL

HIERACIUM L.

We are here publishing only what is necessary to validate the new names and combinations of species being mapped in the Appendix to the Atlas of British Plants. A more detailed paper, bringing up to date the revision by Pugsley, *J. Linn. Soc. (Bot.)* 54 (1948), will follow.

In Sectione ALPINA F. N. Williams

Hieracium tenuifrons Sell & C. West, sp. nov.

Ab *H. alpino* L. squamis involucri angustioribus, stylis obscuris et ligulorum pilis paucioribus differt, praeterea ab *H. pseudopetiolo* (Zahn) Roffey squamis longioribus angustioribus et capitulis latoribus distinguitur.

Holotype: Fionn Ghleann, Glen Etive, v.c. 98, Argyll, July 1954, C. West (CGE).

Planta phyllopoa. Caulis 13-25 (-36) cm altus, valde striatus, flexuosus, pilis aliis simplicibus pallidis nonnunquam basi nigris longis vel longissimis (ad 5 mm), aliis stellatis numerosis, aliis glanduliferis numerosis brevissimis flaviusculo-brunneis vel atriusculis vestitus. Folia medio-viridia; basalia numerosa; primigenia obovata, obtusa, denticulata, basi cuneata; cetera oblanceolata vel obovata; obtusa, denticulata vel leviter dentata, basi attenuata, petiolis mediocribus vel longis; caulina 1-3 (-7), anguste oblanceolata

Watsonia 6 (5), 1967.

vel linearia, obtusa vel subacuta, integra vel raro denticulata, basi attenuata, sessilia vel breviter petiolata; omnia utrinque et margine pilis simplicibus longis pallidis basi nigris, et margine pilis glanduliferis numerosis brevissimis vestita. Anthela capitulo unico. Involucris squamae 14–16 mm longae, 1.0–1.25 mm latae, atriusculo-virides, lineares, plus minusve acutae, pilis aliis simplicibus densissimis longis vel longissimis (ad 5 mm) pallidis, aliis glanduliferis numerosis brevissimis obscuris, aliis stellatis nullis obsitae. Ligulae saturate flavae, apice pilis brevibus vel brevissimis vestitae. Styli obscuri. Receptaculi alveoli margine breviter dentati. Cypsela obscura, 3–3.5 mm longa.

Hieracium notabile Sell & C. West, sp. nov.

H. eximium Backh., *H. marginatum* Sell & C. West, *H. memorabile* Sell & C. West et *H. backhousei* F. J. Hanb. quoad faciem simulat. Ab *H. memorabile* et *H. backhousei* foliis obtusis integris vel denticulatis differt, praeterea ab *H. eximio* et *H. marginato* squamis involucris latioribus obtusioribus distinguitur.

Holotype: Ben More, v.c. 88, Mid-Perth, 16 July 1910, E. S. Marshall no. 3489 (CGE).

Planta phyllopoða. Caulis 17–26 cm altus, valde striatus, flexuosus, parte basali interdum purpureo-tincta, pilis aliis stellatis paucis, aliis simplicibus numerosis inaequalibus brevibus mediocribus longisque basi nigris patentibus, aliis glanduliferis brevissimis paucis obscuris vestitus. Folia pallide viridia; basalia pauca; primigena late elliptica, mucronulata, integra, basi attenuata; cetera anguste elliptica vel elliptica, raro late elliptica, obtusomucronata vel subacuta, integra vel dentibus parvis paucis vel interdum dentibus tenuibus cuspidatis muniter, basi gradatim attenuata, petiolis alatis; caulina 2–3, inferioribus basalibus similibus, superioribus bracteiformibus; omnia utrinque et margine pilis simplicibus numerosis longis saepe fere setiformibus, et margine pilis glanduliferis numerosis brevissimis vestita. Anthela capitulo unico. Involucris squamae 12–16 mm longae, 1–1.5 mm latae, atriusculo-virides, lineares, obtusae vel subacutae, raro acutae, pilis simplicibus densis inaequalibus longis pallidis, pilis glanduliferis nullis, apice pilis stellatis paucis obsitae. Ligulae saturate flavae, apice et nonnunquam in parte aversa pilis simplicibus brevibus vel brevissimis vestitae. Styli obscuri. Cypselae obscurae, circa 4 mm longae.

Hieracium marginatum Sell & C. West, stat. et nom. nov.

Basionym: *H. globosiflorum* var. *lancifolium* Pugsl., *J. Linn. Soc. (Bot.)* **54**, 47 (1948)

(Holotype: Ben Laoghal, v.c. 108, W. Sutherland, 2,300 ft, 2 August 1897, E. S. Marshall no. 2042 (BM)).

Hieracium memorabile Sell & C. West, sp. nov.

H. notabile Sell & C. West, *H. eximium* Backh., *H. marginatum* Sell & C. West et *H. backhousei* F. J. Hanb. quoad faciem simulat. Ab *H. notabile* squamis involucris angustioribus acutis, ab *H. eximio* squamis ligulisque pilis brevioribus, ab *H. backhousei* foliis pilosioribus stylisque obscuris distinguitur.

Holotype: Beinn an Sochaich, 2,500–3,000 ft, v.c. 97, W. Inverness, July 1896, E. S. Marshall and W. A. Shoolbred in Linton, *Set of Brit. Hierac.* no. 55 (CGE).

Planta phyllopoða. Caulis 15–24 cm altus, valde striatus, in parte basali nonnunquam purpureus, pilis aliis simplicibus longis vel longissimis (ad 6 mm longis) pallidis basi nigris, aliis stellatis inferne sparsis superne numerosioribus, aliis glanduliferis paucis vel numerosis brevissimis brevibus vel raro mediocribus obscuris vestitus. Folia saturate viridia; basalia plerumque numerosa; primigena suborbicularia, mucronulata, leviter dentata, basi abrupte contracta, petiolis brevibus; cetera dimorpha, exteriora late elliptica, mucronulata, dentata vel inciso-dentata, dentibus nonnunquam cuspidatis vel mammiformibus, basi cuneata, interiora anguste elliptica vel elliptica, plus minusve acuta, dentata vel inciso-dentata, dentibus saepe inaequalibus nonnunquam cuspidatis, basi attenuata; caulina 1–2 bracteiformia; omnia utrinque et margine pilis simplicibus plus minusve numerosis mediocribus et longis gracilibus, et margine pilis glanduliferis plus minusve numerosis brevissimis flaviusculis vestita. Anthela capitulo unico, nonnunquam furcata, utroque ramo capitulo

unico. Involucri squamae 13–16 mm longae, 1–1.5 mm latae, ante anthesin incumbentes, atriusculo-virides, lineari-lanceolatae, acutae, pilis aliis simplicibus inaequalibus longis pallidis basi nigris, aliis glanduliferis paucis brevissimis vel brevibus obscuris gracilibus obsitae. Ligulae saturate flavae, apice et in parte aversa pilis simplicibus numerosis brevissimis vel brevibus vestitae. Styli obscuri. Cypselae obscurae, circa 3.5 mm longae.

Hieracium atraticeps (Pugs.) Sell & C. West, stat. sp. nov.

H. chrysanthum var. *microcephalum* Backh., *Mon. Brit. Hieracia*, 34 (1856) (Lectotype: Lochnagar, 1855, J. Backhouse, jun. (BM)).

H. hanburyi var. *microcephalum* (Backh.) Pugs., *J. Linn. Soc. (Bot.)* **54**, 51 (1948) quoad basionym exclud. descript.

H. hanburyi var. *atraticeps* Pugs., *J. Linn. Soc. (Bot.)* **54**, 51 (1948) (Holotype: Lochnagar, 1887, E. F. Linton (BM)).

H. chrysanthum var. *microcephalum* Backh. was based on specimens collected from Lochnagar (Aberdeen), Clova (Angus), and Striding Edge and Glaramara (Cumberland). Plants in the Backhouse herbarium from Lochnagar are *H. atraticeps* and those from Cumberland *H. subgracilentipes* (Zahn) Roffey. No Backhouse specimens from Clova have been traced, but *H. atraticeps* occurs there. It is thus safe to assume that Backhouse included within his taxon two of ours. The original diagnosis applies almost equally well to both, with perhaps a slight tendency to fit *H. atraticeps* better. In the discussion that follows the diagnosis, there is also a slight tendency to suggest that the Cumberland form is slightly aberrant. We have therefore chosen a Lochnagar plant as the lectotype. Pugsley (1948) cited as a type of *H. chrysanthum* var. *microcephalum* an E. F. Linton specimen collected at Clova in 1890. This of course is impossible by the International Code. The plant he described is a slight variation of *H. hanburyi* Pugs. On the same page he described *H. hanburyi* var. *atraticeps* giving as its type an E. F. Linton specimen collected at Lochnagar in 1887, and citing also the specimen we have now selected as the lectotype of *H. chrysanthum* var. *microcephalum*.

In Sectione SUBALPINA Pugs.

Hieracium diversidens Sell & C. West, sp. nov.

Ab *H. submuroro* Lindeb. squamis capitulorum brevioribus pilis glanduliferis paucioribus distinguitur.

Holotype: rocks at 1,700 ft, Allt Odhar, near Fortingal, v.c. 88, Mid-Perth, 18 July 1913, E. S. Marshall no. 3831 (CGE).

Planta phyllopoda. Caulis ad 50 cm altus, valde striatus, sparse stellato-pilosus, inferne pilis simplicibus sparsis pallidis, superne raro pilis glanduliferis paucis brevissimis vel brevibus obscuris vestitus. Folia pallide viridia; basalia pauca; primigenia suborbicularia, mucronulata, denticulata, basi abrupte contracta; cetera dimorpha, exteriora late elliptica, mucronulata, denticulata vel leviter dentata, basi abrupte contracta, interiora elliptica vel late elliptica, obtusa vel acuta, denticulata vel irregulariter dentata, dentibus nonnunquam anguste mammiformibus, basi breve cuneata vel subtruncata; caulina 0–1, bracteiformia; omnia utrinque glabra vel pilis simplicibus paucis mediocribus, margine pilis aliis simplicibus numerosis brevibus et interdum aliis glanduliferis brevissimis flaviusculis vestita; petioli pilis simplicibus densis longis flexuosis obsiti. Anthela laxa cymosa, capitulis 1–4; pedunculi suberecti, mediocres, pilis aliis stellatis numerosis, aliis simplicibus paucis brevibus vel mediocribus obscuris, aliis glanduliferis sparsis brevissimis vel brevibus obscuris obsiti. Involucri squamae 9–10 mm longae, 1 (–1.25) mm latae, ante anthesin porrectae, atriusculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, plus minusve acutae, pilis aliis stellatis sparsis, aliis simplicibus numerosis brevibus vel mediocribus obscuris, aliis glanduliferis paucioribus brevissimis vel brevibus obscuris vestitae. Ligulae saturate flavae, apice pilis simplicibus numerosis brevissimis vestitae. Styli obscuri. Cypselae obscurae, circa 3 mm longae.

Hieracium hastiforme Sell & C. West, sp. nov.

Holotype: Cliffs, Glas Carnoch Burn [near Altguish Inn], v.c. 106, E. Ross, 24 July 1909, W. A. Shoolbred no. 716 (CGE).

Planta phyllopoda. Caulis ad 45 cm altus, gracilis, valde striatus, e basi nonnunquam purpureus, pilosus, pilis simplicibus plus minusve numerosis longis pallidis (superne basi nigris), pilis stellatis paucis, et superne pilis glanduliferis sparsis brevibus vel brevissimis obscuris vestitus. Folia pallide viridia; basalia pauca; primigena nobis ignota; plurima lanceolata, raro elliptica, plurima acuta, raro obtusa, denticulata vel dentata, dentibus saepe anguste mammiformibus, basi plus minusve cuneata, petiolis longis; caulina 1-2, inferius basalibus simile, superius bracteiforme; omnia superne glabra vel pilis simplicibus paucis mediocribus, inferne pilis simplicibus paucis mediocribus, caulina inferne praecipuae pilis stellatis plus minusve numerosis omnia in marginibus scaberulis vel pilis simplicibus numerosis brevibus vel mediocribus vestita; petioli pilis simplicibus numerosis mediocribus longisque obsiti. Anthela cymosa, capitulis 1-3; pedunculi longi, suberecti, pilis stellatis numerosis, pilis glanduliferis numerosis brevibus brevissimisque obscuris, pilis simplicibus paucioribus brevibus mediocribusque obscuris vel basi nigris obsiti. Involucri squamae 12-13 mm longae, 1-1.5 mm latae, ante anthesin incumbentes, atriussculo-virides, interiores margine pallidae, lineares, obtusae vel subacutae, pilis aliis stellatis sparsis, aliis simplicibus valde numerosis brevissimis obscuris vestitae. Ligulae saturate luteae (fide E. S. Marshall), apice glabrae vel puberulae. Styli obscuri. Cypselae non visae.

Hieracium cuspidens Sell & C. West, sp. nov.

Ab omnibus speciebus affinis foliis alte irregulariter dentatis distinguitur.

Holotype: Rocky gorge above a subalpine streamlet (1,400 ft), west of the road from Fortingal to Fearnan, v.c. 88, Mid-Perth, 3 July 1913, E. S. Marshall no. 3867 (CGE).

Planta phyllopoda. Caulis ad 50 (ad 60) cm altus, valde striatus, parte basali plerumque purpureo, pilis aliis simplicibus numerosis mediocribus longisque pallidis (superioribus basi nigris), aliis glanduliferis subnumerosis brevissimis obscuris, superne pilis stellatis subnumerosis vestitis. Folia pallide viridia, nonnunquam purpureo-tincta; basalia pauca; primigenia suborbicularia, mucronulata, subintegra, basi rotundata; cetera plurima lanceolata, nonnunquam elliptica vel anguste elliptica, subacuta vel acuta, dentata vel inciso-dentata, dentibus inaequalibus plurimis mammiformibus vel anguste mammiformibus et saepe cuspidatis, nonnunquam ad basim dentibus longis angustis et interdum cum eis in petiolis longis descendentibus, basi cuneata; caulina 0-1, basalibus similes vel bracteiformia; omnia superne glabra vel pilis simplicibus paucis brevibus et mediocribus, inferne pilis simplicibus paucis vel subnumerosis brevibus mediocribusque, margine puberula vel pilis simplicibus plus minusve numerosis brevibus mediocribusque vestita; petioli pilis simplicibus densis mediocribus longisque obsiti. Anthela compacte cymosa, capitulis 1-3 (-9 in specim. cult.); pedunculi mediocres, suberecti, pilis aliis stellatis numerosis, aliis simplicibus plus minusve numerosis brevibus mediocribusque basi nigris, aliis glanduliferis brevissimis vel brevibus obscuris obsiti. Involucri squamae 11-13 mm longae, 1-1.5 mm latae, ante anthesin incumbentes, atriussculo-virides, interiores marginibus pallidioribus, linearilanceolatae, obtusae, pilis stellatis numerosis margine et apice, pilis aliis simplicibus plus minusve numerosis brevibus mediocribusque basi nigris et aliis glanduliferis brevissimis brevibusque vestitae. Ligulae saturate flavae (fide E. S. Marshall), apice puberulae. Styli obscuri. Cypselae obscurae, circa 3 mm longae.

Hieracium glandulidens Sell & C. West, sp. nov.

Ab *H. hyparcticoide* Pugsl. squamis involucri brevioribus, plerumque foliis latioribus cypselisque brevioribus differt.

Holotype: near Inchnadamph, v.c. 108, W. Sutherland, 18 July 1908, E. S. Marshall no. 3295 (CGE).

Planta phyllopoda. Caulis 30-60 cm altus, valde striatus, parte basali nonnunquam leviter purpureo, pilis simplicibus paucis pallidis mediocribus longisque, superne pilis

stellatis paucis et pilis glanduliferis subnumerosis brevissimis brevibusque obscuris vestitus. Folia saturate viridia; basalia plerumque pauca; primigena suborbicularia, mucronulata, subintegra, basi rotundata; cetera variabilia, late elliptica, ovata vel lanceolata, obtusa, acuta vel acuminata, glanduloso-denticulata, nonnunquam dentibus paucis mammiformibus cuspidatis, basi cuneata; caulinum 0-1, basalibus simile; omnia superne glabra vel pilis aliis simplicibus paucis mediocribus, inferne margineque et in petiolis longis pilis subnumerosis brevibus mediocribus longisque vestita. Anthela compacte cymosa, capitulis 1-5; pedunculi longi, suberecti, pilis aliis stellatis numerosis, aliis glanduliferis numerosis brevissimis brevibusque obscuris, aliis simplicibus paucis vel numerosis, brevibus basi nigris obsiti. Involucri squamae 10-12 mm longae, 1-1.5 mm latae, ante anthesin incumbentes, atriussculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, subacutae vel acutae, pilis stellatis margine sparsis et e apice numerosis, pilis aliis simplicibus numerosis, brevibus mediocribusque, basi nigris et aliis glanduliferis numerosis brevissimis brevibusque obscuris vestitae. Ligulae saturate flavae, apice pilis simplicibus brevissimis paucis obsitae. Styli obscuri. Alveolae receptaculi margine longidentatae. Cypselae obscurae, circa 3 mm longae.

Hieracium chrysolorum Sell & C. West, sp. nov.

Ab *H. clovense* E. F. Linton foliis majoribus saepe ellipticioribus obtusioribus emaculatis et capitulis majoribus differt.

Holotype: Midlaw Burn, Moffat, v.c. 72, Dumfries, July 1951, C. West (CGE).

Planta phyllopoda. Caulis 18-30 cm altus, valde striatus, parte basali nonnunquam leviter purpureo-tincto, pilis aliis simplicibus subnumerosis longis pallidis (superne basi nigris), aliis stellatis paucis, superne aliis glanduliferis paucis vel numerosis brevissimis brevibusque obscuris vestitus. Folia caesio-viridia; basalia plerumque numerosa; primigena suborbicularia, mucronulata, subintegra, basi rotundata; cetera suborbicularia, ovato-elliptica vel elliptica, plurima obtusa vel subacuta, raro acuta, denticulata vel grosse dentata, dentibus obtusis vel acutis mammiformibus, basi cuneata vel abrupte contracta, raro rotundata; caulinum 0-1, lanceolatum vel anguste ellipticum, acuminatum, acute dentatum, basi abrupte contractum vel cuneatum, petiolo brevi; omnia utrinque glabra vel pilis simplicibus paucis mediocribus longisque, in marginibus petiolisque pilis simplicibus numerosis mediocribus longisque, caulina subtus pilis stellatis numerosis vestita. Anthela corymboso-cymosa, capitulis 2-6; pedunculi mediocres vel longi, suberecti, pilis aliis stellatis numerosis, aliis glanduliferis numerosis brevissimis vel brevibus obscuris, nonnunquam pilo simplice interdum mediocre basi nigro obsiti. Involucri squamae 11-13 mm longae, 1-1.5 mm latae, ante anthesin incumbentes, interiora marginibus pallidioribus, lineari-lanceolatae, obtusae vel subacutae, pilis aliis stellatis paucis, aliis glanduliferis numerosis inaequalibus brevissimis brevibusque mediocribusque obscuris, pilis simplicibus aliquando mediocribus basi nigris vestitae. Ligulae flavae, glabrae. Styli flavi. Cypselae non visae.

Hieracium nigrisquamum Sell & C. West, sp. nov.

Ab *H. dasythrice* (E. F. Linton) Pugsl. squamis involucri longioribus pilis aliis simplicibus paucioribus obscurioribus aliis stellatis paucioribus, aliis glanduliferis numerosioribus vestitis differt.

Holotype: On rocks, at about 2,500 ft, Coire nan Gall, north of Loch Laggan, v.c. 97, W. Inverness, 7 August 1916, E. S. Marshall no. 4308 (CGE).

Planta phyllopoda. Caulis 30-55 cm altus, valde striatus, parte basali plerumque leviter purpureo, pilis aliis stellatis sparsis, aliis simplicibus paucis mediocribus vel longis pallidis (superne basi nigris) et superne aliis glanduliferis paucissimis brevibus vel brevissimis obscuris vestitus. Folia medio-viridia, nonnunquam purpureo-tincta; basalia pauca vel numerosa; primigena suborbicularia, mucronulata, subintegra, basi rotunda; cetera plerumque elliptica vel late elliptica, raro lanceolata, plurima subacuta, interdum obtusomucronulata vel acuta; plerumque denticulata, nonnunquam integra vel ad basim dentibus paucis parvis, basi cuneata vel abrupte contracta, petiolis longis; caulina 0-1 (-2), plerumque

bracteiformia, sed nonnunquam basalibus similia; omnia superne glabra vel pilis simplicibus paucis brevibus vel mediocribus, inferne et margine pilis simplicibus numerosioribus mediocribus vel longis, margine pilis glanduliferis paucis brevissimis flaviusculis, nonnunquam utrinque pilis stellatis paucis vestita; petioli pilis simplicibus longis obsiti. Anthela laxa cymosa, capitulis 2–8, nonnunquam ramum ex axilla folii caulini superioris emittens; pedunculi plerumque longi, pilis aliis stellatis numerosis vel densis, aliis simplicibus numerosis brevibus vel mediocribus obscuris et aliis glanduliferis paucis vel numerosis brevibus vel brevissimis obscuris obsiti. Involucri squamae 10–12 mm longae, 1–1.25 mm latae, ante anthesin porrectae vel incumbentes, atriusculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, obtusae vel acutae, pilis aliis stellatis paucis, aliis simplicibus numerosis mediocribus vel longis obscuris, aliis glanduliferis plus minusve numerosis brevibus vel mediocribus obscuris vestitae. Ligulae pallide flavae, apice pilis simplicibus numerosis brevissimis obsitae. Styli obscuri. Cypselae obscurae, 4–4.25 mm longae.

Hieracium pseudanglicoides J. E. Raven, Sell & C. West, sp. nov.

Ab *H. pseudanglico* Pugsl. squamis involucri brevioribus foliisque angustioribus pilis stellatis vestitis differt, praeterea ab plantis parvis *H. flocculosi* Backh. squamis involucri plerumque brevioribus pilis aliis glanduliferis numerosioribus et aliis simplicibus pallidioribus vestitis, plerumque foliis angustioribus cypselisque longioribus distinguitur.

Holotype: Rock ledges, corry of Ben Dourain, v.c. 98, Argyll, G.R. 27/330382, July 1953, M. C. F. Proctor & K. M. Goodway no. G3/94 (CGE).

Planta phyllopoða. Caulis 10–50 cm altus, valde striatus, plerumque parte basali leviter purpureo, pilis aliis simplicibus paucis mediocribus vel longis pallidis, aliis stellatis paucis, et superne nonnunquam aliis glanduliferis brevibus vel brevissimis vestitus. Folia pallide viridia, raro purpureo-tincta; basalia pauca vel numerosa; primigena late elliptica, obtuso-mucronulata, integra, basi rotundata; cetera plerumque anguste elliptica, nonnunquam elliptica, obtusa, subacuta vel nonnunquam acuta, plerumque integra, raro dentibus parvis paucis, basi cuneata; caulina 1–2 (–3), basalibus similia vel bracteiformia; omnia superne pilis simplicibus nullis vel utrinque pilis simplicibus plus minusve numerosis mediocribus vel longis et pilis stellatis numerosis, in marginibus petiolisque pilis simplicibus numerosis mediocribus vel longis vestita. Anthela laxa cymosa, capitulis 1–2 (–10), raro ramum longum ex axillo folii caulini superioris emittens; pedunculi longi, erecti, pilis aliis stellatis subnumerosis, aliis glanduliferis numerosis brevissimis vel brevibus obscuris, aliis simplicibus subnumerosis brevibus mediocribus longisque obscuris obsiti. Squamae 10–13 mm longae, circa 1 mm latae, ante anthesin porrectae, atriusculo-virides, nonnunquam interiores marginibus pallidioribus, apice pilis aliis stellatis densis et ad basim aliis stellatis paucis, pilis aliis simplicibus numerosis brevibus mediocribusque obscuris, aliis glanduliferis numerosis brevissimis vel brevibus obscuris vestitae. Ligulae pallide flavae, apice glabro vel puberulo. Styli obscuro. Cypselae obscurae, circa 5 mm longae.

This species was first recognized as new, and the epithet suggested by J. E. Raven, who has joined us as a co-author in describing it.

In Sectione CERINTHOIDEA Koch

Hieracium magniceps Sell & C. West, sp. nov.

Ab *H. irico* Fries pilis paucioribus foliis late illipticis differt; preaterea ab *H. langwellense* F. J. Hanb. in patibus omnibus majoribus distinguitur.

Holotype: Grassy bank of the Shee Water, near the Spittal of Glen Shee, E. Perth, v.c. 89, 19 July 1959, N. D. Simpson, P. D. Sell & C. West (CGE).

Planta phyllopoða. Caulis ad 60 cm altus, robustus, plerumque parte basali purpureo, pilis aliis simplicibus paucis vel subnumerosis longis pallidis nonnunquam basi nigris, aliis stellatis raris vestitus; pili glanduliferi nulli. Folia medio-viridia; basalia pauca; primigena non visa; cetera magna, late elliptica, obtusa vel acuta, leviter undulato-dentata, basi

attenuata; caulina 2-4, magna, basalibus similia; omnia utrinque et margine pilis simplicibus dispersis nonnunquam fere setiformibus pallidis mediocribus vestita; petioli longi alati pilis simplicibus pallidis mediocribus vel longis obsiti. Anthela furcato-cymosa, capitulis 5-6; pedunculi plerumque longi, suberecti, pilis aliis stellatis numerosis, aliis simplicibus brevibus mediocribus vel longis pallidis basi nigris, aliis glanduliferis paucis brevissimis vel brevibus obscuris obsiti. Involucri squamae 12-15 mm longae, circa 1.5 mm latae, ante anthesin incumbentes, atriussculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, subacutae vel acutae, pilis aliis stellatis numerosis praecipue in marginibus, aliis simplicibus numerosis pallidis basi nigris brevibus mediocribus vel longis, aliis glanduliferis paucis brevissimis obscuris vestitae. Ligulae saturate flavae, apice pilis simplicibus numerosis brevissimis obsitae. Styli obscuri. Cypselae non visae.

In Sectione OREADEA Zahn

Hieracium praetermissum Sell & C. West, sp. nov.

Ab *H. ebudico* Pugsl., *H. sarcophylloide* Dahlst. et *H. caledonico* F. J. Hanb. facie simile squamis capitulorum pilis stellatis numerosioribus vestitis differt.

Holotype: Limestone cliffs, 3-4 miles east of Durness, v.c. 108, W. Sutherland, 7 June 1900, E. S. Marshall no. 2336 (CGE).

Planta phyllopoda. Caulis ad 40 cm altus, plerumque parte basale purpureo, pilis aliis simplicibus dispersis (raro numerosis) pallidis longis, aliis stellatis dispersis vestitus. Folia medio-caesio-viridia, plerumque superne maculis brunneo-purpureis magnis et parvis ornata, inferne purpureo-tincta; basalia numerosa; primigena suborbicularia, mucronulata, subintegra, basi rotundata, cetera ovata vel elliptica, nonnunquam lanceolata, plerumque obtuso-mucronata, nonnunquam acuta, raro cuspidata, plerumque dentata, raro denticulata, dentibus inaequalibus ascendentibus acutis apiculatis plerumque basi cuneata, sed in paucis locis basi subtruncata, nonnunquam dentibus in petiolis descendentibus; caulinum plerumque -1, in caule inferno basalibus simile petiolatum, raro 0; omnia superne glabra vel pilis simplicibus dispersis pallidis mediocribus raro fere setiformibus, inferne et margine pilis simplicibus plus minusve numerosis pallidis mediocribus vestita, petioli pilis simplicibus densis longis obsiti. Anthela anguste cymosa, capitulis 2-9; pedunculi mediocres vel longi, suberecti, pilis aliis stellatis numerosis, aliis glanduliferis paucis brevissimis obscuris, aliis simplicibus paucis pallidis interdum basi nigris brevibus, pilis glanduliferis simplicibusque raro numerosioribus. Involucri squamae 12-14 mm longae, 1-1.5 mm latae, ante anthesin incumbentes, atriussculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, plerumque obtusae, raro subacutae, pilis aliis stellatis numerosis praecipue ad margines et apicem, aliis simplicibus plus minusve densis pallidis basi nigris mediocribus vel longis, aliis glanduliferis paucis brevissimis vel brevibus obscuris vestitae. Ligulae saturate flavae, apice pilis simplicibus brevissimis obsitae. Styli obscuri. Receptaculi alveoli margine longe dentati. Cypselae obscurae, circa 4 mm longae.

In Sectione VULGATA F. N. Williams

Hieracium pruinae (Zahn) Sell & C. West, stat. sp. nov.

H. murorum subsp. *pruinae* Zahn in Engler, *Pflanzenreich* 76 (IV, 280), 328 (1921).

H. euprepes var. *pruiniferum* W. R. Linton, *Brit. Hieracia*, 57 (1905).

Hieracium discophyllum Sell & C. West, sp. nov.

Ab *H. asteridiophyllo* Sell & C. West foliis suborbiculariis pilis stellatis nullis differt, praeterea ab *H. pellucido* Laest. simili squamis capitulorum longioribus pilis simplicibus glanduliferisque vestitis distinguitur.

Holotype: Pwll Byfre, v.c. 42, Brecon, 10 July 1929, H. J. Riddelsdell (CGE).

Planta phyllopoda. Caulis ad 40 cm altus, robustus, plerumque parte basale purpureo, pilis aliis simplicibus interdum pallidis mediocribus vel longis, aliis stellatis dispersis

vestitus. Folia flaviusculo-viridia, supra maculis minutis brunneo-purpureis ornata, subter purpureo-tincta; basalia pauca vel numerosa; primigena suborbicularia, mucronulata, integra vel denticulata, basi rotundata; cetera suborbicularia, ovata vel late elliptica, obtuse-mucronulata, regulariter denticulata e basi dentibus leviter altis apiculatis, dentibus nonnunquam in petiolis descendentibus; basi rotundata vel subtruncata; caulina 1 (–2), basalibus similes, petiolata; omnia superne glabra, inferne pilis simplicibus dispersis brevibus vel mediocribus pallidis vestita; petioli pilis simplicibus numerosis longis pallidis obsiti. Anthela late cymoso-corymbosa, capitulis 3–23; pedunculi mediocres, suberecti, pilis aliis stellatis densis, aliis glanduliferis dispersis brevissimis obscuris, aliis simplicibus paucis brevibus pallidis obsiti. Involucri squamae 9–11 mm longae, 1.25–1.5 mm latae, ante anthesin incumbentes, atriussculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, abrupte angustatae ad apices obtusae vel subacutae, pilis aliis stellatis numerosis praecipue in marginibus apicibusque, aliis glanduliferis numerosis brevibus vel brevissimis obscuris, aliis simplicibus paucioribus brevibus vel mediocribus vestitae. Ligulae saturate flavae, glabrae. Styli obscuri. Receptaculi alveoli margine longe dentati. Cypsela obscurae, 3.5–4 mm longae.

Hieracium piligerum (Pugsl.) Sell & C. West, stat. sp. nov.

H. variicolor var. *piligerum* Pugsl., *J. Linn. Soc. (Bot.)* **54**, 156 (1948).

Hieracium mucronellum Sell & C. West, sp. nov.

Ab *H. maculoso* (Stenström) Omang caulibus pilis simplicibus destitutis, foliis pedunculisque pilis paucioribus vestitis, et foliis praecipue obtusioribus distinguitur.

Holotype: Near Bettyhill, v.c. 108, W. Sutherland, 6 July 1951, J. E. Raven (CGE).

Planta phyllopoda. Caulis ad 50 cm altus, gracilis, flexuosus, valde striatus, parte basali saepe leviter purpureo, superne pilis stellatis dispersis, pilis simplicibus glanduliferisque nullus. Folia medio- vel obscure viridia, superne maculis minutis brunneo-purpureis conspersa, inferne purpureo-tincta; basalia numerosa; primigena ovata, obtuso-mucronata, subintegra, basi rotundata; cetera variabilia, elliptica, late elliptica, ovata, oblonga vel lanceolata, obtuso-mucronulata vel acuta, leviter apiculato-dentata vel mammiformidentata, basi subtruncata, dentibus in petiolis nonnunquam descendentibus; caulinum 0–1, in parte basali caulis divaricatum, lanceolatum, longe acutum, petiolatum, dentatum omnia plerumque superne glabra, inferne et in marginibus pilis simplicibus dispersis mediocribus vel longis pallidis vestita; petioli pilis simplicibus densis longis obsiti. Anthela compacte cymosa, capitulis 2–8; pedunculi mediocres vel longi, suberecti, pilis aliis stellatis densis, aliis glanduliferis dispersis brevissimis obscuris, aliis simplicibus nullis. Involucri squamae 9–10 mm longae, 0.75–1 mm latae, ante anthesin incumbentes, atriussculo-virides, interiores marginibus pallidioribus, anguste lineari-lanceolatae, subacutae vel acutae, pilis aliis stellatis dispersis, aliis glanduliferis numerosis brevissimis obscuris, aliis simplicibus numerosis brevibus obscuris vestitae. Ligulae pallide flavae, glabrae. Styli obscuri. Receptaculi alveoli margine breviter dentati. Cypsela obscura, 2.5–3 mm longa.

Hieracium pauculidens Sell & C. West, sp. nov.

Holotype: Abundant on grassy slopes of the coast, Skerryay, W. Sutherland, v.c. 108, 23 June 1900, E. S. Marshall, no. 2327 (CGE).

Planta phyllopoda. Caulis ad 55 cm altus, valde striatus, parte basali leviter purpureo, pilis aliis simplicibus paucis pallidis brevibus vel mediocribus, aliis stellatis paucis vel numerosis, superne aliis glanduliferis paucis brevibus obscuris vestitus. Folia medio-viridia, saepe purpureo-tincta; basalia plerumque pauca; primigena suborbicularia, mucronulata, subintegra, basi plus minusve rotundata; cetera ovata vel late elliptica, obtuso-mucronulata vel cuspidata, subintegra, minute denticulata vel raro dentibus paucis, basi inaequaliter rotundata vel subtruncata; caulina 0 vel raro 1, lanceolata, longe acuta, subintegra, basi cuneata, petiolata; omnia utrinque et in marginibus pilis simplicibus plus minusve numerosis mediocribus pallidis vestita, petioli pilis simplicibus densis mediocribus vel longis obsiti;

caulina inferne pilis stellatis dispersis vestita. Anthela compacte cymosa, capitulis 2–6; pedunculi breves vel mediocres, pilis aliis stellatis numerosis, aliis glanduliferis numerosis brevibus obscuris, aliis simplicibus paucioribus basi nigris obsiti. Involucri squamae 9–10·5 mm longae, circa 1 mm latae, ante anthesin plus minusve incumbentes, atriussculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, obtusae vel acutae, pilis aliis stellatis dispersis praecipue ad marginem, aliis glanduliferis numerosis brevibus vel brevissimis, aliis simplicibus numerosis pallidis basi nigris brevibus vel mediocribus vestitae. Ligulae pallide luteae, glabrae. Styli flavi. Receptaculi alveoli margine breviter dentati. Cypselae obscurae, circa 3·5 mm longae.

Hieracium variifolium Sell & C. West, sp. nov.

Ab *H. anguino* (W. R. Linton) Roffey foliis latioribus magis dentatis capitulis numerosioribus squamis involucri vestitis differt; praeterea ab *H. prolixo* Nörrl. (facie simili) pedunculis pilis simplicibus numerosioribus vestitis, squamis involucri longioribus et capitulis angustioribus distinguitur.

Holotype: Rocks just above the road at Coldbackie, v.c. 108, W. Sutherland, G.R. 29/612599, 8 June 1965, J. N. Mills & C. West (CGE).

Planta phyllopora. Caulis ad 40 cm altus, inferne nonnunquam leviter purpureus pilis aliis simplicibus paucis mediocribus vel longis, pallidis, aliis stellatis paucis, aliis glanduliferis paucis brevissimis obscuris vestitus. Folia medio-viridia, superne plerumque maculis magnis et parvis purpureo-brunneis ornata, inferne purpureo-tincta; basalia numerosa; primigena subrotunda, mucronulata, minute denticulata, basi rotundata; cetera variabilia, ovata vel late elliptica, obtuso-mucronulata vel acuta, saepe cuspidata, denticulata vel dentata, dentibus saepe anguste vel late mammiformibus, inferioribus saepe unguiculato-mammiformibus, basi inaequaliter subtruncata vel rotundata, dentibus nonnunquam in petiolis descendentibus; caulinum 0 (vel 1), lanceolatum, longe acutum, leviter dentatum, petiolatum; omnia superne glabra, inferne et margine pilis simplicibus pallidis mediocribus vestita; petioli pilis simplicibus densis longis obsiti, caulina pilis stellatis paucis vestita. Anthela anguste cymosa, capitulis 2–5 (–8); pedunculi mediocres vel longi, suberecti, praecipue acladio brevi, pilis aliis stellatis plus minusve numerosis, aliis glanduliferis numerosis brevibus obscuris, aliis simplicibus numerosis pallidibus nigris brevibus vel mediocribus obsiti. Involucri squamae 12–15 mm longae, circa 1 mm latae, ante anthesin porrectae ad apicem incurvatae, atriussculo-virides, interiores marginibus pallidioribus vel viridiusculae, anguste lineari-lanceolatae, subacutae vel acutae, pilis aliis stellatis sparsis, aliis glanduliferis numerosis brevissimis vel brevibus obscuris, aliis simplicibus numerosis obscuris vel basi nigris brevibus vel mediocribus vestitae. Ligulae saturate flavae, apice puberulae. Styli obscuri. Receptaculi alveoli breviter dentati. Cypselae obscurae, circa 4 mm longae.

Hieracium maculoides Sell & C. West, sp. nov.

H. maculosum (Stenstrom) Omang, *H. maculatum* Sm. et *H. glanduliceps* Sell & C. West quoad faciem simulat. Ab *H. maculoso* ambitu et dentibus foliorum et squamis longioribus differt; praeterea ab *H. maculato* et *H. glandulicipite* squamis capitulorum pilis simplicibus numerosis vestitis distinguitur.

Holotype: Scaurs above Dale Beck, Ingleborough, v.c. 64, M.W. Yorks, 7 July 1902, A. Ley (CGE).

Planta phyllopora. Caulis ad 35 cm altus, nonnunquam parte basali leviter purpureo, pilis aliis simplicibus paucis vel numerosis mediocribus vel longis pallidis, aliis stellatis dispersis vestitus; pili glanduliferi nulli. Folia pallide viridia, superne maculis magnis parvisque purpureo-brunneis ornata, inferne saepe purpureo-tincta; basalia plerumque pauca; primigena suborbicularia, mucronulata, subintegra, basi rotundata; cetera ovata, lanceolata, elliptica vel late elliptica, obtusa vel acuta, basi cuneata, denticulata vel dentata, dentibus saepe apiculatis; caulina 0–2 (–3), inferiora basalibus similia, superiora linearia vel bracteiformia; omnia utrinque et margine pilis simplicibus paucis vel numerosis pallidis

mediocribus vestita, petioli mediocres pilis simplicibus densis pallidis longis obsiti. Anthela anguste compacteque cymosa, capitulis 1–6; pedunculi mediocres vel longi, suberecti, pilis aliis stellatis densis, aliis simplicibus paucis vel numerosis pallidis nonnunquam basi nigris brevibus vel mediocribus, aliis glanduliferis paucioribus brevissimis vel brevibus obscuris obsiti. Involucri squamae 10–12 mm longae, circa 1 mm latae, ante anthesin incumbentes, atriusculo-virides, interiores marginibus pallidioribus, lineari-lanceolatae, subacutae vel acutae, pilis aliis stellatis dispersis, aliis simplicibus numerosis mediocribus vel longis pallidis basi nigris raro aliis glanduliferis paucis brevissimis obscuris vestitae. Ligulae flavae, apice puberulae. Styli obscuri. Receptaculi alveoli margine longe dentati. Cypselae obscurae, circa 4 mm longae.

Hieracium glanduliceps Sell & C. West, sp. nov.

Ab *H. maculato* Sm. foliis basi abrupte contractis vel subtruncatis et squamis involucri pilis glanduliferis inaequalibus differt, praeterea ab *H. maculoso* (Stenström) Omang et *H. maculoides* Sell & C. West facie simile praecipue foliis caulinis et squamis capitulorum pilis glanduliferis inaequalibus vestitis distinguitur.

Holotype: Keld Head Scaur, Ingleton, v.c. 64, M.W. Yorks, 2 July 1903, A Ley (CGE).

Planta phyllopoda. Caulis ad 40 cm altus, valde striatus, flexuosus, pilis aliis simplicibus numerosis mediocribus vel longis pallidis, aliis stellatis dispersis, aliis glanduliferis nullis. Folia obscure viridia, superne maculis magnis parvisque purpureis ornata, utrinque purpureo-tincta; basalia pauca vel numerosa; primigena subrotundata, mucronulata, basi rotunda; cetera ovata, ovato-lanceolata, vel raro oblonga, obtuse mucronulata vel acuta, denticulata vel dentata, dentibus unguiculato-mammiformibus vel mammiformibus, basi abrupte contracta vel subtruncata; caulina 1–3, infima basalibus similia petiolataque, superiora lanceolata vel linearia, acuta, dentata ut in foliis basalibus, sessilia; omnia superne glabra vel utrinque et margine pilis simplicibus paucis vel numerosis pallidis mediocribus vestita; petioli pilis simplicibus densis mediocribus vel longis pallidis obsiti. Anthela anguste cymosa, nonnunquam ramum longum ex axilla folii caulini superioris emittens; capitulis 1–8 (–10); pedunculi mediocres vel longi, suberecti, pilis aliis stellatis numerosis, aliis glanduliferis numerosis brevissimis obscuris, aliis simplicibus paucis vel numerosis brevibus obscuris vestiti. Involucri squamae 10–11 mm longae, circa 1 mm latae, ante anthesin incumbentes, atriusculo-virides, interiores marginibus pallidioribus, anguste lineari-lanceolatae, subacutae vel acutae, pilis aliis stellatis dispersis, aliis glanduliferis numerosis brevissimis brevibus et mediocribus obscuris, aliis simplicibus paucis mediocribus obscuris vestitae. Ligulae flavae, glabrae. Styli obscuri. Receptaculi alveoli margine breviter dentati. Cypselae obscurae, 3–3·5 mm longae.

In Sectione TRIDENTATA F. N. Williams

Hieracium sparsifrons Sell & C. West, nom. nov.

H. sparsifolium var. *oligodon* E. F. Linton ex W. R. Linton, *Brit. Hieracia*, 78 (1905).

H. oligodon (E. F. Linton ex W. R. Linton) Pugsl., *J. Ecol.* 33, 346 (1946), non Naeg. & Peter, *Hier. Mittel-Eur.* 2, 51 (1886).

Hieracium ornatilorum Sell & C. West, sp. nov.

Ab *H. eboracense* Pugsl. squamis involucri alio modo vestitis distinguitur.

Holotype: Great Scar Limestone, Grassington, v.c. 64, M.W. Yorks, 570 ft alt., 11 August 1909, J. Cryer (CGE).

Planta aphyllopoda. Caulis ad 110 cm altus, nonnunquam leviter purpureus, pilis aliis simplicibus sparsis brevibus mediocribus vel longis pallidis, aliis stellatis paucis vestitus. Folia ?obscure viridia; omnia caulina, 10–17, inferiora mediaque elliptica, obtusa vel subacuta, dentata, basi cuneata, plerumque sessilia, raro breviter petiolata; superiora ovata vel lanceolata, acuta, acute alteque dentata, basi rotundata, sessilia; omnia

utrinque glabra vel pilis simplicibus paucis pallidis mediocribus, margine pilis simplicibus subnumerosis pallidis mediocribus vestita. Anthela divaricate cymosa, capitulis 2–12; pedunculi mediocres vel raro longi, divaricati, pilis aliis stellatis densis, aliis simplicibus paucis brevibus vel mediocribus pallidis, raro aliis glanduliferis brevissimis obscuris obsiti. Involucri squamae 11–13 mm longae, circa 1·5 mm latae, ante anthesin incumbentes, atriusculo-virides, interiores marginibus pallidioribus, sublineares, obtusae, pilis aliis simplicibus paucis brevibus vel mediocribus obscuris, aliis glanduliferis paucioribus brevissimis vel brevibus obscuris vestitae. Ligulae ? saturate flavae, glabrae. Styli obscuri. Receptaculi alveoli margine ? breviter dentati. Cypselae obscurae, circa 3·5 mm longae.

In Sectione UMBELLATA F. N. Williams

HIERACIUM UMBELLATUM L., *Sp. Pl.*, 804 (1753).

subsp. **bichlorophyllum** (Druce & Zahn) Sell & C. West, comb. nov.

H. laevigatum subsp. *bichlorophyllum* Druce & Zahn, *Rep. Bot. Exch. Club Brit. Isl.* **9**, 561 (1932 for 1931).

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PILOSELLA Hill, *Brit. Herb.*, 441 (1756).

The reasons for recognizing *Pilosella* as a distinct genus will be given in a later paper.

PILOSELLA PELETERANA (Mérat) C. H. & F. W. Schultz

subsp. **PELETERANA**

Hieracium peleterianum Mérat, *Nouv. Fl. Env. Par.*, 305 (1812).

P. peleteriana (Mérat) C. H. & F. W. Schultz, *Flora (Regensb.)* **45**, 421 (1862).

subsp. **tenuiscapa** (Pugschl.) Sell & C. West, comb. et stat. nov.

Hieracium peleterianum var. *tenuiscapum* Pugschl., *J. Linn. Soc. (Bot.)* **54**, 313 (1948).

PILOSELLA OFFICINARUM C. H. & F. W. Schultz

subsp. **concinata** (F. J. Hanb.) Sell & C. West, comb. et stat. nov.

Hieracium pilosella var. *concinatum* F. J. Hanb., *Ill. Mon. Brit. Hier.*, 6 (1889).

subsp. **OFFICINARUM**

Hieracium pilosella L., *Sp. Pl.*, 800 (1753).

Hieracium repens S. F. Gray, *Nat. Arr. Brit. Pl.* **2**, 421 (1821) nom. superfl. illegit. pro

H. pilosella L., non *H. repens* Willd., *Sp. Pl.* **3** (3), 1564 (1803).

H. canum Vuk., *Hierac. Croatica*, 6 (1858), nom. superfl. illegit. pro *H. pilosella* L.

Pilosella officinarum C. H. & F. W. Schultz, *Flora (Regensb.)* **45**, 421 (1862), nom. nov. pro *Hieracium pilosella* L.

subsp. **nigrescens** (Fries) Sell & C. West, comb. nov.

H. pilosella var. *nigrescens* Fries, *Symb. Hist. Hierac.*, 2 (1848).

subsp. **tricholepia** (Naegeli & Peter) Sell & C. West, comb. nov.

H. pilosella subsp. *tricholepium* Naegeli & Peter, *Hierac. Mitt.-Eur.* **1**, 138 (1885).

subsp. **trichoscapa** (Naegeli & Peter) Sell & C. West, comb. nov.

H. pilosella subsp. *trichoscapum* Naegeli & Peter, *Hierac. Mitt.-Eur.* **1**, 133 (1885).

Pilosella flagellaris (Willd.) Sell & C. West, comb. nov.,

subsp. **flagellaris**

Hieracium flagellare Willd., *Enum. Pl. Hort. Berol. Suppl.*, 54 (1814, dated 1813).

Planta ad 35 cm alta, capitulis 2–4 (–7); pedunculi pilis simplicibus plus minusve numerosis ad 2 raro 3 mm longis obsiti; squamae involucris pilis simplicibus paucis vel subnumerosis ad 1·5 mm longis vestitae.

Naturalized in a few localities in great Britain, widespread in Continental Europe.

subsp. **bicapitata** Sell & C. West, subsp. nov.

Holotype: North-west of Hoove, Zetland, v.c. 112, 27 June 1963, W. Scott (CGE).

Planta ad 18 cm alta, saepe capitulis 2; pedunculi pilis simplicibus, numerosis ad 7·5 mm longis obsiti; squamae capitulorum pilis simplicibus densis ad 2·5 mm longis vestitae.

Known only from Zetland where it is apparently native. If native, the only taxon in the genus indigenous to the Islands.

Pilosella lactucella (Wallr.) Sell & C. West, comb. nov.

subsp. **lactucella**

Hieracium lactucella Wallr., *Sched. Crit.* **1**, 408 (1822).

subsp. **helveola** (Dahlst.) Sell & C. West, comb. nov.

H. floribundum subsp. *helveolum* Dahlst., *Hierac. Exsicc.* **4**, nos. 14 & 15 (1891); *Acta Hort. Berg.* **2** (4), 13 (1894).

Pilosella caespitosa (Dumort.) Sell & C. West, comb. nov.

Hieracium caespitosum Dumort., *Fl. Belg.*, 62 (1827).

Hieracium pratense Tausch., *Flora (Regensb.)* **11** Erg., 56 (1828).

subsp. **colliniformis** (Naegeli & Peter) Sell & C. West, comb. nov.

Hieracium collinum subsp. *colliniforme* Naegeli & Peter, *Hierac. Mitt.-Eur.* **1**, 308 (1885).

PILOSELLA AURANTIACA (L.) C. H. & F. W. Schultz

subsp. **AURANTIACA**

Hieracium aurantiacum L., *Sp. Pl.*, 801 (1753).

P. aurantiaca (L.) C. H. & F. W. Schultz, *Flora (Regensb.)* **45**, 426 (1862).

subsp. **brunneocrocea** (Pugs.) Sell & C. West, comb. et stat. nov.

Hieracium brunneocroceum Pugs., *J. Bot., Lond.* **59**, 67 (1921).

PILOSELLA PRAEALTA (Vill. ex Gochnat) C. H. & F. W. Schultz

subsp. **PRAEALTA**

Hieracium praealtum Vill. ex Gochnat, *Tent. Pl. Cich.*, 17 (1808).

P. praealta (Vill. ex Gochnat) C. H. & F. W. Schultz, *Flora (Regensb.)* **45**, 429 (1862).

subsp. **arvorum** (Naegeli & Peter) Sell & C. West, comb. nov.

Hieracium magyricum subsp. *arvorum* Naegeli & Peter, *Hierac. Mitt.-Eur.* **1**, 586 (1885).

subsp. **spraguei** (Pugs.) Sell & C. West, comb. et stat. nov.

Hieracium spraguei Pugs., *J. Linn. Soc. London (Bot.)* **54**, 328 (1948).

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POTAMOGETON BERCHTOLDII × NATANS = P. × VARIIFOLIUS Thore, *Essai Chlor. Dép. Landes*, 47 (1803) ('*varii-folius*') (pro sp.).

P. gramineus subsp. *variifolius* (Thore) Nyman, *Consp. Fl. Eur.*, 682 (1882).

P. natans × *trichoides* Hagstr., *K. Svenska Vetensk. Handl., N.F.* **55** (5), 193 (1916).

P. javanicus subsp. *variifolius* (Thore) P. Fourn., *Quatre Fl. Fr.*, 140 (1935).

This remarkable hybrid was first described (as a species) by Thore from Dép. Landes in south-west France; it occurs also in the adjoining Dép. Gironde. It was unknown from outside this area until a plant apparently identical with it in all respects was discovered in Ireland by D. McClintock in August 1957, in the Glenamoy River below Glenamoy Bridge, West Mayo (v.c. H 27) (BM). The same plant was again found in the Glenamoy River by A. C. Jermy on 18 July 1962 (BM), growing in company with *P. natans* in a side eddy away from the fast-flowing stream.

P. × variifolius has always been a botanical puzzle. Shortly after its original description De Candolle, in Lam. & DC., *Fl. Fr.* ed. 3, 3, 184 (1805), referred it to *P. fluitans*, as also did A. Bennett, *J. Bot., Lond.* 29, 75 (1891). Nyman (1882), however, treated it as a subspecies of *P. gramineus*, and it was placed in the synonymy of that species by K. Richter, *Pl. Eur.* 1, 13 (1890). Graebner, in his monograph of *Potamogeton* in Engler, *Pflanzenr.* 4 (11), 48 (1907), treated it as a '*Planta dubia*' apparently related to the tropical and subtropical *P. octandrus* (*P. javanicus*); and P. Fournier (1935), following this up, went so far as to recognize it formally as a subspecies of *P. javanicus*.

The idea that *P. × variifolius* is in any way closely allied to *P. octandrus* is quite fanciful. In fact, as Hagström (1916) pointed out, the plant is sterile and must be of hybrid origin. Such an origin had been suggested by Rouy, *Fl. Fr.* 13, 304 (1912), with *P. polygonifolius* and *P. gramineus* as putative parent species. Hagström, however, rejected this suggested parentage, stating that the leaf characters 'point in the direction of *P. natans* and some narrow-leaved species'. After discussing the plant further he decided that the narrow-leaved parent must be *P. trichoides* and he accordingly treated *P. × variifolius* as *P. natans × trichoides*.

We are in full agreement with Hagström that *P. × variifolius* must be a hybrid between *P. natans* and one of the narrow-leaved ('pusilloid') species. It has floating leaves which, though much smaller, resemble those of *P. natans* and often show an indication of the discoloured joint at the top of the petiole which is characteristic of that species, and it has numerous narrowly linear submerged leaves which resemble the phyllodes of *P. natans* though more delicate in texture and with a nervation suggesting the influence of one of the 'pusilloid' species. Surprising though such a combination of parents may be, we can think of no other explanation for the origin of *P. × variifolius*; but while in accord with Hagström on this point we have always had doubts about his choice of *P. trichoides* as the 'pusilloid' parent. *P. × variifolius*, like *P. natans*, has four-carpellate flowers, whereas in *P. trichoides* the number of carpels is normally reduced to one (rarely two or three). Hagström mentioned this point, but regarded it as an instance where '*P. natans* is prevailing over *P. trichoides*'. Our own investigations have shown, however, that in hybrids between *P. trichoides* and four-carpellate species the number of carpels is reduced to 1–3, as in *P. crispus × trichoides* (*P. × bennettii*) and *P. pusillus × trichoides* (*P. × grovesii*; see below), and if *P. × variifolius* were *P. natans × trichoides* we should expect a similar reduction.

The discovery of *P. × variifolius* in West Mayo confirms our doubts about the parentage *P. natans × trichoides*, for *P. trichoides* is not known from Ireland, and we have no reason to suppose that the hybrid has not arisen *in situ* in West Mayo where it occurs along with *P. natans*. We conclude, therefore, that the 'pusilloid' parent must be a species other than *P. trichoides*, and the only possibilities are *P. berchtoldii* and *P. obtusifolius*, both of which have four-carpellate flowers and open stipules as in *P. × variifolius*. We can see no sign of any influence of *P. obtusifolius* in the hybrid, but the venation of the submerged leaves strongly suggests *P. berchtoldii*, a common and widely distributed species which occurs in West Mayo. The formula *P. berchtoldii × natans* is therefore here proposed for *P. × variifolius*.

POTAMOGETON ALPINUS × LUCENS = *P. × NERVIGER* Wulfg. in J. A. & J. H. Schult., *Mant.* 3, 359 (1827) (pro sp.).

P. rufescens var. *nerviger* (Wulfg.) Nyman, *Consp. Fl. Eur.*, 681 (1882).

P. rufescens subsp. *nerviger* (Wulfg.) K. Richter, *Pl. Eur.* 1, 12 (1890).

P. alpinus subvar. *nerviger* (Wulfg.) Ascherson & Graebner, *Syn. Mitteleur. Fl.*, 1, 311 (1897).

P. alpinus × praelongus Hagstr., *K. Svenska Vetensk. Handl., N. F.* 55 (5), 149 (1916) pro parte, excl. pl. angl.

P. alpinus × heterophyllus Galenis, *Lietuvos TSR Fl.* 2, 63 (1963).

The hybrid *P. alpinus × lucens* is known in the British Isles only from the River Fergus in Clare (v.c. H 9), where it was discovered above Inchiquin Lough by J. G. Dony

on 3 August 1947 (BM) and re-collected by him on 30 July 1948 (BM); it was also collected above Poplar Bridge, Killinaboy, by G. Taylor on 31 August 1962 (BM).

P. × nerviger Wölg. was originally described (as a species) from Lithuania. During the last century it was variously treated as a variety, subspecies or subvariety of *P. alpinus* (*P. rufescens*), and its affinity with that species is obvious. In 1907 G. Fischer, *Ber. Bayer. Bot. Ges.* **11**, 46, suggested that it might be the hybrid *P. alpinus* × *lucens* though he could find no anatomical confirmation for this. Hagström (1916) made no comment on Fischer's suggestion but identified Wölg's Lithuanian plant with the British *P. × griffithii* under the formula *P. alpinus* × *praelongus*. As already explained in *J. Bot., Lond.* **77**, 280 (1939), we believe this formula to be correct for *P. × griffithii*, but not for *P. × nerviger*, which, following Fischer's suggestion, we accept as *P. alpinus* × *lucens*. Recently Galenis (1963) has treated *P. × nerviger* as a hybrid between *P. alpinus* and *P. gramineus* (*P. heterophyllus*), but we do not know the justification for this.

POTAMOGETON CRISPUS × PRAELONGUS = *P. × undulatus* Wölg. in J. A. & J. H. Schult., *Mant.* **3**, 360 (1827) (pro sp.). Dandy & Taylor, *Bot. Soc. & Exch. Club Brit. Is.* **12**, 425 (1942); *J. Bot., Lond.* **80**, 118 (1943).

P. crispus × *praelongus* Casp., *Schr. Phys.-ök. Ges. Königsberg* **18**, 98 (1877).

P. praelongus × *crispus* Ascherson & Graebner, *Syn. Mitteleur. Fl.* **1**, 338 (1897).

The hybrid *P. crispus* × *praelongus* was first recognized by Caspary (1877) from localities now in Poland. *P. × undulatus* Wölg., which had already been described (as a species) from Lithuania, was later identified correctly as the same hybrid. There are authentic records of it also from Germany and Denmark.

In the British Isles *P. × undulatus* was first found in 1906 in the River Lagan at Belfast, Antrim (v.c. H 39), where it was re-collected in September 1952 by G. Taylor (BM); it also occurs in the Six Mile Water at Antrim in the same vice-county. In addition to these Irish localities a Welsh station for the hybrid is now known. It was found in Llyn Hilyn, Radnor (v.c. 43), by J. A. Webb in 1938 (NMW), in company with *P. crispus* and *P. praelongus*; and it was collected there again by C. I. & N. Y. Sandwith in July 1945 (BM), along with *P. crispus* and *P. praelongus*.

Potamogeton pusillus × trichoides = *P. × grovesii* Dandy & Taylor, hybr. nov.; inter parentes manifeste media, *P. trichoidi* facie similior sed stipulis basin versus tubulosis differt; a *P. pusillo* floribus 1–3-carpellatis praecipue distinguitur.

Holotype: England, East Norfolk (v.c. 27), dike between Ingham and Palling, 11 August 1897, J. Groves (BM).

P. trinervius sensu Dandy, *List Brit. Vasc. Pl.* 134 (1958), non G. Fisch.

This apparently very rare hybrid is known to us only from a single locality between Ingham and Palling in East Norfolk (v.c. 27), where on 11 August 1897 James Groves made a voluminous gathering of 'pusilloid' pondweeds which he distributed extensively through the Botanical Exchange Club under the name *P. trichoides*, and which he recorded as *P. trichoides* in *Bot. Exch. Club Rep.* **1897**, 569 (1898). The gathering does indeed contain specimens of *P. trichoides*, but examination of many sheets of it shows that altogether it comprises three different plants: *P. trichoides*, *P. pusillus* and their hybrid *P. pusillus* × *trichoides*. Thus every sheet of this gathering requires careful scrutiny to decide which of the three taxa are represented. *P. pusillus* and *P. trichoides* by themselves are very easily distinguishable, differing in leaf nervation, stipules, winter-buds, flowers and fruit. The hybrid, being intermediate in its characters, is of course more difficult to distinguish: in general appearance it more closely resembles *P. trichoides*, but it differs from that species, which has open stipules, in having the stipules tubular towards the base as in *P. pusillus*; it differs from *P. pusillus*, which has four-carpellate flowers, in having the carpels reduced in number to 1–3 as in *P. trichoides*. The flower spikes in the hybrid are mostly quite abortive; occasionally a drupelet is developed, but it may not have been viable.

An identical hybrid was later collected (with *P. trichoides*) on 1 August 1900 by A. and J. Bennett and C. E. Salmon in the New Cut between Stalham and Palling (GL), this presumably being the same as Groves's original locality.

The name *P. trinervius* G. Fisch., *Ber. Bayer. Bot. Ges.* **11**, 29, 123 (1907), has been erroneously used for this hybrid. It was published by G. Fischer for Bavarian plants to which he attributed the parentage *P. panormitanus* $\times$ *trichoides*, i.e. *P. pusillus* $\times$ *trichoides*. He stated that there were two forms of the hybrid, one like *P. pusillus* (*P. panormitanus*) but more delicate, the other resembling *P. trichoides* but with the broader three-nerved leaves of *P. pusillus* (the leaves of *P. trichoides* are in fact three-nerved but only the midrib is readily discernible). By the courtesy of Professor H. Merxmüller we have been able to examine Fischer's original material, now at Munich (M), and we find that all his specimens of the first (slender) form are in fact *P. trichoides*, while all those of the second (three-nerved) form are *P. pusillus*; one gathering, from Gaustadter Weiher, July 1905, is a mixture of the two species (the supposed parents), but we can find no trace of a hybrid. A sheet of this mixed gathering from Gaustadter Weiher and one of *P. pusillus* from Godeldorfer Weiher are the only sheets actually labelled with the binomial *P. trinervius*, and as the epithet *trinervius* clearly refers to the form with obviously three-nerved leaves (i.e. *P. pusillus*) we choose the specimen on this latter sheet as lectotype; it was collected in Godeldorfer Weiher in July 1902 by G. Fischer, and labelled '*Potamogeton trinervius* Fischer = *P. panormitanus* $\times$ *trichoides*'. It appears that Hagström must have suggested the formula (though not the binomial) as there is a note 'dt. Hagström' at the bottom of the label. The name *P. trinervius* thus becomes a synonym of *P. pusillus*, and the hybrid *P. pusillus* $\times$ *trichoides* from East Norfolk is left without a binomial. We therefore name it after its discoverer, James Groves (1858–1933).

J. E. DANDY
G. TAYLOR

DACTYLORHIZA INCARNATA (L.) Soó

subsp. **gemmana** (Pugs.) Sell, comb. nov.

Orchis latifolia var. *gemmana* Pugs., *J. Linn. Soc. (Bot.)* **49**, 578 (1935).

subsp. **cruenta** (O. F. Muell.) Sell, comb. nov.

Orchis cruenta O. F. Muell., *Fl. Dan.* **5** (15), t. 876 (1782).

I agree with J. Heslop-Harrison (*Ber. Geobot. Forsch. Inst. Rübel* **1953**, 53–82 (1954)) and A. R. Clapham (Clapham, Tutin & E. F. Warburg, *Fl. Brit. Is.* ed. 2, 1044 (1962)) in considering the above taxa to be subspecies of *Dactylorchis incarnata* (L.) Vermeul. and now make the necessary transferences to the correct generic name *Dactylorhiza* Nevski.

P. D. SELL

CATAPODIUM RIGIDUM (L.) C. E. Hubbard

subsp. **majus** (C. Presl) Perring & Sell, comb. et stat. nov.

Sclerochloa rigida var. *major* C. Presl, *Fl. Sic.*, xlv (1826) (based on *Sclerochloa patens* C. Presl).

Sclerochloa patens C. Presl, *Cyp. Gram. Sic.*, 45 (1820).

Subsp. *majus* can be distinguished from subsp. *rigidum* by its taller habit, wider leaves and open pyramidal inflorescence. It occurs in the south and west of the British Isles, often near the sea, and abroad in south-west Europe and much of the Mediterranean region.

F. H. PERRING
P. D. SELL

CATABROSA AQUATICA (L.) Beauv.

subsp. **minor** (Bab.) Perring & Sell, stat. nov.

C. aquatica var. *uniflora* S. F. Gray, *Nat. Arr. Brit. Pl.* **2**, 133 (1821).

Watsonia **6** (5), 1967.

C. aquatica var. *littoralis* Parnell, *Brit. Grass.*, 228, t. 102 (1842).

C. aquatica var. *minor* Bab., *Man. Brit. Bot.*, 366 (1843) (Lectotype: Sand of the sea shore, Hoylake, 24 August 1804, T. Gisborne (CGE)).

Subsp. *minor* differs from subsp. *aquatica* in having shorter culms, leaves and panicles, and in the spikelets being only 1-flowered. It occurs in poor wet sandy soils near the sea at various places on the north and west coasts of Britain. No specimens have been seen from outside Britain.

F. H. PERRING

P. D. SELL

BOOK REVIEWS

Flora Europaea. Volume 1. Lycopodiaceae to Platanaceae. Edited by T. G. Tutin, V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters and D. A. Webb, with the assistance of P. W. Ball and A. O. Chater. Pp. xxxii+464 with 5 maps. Cambridge, University Press, 1964. Price £4 4s. 0d.

The publication of a European Flora was discussed for the first time in 1954 during the 8th International Botanical Congress in Paris. It is amazing that this British initiative materialized so quickly. This is no doubt due to the activities of the very energetic Executive Committee of which T. G. Tutin is president and V. H. Heywood secretary. The difficulties they have encountered during their gigantic undertaking must have been enormous. Not only did they have to find skilled collaborators, but they also had to strive for uniformity of treatment. Even before the first rough draft could be made, a number of conferences and progress reports proved to be necessary, which eventually culminated in the publication of a booklet entitled: *The presentation of taxonomic information: A short guide for contributors to Flora Europaea* (1958).

The all-British composition of the Editorial Committee and the Organizing Committee must have been advantageous, because a frequent and close contact between their members was possible which must have contributed substantially towards the early publication and the reasonable uniformity. It is true that the Committees are supported in their task by a number of 'advisory Editors' and that a considerable number of prominent botanists all over Europe act as Regional Advisers or supplied geographical data and technical information, but it remains an achievement of the first order just the same.

The *Flora Europaea* certainly meets a long-felt want in that improved methods of communication enable many European botanists to visit foreign countries more easily. There are of course many Floras, and some quite good ones among them, but several of these are not exactly up-to-date or are written in an alien tongue. Judged by contemporary standards, only very few Floras deal adequately with 'critical' groups, follow a sufficiently modern species concept and use a nomenclature which is not hopelessly out of date. The drawbacks are more particularly noticeable in Floras covering parts of S.E. Europe and the Mediterranean countries.

The new *Flora* is arranged roughly according to the Englerian system (as used in Engler & Diels, *Syllabus der Pflanzenfamilien*, 11th ed., 1936). In a general preliminary survey the various families of the Spermatophyta are classified in a number of orders, but this kind of arrangement was relinquished in the case of the Pteridophyta, presumably because there is but little unanimity concerning the taxonomic significance of the various hierarchic subdivisions proposed for this group. Twenty-one families of ferns are treated under the heading Filicopsida, without the distinction of, e.g., *Ophioglossales*, *Osmundales* and *Salvinales* although these orders at least are recognized by several leading pteridologists. Still, the subdivision of the ferns into such a large number of families, several of which are included in 'Polypodiaceae' even in some recent floras, will delight many a fern specialist.

Conceivably, the *Flora of the British Isles* by Clapham, Tutin & Warburg has served as a model for the set-up of this *Flora Europaea*. This is certainly no objection, because this flora is, in the reviewer's opinion, the best European one, with very clear dichotomous keys and pithy descriptions of the species. In the *Flora Europaea* also a morphological description of every species is given which, though concise, is to the point. Taxa below the rank of subspecies are wisely left out of consideration. Not only would this have made the Flora much too unwieldy, but at the present state of our knowledge this might easily have given rise to much disagreement. Moreover, the relative uniformity of treatment could not possibly have been attained, because the infraspecific categories of some forms have been much more extensively studied than those of other taxa. In a book with so many co-authors, fifty-one collaborators having contributed to this first volume alone, a consistent uniformity of treatment could not possibly have been achieved, some systematists being born 'splitters' and others tending towards 'lumping'. This does not only apply to the possible differences in the species concept, but also to their different ideas concerning generic delimitations which are sometimes rather broad and in other cases (and this seems to be the modern trend) are drawn much more narrowly. As an example, many botanists may find it difficult to become accustomed to the subdivision of the old 'established' genus *Lycopodium* into the four generic *Huperzia*, *Lepidotis*, *Lycopodium* (*sensu stricto*) and *Diphasium*. (Recently the genus *Lycopodiella* has been described, to which *L. inundatum* belongs.) Likewise, some workers may not feel too happy about the segregation of some species, formerly generally treated under *Sempervivum*, under the generic name *Jovibarba*. *Consolida* is considered as a separate genus apart from *Delphinium* but, on the contrary, *Batrachium* has not been separated from *Ranunculus*. On the whole the species concept is rather narrow. It may be a consolation to those who may not so willingly accept 'small' species that such a 'modern' classification has at least the advantage

of more readily becoming an incentive for new research. Most of the recent opinions are based on painstaking and specialized biotaxonomical studies, often including an experimental approach. Nevertheless one may wonder why sometimes the specific variability is so summarily treated, e.g. under *Capparis spinosa*, of which species is said 'incl. *C. rupestris*', and of which the var. *inermis* is briefly discussed. In the author's opinion, *Capparis rupestris*, though treated in several Floras as a distinct species, does not even qualify as a subspecies of *C. spinosa*; however, this remains a matter of personal opinion.

New taxa, new names and new combinations are described previous to their publication in the *Flora* in the form of a series of notes in *Fedde's Repertorium (Notulae Systematicae ad Floram Europaeam spectantes)*, of which the first appeared in 1961. As far as can be ascertained, so much attention has been paid to the nomenclatural details, that in most cases the names have truly been brought up to date. A notable exception is the name *Parietaria diffusa* Mert. & Koch which is now generally thought to be conspecific with the older *P. judaica* L. (the 'current' name of many floras is *P. ramiflora* Moench). Such an omission can of course gladly be forgiven. Apart from the phytophographical specific descriptions, the specific chromosome number, if available, is always indicated. We may expect that this information will have to be thoroughly revised after some decades when our knowledge will have considerably increased, not only because the hitherto unknown chromosome numbers of many plants will have become known, but also because the infraspecific variation of the chromosome number may prove to be more common than one is wont to admit at present. Cases of apogamy are not always mentioned. Among the ferns, apogamy is reported as occurring in *Pteris cretica*, but nothing is said about the reproduction of *Dryopteris borreii* which most probably also propagates as an obligate apomict. Ecological data are conspicuously scarce and only supplied if the information is valid throughout the European range of the taxon concerned (and apparently only if it can be given in a concise and unambiguous form). The practical result of this editorial policy is that in the majority of the cases ecological characteristics are entirely lacking. In this respect, too, there is much room for improvement in future editions. The distribution of every species within the geographical boundaries of Europe is always mentioned, the countries generally being indicated by standard abbreviations. In this respect the data of the *Flora* are sometimes incomplete and there are certain omissions (e.g. concerning species of *Asplenium*). It is to be regretted that the distribution outside the European continent is only given in exceptional cases. In their introduction the Editors state that the extra-European areas of distribution are only mentioned in those cases in which the European range of the taxon in question is small and forms only a fraction of the total area of distribution. It must be admitted that the information concerning the extra-European distribution of European taxa is not always reliable and that in several cases taxonomic problems are immediately involved such as the status of supposedly conspecific forms and of a number of (for instance American) reputed vicariads. However, in many cases the distributional area is sufficiently known and worth mentioning.

Apart from a list of basic and standard Floras, an extensive and very useful bibliography of the titles of books and periodicals cited in the text, and mainly referring to the original descriptions of the various taxa, is included. The glossary of technical terms will undoubtedly prove to be a good 'service' to 'continentals' and other alien botanists.

In conclusion, it may be said that one must admire the achievements of the Editorial Board. The *Flora* will be a source of information and of inspiration. The minor errors and omissions were perhaps unavoidable and do, in any event, not detract much from the outstanding merits of this book. The present volume is of an excellent typographical quality. It is a good thing that no expenses were spared, so that the book stands a good chance of surviving the excessive handling it is surely to be submitted to. There can be very little doubt that this *Flora* will be gratefully welcomed by many botanists, professionals and amateurs alike, and that they will start looking forward to the appearance of the next volume.

S. SEGAL

Principles of Angiosperm Taxonomy. P. H. Davis and V. H. Heywood. Pp. xx+556, with 42 figures in the text. Oliver & Boyd, Edinburgh. 1963. Reprinted with corrections and supplementary bibliography, 1965. Price (hard covers) £4. 15s., (paperback) £3. 15s.

The first thing that must be said about this book is that (as the cliché has it) it fills a long felt want. I remember clearly from my own student days feeling that, while it was (in principle at least) easy enough to learn about the *results* of the taxonomic activity of the last two centuries, it seemed to be nearly impossible to learn anything about the principles and methods by which these results had been achieved. Taxonomists, evidently, were born, not made.

The authors of *Principles of Angiosperm Taxonomy* are both practising taxonomists whose work is widely known and respected. Starting from a consideration of basic taxonomic ideas, they trace the development of plant taxonomy from Theophrastus to the present day, giving an admirable outline of the contribution of pre-Darwinian taxonomists, and of the influence of evolutionary ideas on taxonomy in

general, and the development of classificatory 'systems' in particular. They consider the taxonomic hierarchy and the units of plant classification as we have inherited them, and then return to examine the concept of characters, the construction and definition of taxonomic groups, and the evolutionary interpretation of comparative data. They give a brief and critical (but sympathetic) discussion of numerical taxonomy. Chapters 5-7 are devoted to consideration of the particular properties and problems of morphological, cytological and chemical characters respectively. Chapter 8 deals with field and herbarium techniques, including a short section on typification and nomenclature, and the following chapter contains a great deal of useful information and advice on the presentation of taxonomic results. The remaining five chapters—'Modification of the phenotype', 'Variation within populations', 'Populations and the environment', 'Evolution and the differentiation of species' and 'Hybridization and taxonomy'—are essentially 'biosystematics' or 'experimental taxonomy', and deal with the biological background of the taxonomic situations that may be encountered in the field or the herbarium. The short section of 'Conclusions' is worth repeated reading.

The authors take an essentially phenetic standpoint, and consider that 'In the Angiosperms classifications based on phylogeny are unattainable except for certain special cases and then mostly at or near species level.' I think this reflects the general consensus among present-day plant taxonomists. Indeed, I am not at all clear in just what sense *any* taxonomists have ever believed that their classifications were 'based on phylogeny'. This is a catchphrase one occasionally hears vehemently defended; do its users think out its implications to their conclusions? The authors' attitude to biosystematic evidence may be found more controversial, but here again I think we have been moving towards a consensus in the last decade or so, and that a majority of plant taxonomists will accept the authors' propositions that 'Taxonomic species represent different evolutionary situations. No assumptions about their breeding relationships are implicit in their definition, and it must not be assumed that sexual species comprise only interbreeding individuals, unless this can be demonstrated.'

A book about as large a subject as Angiosperm taxonomy is inevitably selective. I have found no serious omissions, and in general the examples are well chosen. The authors have delved widely and deep in the literature bearing on their subject, and their material is critically handled and well integrated. Other authors might well have arranged the book differently; it could be argued that a consideration of practical taxonomic units and the material of Chapters 8 and 9 would have been better placed after the biosystematic chapters. However, the logic of a book designed to be read and re-read is not necessarily the logic of an essay or a course of lectures, and the usefulness of the book is unaffected. I would recommend 'Davis & Heywood' unreservedly to students as a firmly based exposition of the ideas and practices of mainstream plant taxonomy in the 1960s. But obviously not all students will have the ability and willingness to tackle a long book which does not shirk the complexities or difficulties of a complex and difficult subject. There is still room for a much shorter, cheaper, tautly argued book covering some of the more essential ground of the present one.

The book is well produced; one wishes it were less highly priced, though the price is not exorbitant by present-day standards. The paperback edition is hardly robust enough for its weight, and the amount of use it is likely to get, and is still expensive.

Principles of Angiosperm Taxonomy will no doubt remain the standard work for a very long time to come. The authors have placed us greatly in their debt.

M. C. F. PROCTOR

Principles of Numerical Taxonomy. R. R. Sokal and P. H. A. Sneath. Pp. 359, with 39 figures in the text. W. H. Freeman & Co., Ltd., San Francisco and London. 1963. Price £3.

'The ideas on which numerical taxonomy rests go back to Adanson. . . . Numerical taxonomy aims to develop methods which are objective and repeatable both in the evaluation of taxonomic affinity and in the erection of taxa.' This book sets out to provide a theoretical basis for numerical taxonomy, to review what has so far been achieved, and to provide the newcomer with a detailed step-by-step description of the procedures employed. The authors have kept their treatment broad 'so as to be applicable to zoology, botany, microbiology, and palaeontology and other related sciences' and hope that it will invite practitioners in these sciences to look at their material in a new way. The chapters dealing with the numerical methods assume a knowledge of elementary statistical methods; the rest of the book demands little or no mathematical background of the reader.

The core of the book is an attempt to set up procedures for a maximum-attribute 'natural' taxonomy on the lines suggested by Gilmour and others. The necessary stages are (a) selection of the individuals or taxa to be classified (operational taxonomic units, or OTUs), (b) selection of characters and evaluation of character-states for all the OTUs, (c) estimation of the taxonomic resemblance between all possible pairs of OTUs, and (d) construction of a taxonomic system from the information so obtained. There remain problems of identification and nomenclature, and of course the evidence may be used for other purposes such as the study of phylogenetic problems.

The authors give a lucid discussion of the character concept, including the problems of dealing with various kinds of multi-state characters, of recognizing homology, and those posed by allometric growth (which impinge on the general problem of reducing complex shapes to minimal sets of independent parameters; an important desideratum of numerical taxonomy which merits consideration at greater length). They emphasize that a reasonably large number of characters (say 50–100) must be used if the results are to be repeatable—and that even 100 characters will be only a small sample of the genotype. They review a large number of possible measures of taxonomic similarity, most of which have at one time or another been used for either ecological or taxonomic data. They conclude that the most useful are the simple matching coefficient (proportion of characters showing the same character-state for two OTUs), or correlation coefficients or Euclidian distances between OTUs after standardization of characters.

The relationships between the OTUs are then examined by attractively simple cluster-analysis methods. Sneath's single-linkage method is the simplest; OTUs are combined into clusters in descending order of their similarities with one another. In the average-linkage methods of Sokal and Michener, once the initial clusters are formed a measure of the similarity of the whole clusters to one another (and to unclustered OTUs) is used. In the successive re-computations of these measures of similarity, clusters may receive the same weight as individual OTUs, or they may be weighted proportionately to the number of OTUs they contain. Single-linkage will tend to give less clear cut answers than the average-linkage methods (but it may perhaps provide a more appropriate model of particular taxonomic situations). The results are presented as 'dendrograms'—hierarchical schemes with the OTUs ranged along one axis and the levels of similarity (or taxonomic distance) at which these join into clusters along the other.

'Numerical taxonomy' can be applied not only to the ordinary purposes of taxonomy, but also to various other problems involving similarity between organisms. As the authors suggest, it could be used to examine environmental effects on a particular species, or to study phylogenetic problems, a subject to which they devote a thoughtful and stimulating chapter.

The book concludes with a discussion of nomenclatural problems, a review of applications of numerical taxonomy up to 1962, a discussion of some objections to numerical taxonomy, a very brief consideration of the extraction of discriminatory features and the preparation of keys, and some speculation on the future of systematics. An appendix sets out computational methods for the procedures discussed in the book.

The problem of homology has obviously given the authors much difficulty, and one feels that considerable philosophical difficulties remain. Logically, it would be possible to reconstruct the organism completely from the full set of unit character states; for taxonomic purposes, we are replacing the organism by a model susceptible to our particular scheme of analysis. But the model may be constructed in different ways. The 'bits' specify the character-states, not the characters, and there seems to be no way of knowing whether we are constructing our models of different organisms in ways which are essentially equivalent for our purpose.

The basic problems of correlations and discontinuity are only briefly and incidentally discussed. Characters may be correlated because they are linked to the same developmental process, because they are affected by the same environmental factor, or because they reflect different genes which tend to be associated together within or between populations. Redundancy of the first two kinds should, as far as possible, be eliminated from taxonomic data; redundancy of the third kind is fundamental to the idea of 'natural' classification. So too is the idea of discontinuity, and it is surely more important that (say) species-limits should follow natural discontinuities than that they should fall at a particular phenon level.

In a subject developing as fast as numerical taxonomy, technical criticism can easily be unfair. Many people will probably find Williams & Dale's (1965) discussion of a theoretical basis for numerical taxonomy more stimulating and intellectually satisfying than Sokal & Sneath's; those authors had the advantage of reading the present book in proof. Others may be encouraged by the fact that the present authors often seem more concerned with empirical considerations than with mathematical niceties. The very powerful R-methods are scarcely considered; the authors do not pursue R-type factor or component analyses to the point of considering the distribution of OTUs in the common-factor or component space. The methods were freely available before this book was written. The Q-methods of Sokal & Sneath are appropriate for assessing levels of similarity between large numbers of diverse OTUs showing many independent directions of variation; they provide no information on discrimination. R-type principal component analysis and allied methods are appropriate where the OTUs are likely to fall into a relatively small number of rather discrete clusters, and where it is of interest to preserve something of the structure of the relationships as well as their magnitude; these methods provide information for discrimination of the clusters, but may lose information unrelated to the major directions of variation between the clusters. Discriminant analysis should surely receive more than a passing mention. The authors criticize the choice of title of *The New Systematics*, so they may be fairly criticized for their scanty treatment of the numerical methods most appropriate at specific and infraspecific levels in a book with the all-embracing title of their own!

This would have been a far better book if it had included many more concrete examples of the application of numerical methods to actual taxonomic situations, and much less criticism of what the authors hold out as the practices of 'conventional taxonomy'. Their criticism largely reflects one of those arguments which (like much political and religious controversy) have more to do with emotionally loaded labels than with reality, and it clouds more important issues. I suspect that a coolly rational appraisal would show rather little difference between the real working beliefs of many 'conventional' taxonomists and those of the authors. The main effect of phylogenetic ideas has probably been to encourage 'natural' (i.e. phenetic) as against artificial classification. So far as weighting is concerned, it seems to me that, in their quite proper anxiety to avoid appearing to condone any form of *a priori* weighting, the authors lay altogether too little stress on the fact that a *posteriori* weighting is an essential goal of taxonomic activity.

There is too ready a generalization from the fact that the present numerical methods give acceptable results in a few selected instances to the implied proposition that all biological taxonomy could be replaced by essentially similar methods. This book by-passes the really difficult problems that beset the plant taxonomist; adequate sampling of widely ranging taxa, plasticity, and the problem of extracting enough characters to describe the plant adequately without excessive and obvious redundancy. A group of students left to their own devices with numerical methods may well (as we have found in practice) produce a classification which faithfully reflects superficial resemblance, with an emphasis on size. Numerical taxonomy does not guarantee good taxonomy. There is little doubt that (for different reasons) insects with complete metamorphosis, or micro-organisms, or even inanimate objects provide easier material for numerical taxonomy than most plants.

These, to my mind, are serious flaws in an otherwise praiseworthy pioneering effort. I fear readers may too easily be provoked to one of two reactions—that numerical taxonomy as it is expounded here has all the answers, or that numerical methods are valueless. In my view both are dangerously wrong. Numerical taxonomy is not in a position to supplant 'conventional' taxonomy (the authors would not claim that it is), but it can contribute much to taxonomy in theoretical insights and in working tools. In appropriate circumstances numerical methods can save time and effort, and the authors are justified in their hope that numerical taxonomy can help us 'to arrive at judgments of affinity . . . without the time and controversy which seem necessary at present for the maturation of taxonomic judgments'. The taxonomist's time is expensive as well as the computer's!

No doubt, with characteristic resilience, taxonomy will absorb into everyday use those parts of numerical taxonomy which are found to be of general value—as in the past it has absorbed and been enriched by the ideas of Darwinism or the 'New Systematics'.

To sum up, here is a book about which one has reservations, but which is nevertheless required reading, and will inevitably stand as something of a classic. One greatly hopes for a second edition in which the reservations can be dispelled.

REFERENCE

- WILLIAMS, W. T. & DALE, M. B. (1965). Fundamental problems in numerical taxonomy. *Adv. Bot. Res.* **2**, 35–68.

M. C. F. PROCTOR

Phenetic and Phylogenetic Classification. Systematics Association Publication No. 6. Edited by V. H. Heywood and J. McNeill. Pp. xi + 164. The Systematics Association, London. 1964. Price 15s.

Phenetic and Phylogenetic Classification is a report of the symposium held by the Systematics Association under this title in Liverpool in April 1964. It includes the text of the papers presented, together with extracts from the discussions which concluded the sessions. The contributors, well chosen, of very varied backgrounds and views, include some distinguished names. A controversial subject, the exigencies of time and space, and an obvious atmosphere of enthusiasm probably all contributed to the clarity and directness with which authors have presented their views. Every taxonomist will find plenty here to disagree with or argue about; this book would make an excellent basis for a series of discussions or seminars in a university taxonomy course.

More or less 'conventional' views are put forward by Burtt and Blackwelder. Burtt produces some provocative examples of classificatory problems in flowering plants; are *Astragalus* and *Oxytropis*, separated by a single character, 'good' genera? Blackwelder talks some robust common sense about taxonomic principles and methods; I particularly liked his list of 'acceptances'. Delevoryas is avowedly phylogenetic in his approach, and discusses the influence of palaeobotanical evidence on classifications of vascular plants. Introducing the session on numerical taxonomy, Sneath outlines succinctly the basic steps in his own numerical approach. Boyce presents a useful comparison of the results of a (Q) principal component

analysis and cluster analyses of data from recent and fossil primate skulls. Edwards & Cavalli-Sforza discuss taxonomic aims, and go on to give a very interesting account of the interpretation of modern taxonomic evidence (on blood groups) in terms of a minimal phylogenetic model. Silvestri & Hill give a valuable discussion of basic general problems (ranging from the taxonomy of DNA chains to that of higher plants and animals); in considering the weighting of characters they outline briefly some conceptually interesting numerical techniques. Kendrick proposes a solution to a tiresome scoring problem. Meeuse, in his critique of numerical taxonomy, rightly emphasizes practical considerations; but these could be pursued further, and one is left feeling that the basic questions remain unanswered. Olson includes some assertions which will provide ready material for argument, and some valuable results from a study of character correlation groups in certain fossil vertebrate skulls, whose taxonomic implications will repay careful thought. The discussions are thoroughly worth reading, and have an immediacy and cogency often lacking in reports of this kind.

The editors are to be congratulated on a well- (and promptly-) produced book.

M. C. F. PROCTOR

Botany: A Laboratory Manual. T. E. Weier, C. R. Stocking and J. M. Tucker. Ed. 3. Pp. viii+165. John Wiley & Sons Ltd., New York and London. 1964. Price £1 3s. 0d.

This book is designed for use in colleges in the United States. It is probable that it is satisfactory there where botany is taught rather differently. One wonders, however, why the publishers have bothered to bring it to the United Kingdom where teaching methods and ideas are such that most teachers will not readily find a use for it. Much of the material is of about 'A' level standard; a few exercises might be used in first-year university courses. Some of the illustrations are of a reasonable standard; others would be considered inadequate at any level. Fig. 14.3 (p. 39) 'Leaf morphology' is particularly poor. Here, leaf venation is illustrated by drawings of three leaves all of which are unnecessarily small—so small that the one intended to show parallel venation has completely indistinct veins. On page 119 appears: '*Diagram the life cycle of . . . as directed by the instructor.*' This sums up the whole book. With a competent instructor it is unnecessary.

J. TIMSON

The Arlington Practical Botany. Book I. Plant Anatomy. Mary-Anne Burns. Pp. 93, 8½ × 11 in. 230 drawings. Arlington Books, London. 1964. Price 15s. 0d.

This book which is the first of a projected series of six is intended for students studying for 'A' level G.C.E. It is a laboratory guide and should also be useful for revision before examinations. It serves its purpose well and can be recommended for use in schools. It might also be of interest to amateur botanists who would like some knowledge of the internal structure of plants. The drawings are the main feature of the book and of quite a high standard although it is a pity that the 'two groups of chromosomes' on p. 9 are not more clearly drawn as there is always a tendency for students to draw these structures badly. The two drawings of leaf structure on p. 71 would have been much improved by being on a larger scale. It is unfortunate that the Latin names of plants are not in italics and that in discussing the various theories of shoot apex structure no dates are given with the authors' names. These are, however, relatively minor criticisms which could easily be avoided in any future edition and in the other volumes of this series. If these volumes maintain the standard of Book I, the series will be a valuable addition to the books available for students at this level.

J. TIMSON

Flowers of the Mediterranean. By Oleg Polunin and Anthony Huxley. Pp. xii+257 with 32 plates in colour. Chatto & Windus Ltd., London. 1965. Price £2 2s. 0d.

There can be no doubt of the need for a good popular guide to the flora of the Mediterranean for the use of British tourists, and this is the public for which this book is intended. It provides pictures and descriptions to help them to identify some of the more conspicuous plants they find, and it should also assist them to take a real interest in the flora. The introductory chapter on the vegetation of the Mediterranean, though far too short, is just what the intelligent visitor needs, and the notes about uses, history, biblical and literary references, etc. added to the descriptions, and especially those on plants of economic importance, provide one of the most valuable features of the book.

The descriptions cover over 700 species in 193 pages. The wording is appropriate for the reader for whom it is intended, but there is little attempt to emphasize diagnostic characters of special importance, and it is unlikely that users will wade through all the characters to enable them to distinguish the plants described from the hundreds of others which find no place in the book.

Over 300 species are illustrated in colour with some of the best reproductions of flower transparencies which have yet appeared. Many of these are exceedingly beautiful and they include pictures which cannot be praised too highly. They show the plants growing in their natural habitat, and to people who already know them they will bring back many happy memories, but as a guide to identification they are far inferior to a good series of drawings in colour. The drawback to colour transparencies, as every experienced lecturer knows, is that several are needed to illustrate each species. A good picture of the flower will seldom show fruit; separate pictures have to be taken to show flower, fruit, leaves, habit, and various details and to reproduce all these would be too expensive. The identification of some of the colour pictures in *Flowers of the Mediterranean* (the Genistas for example) would defeat even the most experienced botanist.

A further 127 species are illustrated on 28 pages of line drawings, and there are also sketches of fruits and other details in the text. These are by Mrs. Barbara Everard and are outstanding for their accuracy and success in conveying a true impression of the plants depicted.

In attempting to include a representative selection of the common conspicuous plants to be found in all parts of the Mediterranean coast the authors have set themselves an impossible task. They have tried to solve it by exercising a strong bias towards flowers found in Greece and the Aegean, Turkey, Lebanon and Palestine, and adding some species found only elsewhere. The book is likely to prove a very much more useful guide for the relatively small number of tourists visiting the eastern part of the region, than for the vast numbers taking the cheaper holidays in Spain, France, Corsica, Sardinia, Italy and Yugoslavia. These will find many abundant conspicuous flowers not mentioned in the book at all. To give reasonable coverage for the ambitious title at least three books of this size are needed, and these should be on a regional basis so that the tourist needs to carry only one at a time. It is to be hoped that Messrs. Polunin and Huxley will follow this up with similar works for parts of the western Mediterranean, but in the meanwhile they have earned our gratitude by providing this inexpensive and well illustrated book which is a joy to own.

J. E. LOUSLEY

Illustrations to the Flora of Delhi. J. K. Maheshwari. Pp. xx+282, with 278 line-drawings. Council of Scientific and Industrial Research, New Delhi. 1966. Price Rs. 28.00 (£2 16s. 0d.; \$8).

Of the 942 species described in the *Flora of Delhi*, by the same author, which was published in 1963, only 278 are illustrated in the present work. However, when one considers that 411 of the species in the *Flora* are cultivated, and that the illustrations are all of indigenous or naturalized species, it is seen that the ratio is not as one-sided as it at first appears. The figures are set out one species to a page, and each is cross-referenced to the main work. A scale is provided for each figure, and in many cases floral dissections and/or enlargements are also displayed. The family to which each species belongs is indicated at the top of the page, and the number of each figure corresponds to the page number.

The illustrations are, on the whole, quite clear and sufficiently diagnostic to enable identifications to be made, although they do vary in quality to a certain extent; not only this, but they also vary somewhat in style which is rather singular since in his preface the author clearly states that the drawings are the work of but one artist, Shri D. M. Sonak. It is, for example, not easy to imagine that the carefully delineated and well-proportioned figure of *Vicoa vestita* on p. 102 proceeded from the same pen as the rather slapdash figure of *Gomphrena celosioides* which appears on p. 179.

Several plants well known to British botanists appear in this work, so that even in the first twenty pages we come upon such familiar species as *Ranunculus sceleratus*, *Coronopus didymus*, *Sisymbrium irio*, *Stellaria media*, *Arenaria serpyllifolia* and *Spergula arvensis*. It thus appears that any botanist from these shores visiting the Delhi area for the first time would have quite a good nucleus to work from as a basis for getting to know the local flora.

In his introduction the author enumerates some nomenclatural changes which have taken place since the publication of the *Flora*, and he also lists thirty-seven additional species recorded from Delhi State in the intervening three years—which would suggest that a certain amount of work remains to be done on the plants from the environs of India's capital.

Although somewhat limited in scope, this set of illustrations may be said to constitute a useful supplement to the *Flora*, and a worthwhile contribution to the steadily-growing volume of literature on the plants of the Indian subcontinent as a whole.

A. R. SMITH

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THE *BROMUS MOLLIS* AGGREGATE IN BRITAIN

By PHILIP SMITH

Department of Botany, University of Edinburgh

ABSTRACT

Experimental studies on taxa within the *Bromus mollis* aggregate (sensu Tutin) have revealed that plants referable to *B. thominii* sensu Tutin are hybrid derivatives of crosses between *B. mollis* L. and *B. lepidus* Holmberg. The name *B. × pseudothominii* Philip Smith (hybr. nov.) is given to this material. It is demonstrated that the selection pressures favouring the persistence of these hybrid forms are associated with their success in contaminating sown pasture grass seed. The name *B. thominii* Hardouin should be applied to a dune species which is shown to be genetically and serologically distinct from inland forms of *B. thominii* sensu Tutin. It is proposed to include the dune material, together with *B. mollis* sensu stricto and *B. ferronii* Mabilie, in a single species for which the correct name is *B. hordeaceus* L. Subspecific rank is given to these component taxa of *B. hordeaceus*, which therefore become: *B. hordeaceus* subsp. *hordeaceus* (syn. *B. mollis* L.); *B. hordeaceus* subsp. *thominii* (Hardouin) Hylander; and *B. hordeaceus* subsp. *ferronii* (Mabilie) Philip Smith.

INTRODUCTION

Tutin (1962) includes *Bromus mollis* L., *B. thominii* Hardouin and *B. ferronii* Mabilie in his conception of the *B. mollis* aggregate. These plants are closely similar morphologically, and seem to have strong affinities with at least three other taxa, namely *B. molliformis* Lloyd, *B. interruptus* (Hackel) Druce and *B. lepidus* Holmberg. Variation in the field in the *B. mollis* agg. is frequently puzzling since all variants of *B. mollis* and '*B. thominii*' often grow together in the same sward, and their taxonomic separation is sometimes apparently arbitrary. Though several features are used to distinguish them (Tutin 1962), in practice the variation in lemma and spikelet sizes is the only character which can be used to discriminate between the two taxa. Both *B. mollis* and '*B. thominii*' are ruderal plants of inland areas, sometimes found in maritime habitats, but *B. ferronii* is a cliff-top plant of very restricted distribution. It is known only from a few localities in the south and west of Britain, and western France. *B. mollis* and '*B. thominii*' appear to be widely distributed in Europe and western Asia and are introduced in most other parts of the world, often becoming well established.

An enquiry into the treatment of these taxa by different authors reveals a wide variety of opinions as to their taxonomic rank and nomenclature. Difficulties also arise because the application of two Linnaean names, *B. mollis* and *B. hordeaceus*, is uncertain. Discussion of Linnaeus' interpretation in the literature (e.g. Munro 1861; Hackel 1884; Holmberg 1924) has further confused the position.

My investigations into these problems, as part of a large-scale experimental treatment of the genus *Bromus*, were begun in 1961, and the present account relates to my first results bearing on the *B. mollis* aggregate. Experimental work with *B. interruptus* is not yet complete, and the relationship of this curious species to the rest of the British bromes will be discussed in a subsequent paper. The results of my work require some nomenclatural changes which are presented first so that the correct names can be used through the rest of the paper.

FORMAL TAXONOMY OF THE MATERIAL

Nomenclature and synonymy

Results of examining the bromes of the Linnaean herbarium in London (LINN) (Smith 1965) indicate that while the modern conception of the species *B. mollis* L. (e.g. in Hubbard 1954, and Tutin 1962) is correct, it is not certain what Linnaeus meant by his name *B. hordeaceus* (*Species Plantarum* ed. 1, 1753). Munro (1861), Hackel (1884) and Holmberg

(1924) have each provided partial explanations of Linnaeus' meaning, which are unfortunately based on mutual misunderstandings and are incorrect. By comparing the Linnaean treatments of *Bromus* in the *Flora Suecica* ed. 1 (1745), *Species Plantarum* eds. 1 and 2 (1753 and 1762) and *Flora Suecica* ed. 2 (1755), one can trace a sequence of change in Linnaeus' ideas about these plants (Smith 1965). Comparison with the Linnaean herbarium provides further information.

Linnaeus' criteria for distinguishing species of *Bromus* are restricted to laxness of panicle, gross spikelet shape, spikelet indumentum and whether the awns are straight or reflexed. Using them he had no difficulty in distinguishing a lax-panicled plant which he named *B. secalinus* from a plant with an erect, dense panicle which he named *B. hordeaceus* L. (*Flora Suecica* ed. 1, 1745). This treatment is repeated in the first edition of the *Species Plantarum* (1753), which is the earliest place of valid publication. In *Flora Suecica* ed. 2 (1755) Linnaeus transferred *B. hordeaceus* to the status of variety β of *B. secalinus*, retaining the epithet 'hordeaceus'. (A printer's error makes it appear as β ; since *B. secalinus* already had one variety, it should correctly have been var. γ .) Linnaeus explains this change: '*Bromus hordeaceus in hortis satus transit in Bromum secalinum, cujus varietas est, ex solo arido et duro pygmaeus.*' Clearly cultivation of a depauperate accession of *B. hordeaceus* L. in the richer soil of a garden had produced a specimen approaching the vigour of *B. secalinus*.

A further evolution of Linnaeus' treatment of these bromes is marked in *Species Plantarum* ed. 2 (1762) which is the last evidence we have of Linnaeus' intentions. 'Var. β hordeaceus' still appears under *Bromus secalinus*, and there is a new entry—*B. mollis*. From the Linnaean phrase name: '*Bromus panicula erectiuscula, spicis ovatis aristis rectis, foliis mollissime villosis*' it is highly likely that the plant referred to is a soft brome, at present called *B. mollis* L. His description is expanded by a footnote: '*Similis B. secalino sed albido-pubescens. Genicula crassiora, cylindrica, subtus inprimis valde hirsuta. Folia utrinque mollis sima vaginis striatis. Panicula brevius pedicellata.*'

Of the six sheets of *Bromus* in the Linnaean herbarium referable to the *B. mollis* agg. sensu Tutin (Smith 1965), sheet 93.5 bears two specimens labelled *B. mollis* by Linnaeus (fide Spencer Savage in the Linnean Society's *Catalogue of the Linnaean Herbarium*). Sheet 93.7 bears a depauperate tussock of a soft brome which though totally unlike *B. secalinus* has been so labelled by Linnaeus. This plant has been named '*B. nanus*' by Weigel.

Together with evidence from his published accounts these specimens indicate that both *B. mollis* L. and *B. hordeaceus* L. applied to a plant within the *B. mollis* agg. sensu Tutin. Linnaeus transferred *B. hordeaceus* to varietal rank beneath *B. secalinus* after cultivation of a specimen resembling that on sheet 93.7. It is possible that this plant was his original collection. This explanation is supported by all the alterations of synonymy throughout the four Linnaean works cited (Smith 1965).

If *B. hordeaceus* L. and *B. mollis* L. are conspecific, the former is the earlier and thus the correct name of the species.

The genotypically depauperate material from dunes described later in this paper appears to be correctly named *B. thominii* Hardouin, judging from material collected and named by Hardouin in the herbaria at Kew (K) and Paris (P). Some of this material is illustrated in Plate 14a. *B. thominii* Hardouin replaced the earlier homonym *B. arenarius* Thomine-Desmazures (1824) non Labillardière (1804). No type of either *B. thominii* or *B. arenarius* Thomine-Desmazures was cited in the original descriptions. Thomine's herbarium material seems to have been lost. His figure (Thomine-Desmazures 1824) plainly indicates material similar to Hardouin's *B. thominii*. Wendelbo (1956) indicated that he thought *B. thominii* sensu Tutin (Tutin 1962) differed from French material collected and named by Hardouin.

The depauperacy of Linnaeus' *B. hordeaceus* has been used by many taxonomists as an indication that the name should apply to small plants like *B. thominii* Hardouin, and not to *B. mollis* L. If the depauperacy was only phenotypic and resulted from growth in hard, dry soils as Linnaeus reported (*Flora Suecica* ed. 2, 1755), then genetically dwarfed

material should not be included in *B. hordeaceus* L., if it is regarded as specifically distinct from more robust specimens (i.e. *B. mollis* L.). The evidence in this paper that plants from sand dunes are genetically depauperate is reinforced by the work of Holmberg (1924), Nilsson (1931, 1937) and Wilson (1956). The two earlier workers regarded this material as specifically distinct and mistakenly named it *B. hordeaceus* L. The evidence above requires that, if such distinct status is accorded to these plants, then the name must be *B. thominii* Hardouin.

Weigel published the name *B. nanus* in 1772 (*Observationes Botanicae*) and refers Linnaeus' sheet 93.7 (LINN) to it. Weigel's conception of this species probably included depauperate material of a number of related species. Sheet 93.7 material probably grew in an exposed place, in black, well-drained soil. It has rather short lemmas and short, weakly divaricate awns, and would be referred to *B. hordeaceus* subsp. *thominii* in the key given below.

As explained above, if all these bromes are included in one species, then the name *B. hordeaceus* has priority over *B. mollis*. In view of the differences between the taxa, discussed in the rest of the paper, I believe that *B. mollis* L. (as in Hubbard 1954, and Tutin 1962), *B. thominii* Hardouin non sensu Tutin, and *B. ferronii* Mabilie are best regarded as subspecies of a single species. Hylander (1945) has also concluded that the dwarfed form from dunes should be regarded as a subspecies in this group, basing his conclusion on Nilsson's (1931, 1937) genetic work, which is discussed below. He has already made the necessary combination: *B. hordeaceus* L. subsp. *thominii* (Hardouin) Hylander.

My conclusions from the evidence presented below are that *B. lepidus* is a distinct species, and that *B. thominii* sensu Tutin is a collection of hybrid derivatives (nothomorphs) which are, however, so common that a suitable binomial is needed for reference. The name *B. × pseudothominii* Philip Smith is therefore proposed. Clearly it is very difficult to describe the limits of what is by definition a segregating hybrid complex. Some variants of *B. × pseudothominii* are very close to pure *B. lepidus*, others resemble pure *B. hordeaceus* subsp. *hordeaceus*. The evidence of the artificial hybridizations reported in this paper, and of field collections, indicate that the commonest variants resemble *B. hordeaceus* more closely than they do *B. lepidus*. The key is written with this fact in mind. In most bromes there is variation in the development of spikelet indumentum from pubescence to glabrosity and this is acknowledged by the recognition of taxonomic forms and varieties based on the indumentum variation alone. It is an equivocal point as to whether the hairy spikelet form of the typically glabrous *B. lepidus* is a genuine expression of intraspecific variation, or whether it may result from a flow of genes for hairiness from *B. hordeaceus*. The same problem exists for glabrous spikelet varieties of *B. hordeaceus*. It is not possible to know whether the types of these varieties are pure intraspecific variants or the products of introgressive hybridization and therefore synonyms of *B. × pseudothominii*. It is likely that such varieties contain genetic material from both sources and therefore it seems wiser to regard them as only *pro parte* synonyms of *B. × pseudothominii*.

The correct nomenclature of the material considered in this paper, together with a selected synonymy, is listed below.

B. HORDEACEUS L., *Sp. Pl.*, 77 (1753).

subsp. *HORDEACEUS*

B. mollis L., *Sp. Pl.* ed. 2, 112 (1762).

subsp. *THOMINII* (Hardouin) Hylander, *Upps. Univ. Årsskr*, 1, (7) 84 (1945).

?*B. nanus* Weigel, *Obs. Botan.* 8 (1772).

B. arenarius Thomine-Desmazures, *Mém. Soc. Linn. Calvados* 1824, 40 (1824) non Labill., *Nov. Holl. Pfl.* 1, 23 (1804).

B. thominii Hardouin, *Congrès Sc. Fr.* 1, 56 (1833) non sensu Tutin in Clapham et al., *Flora of the British Isles*, ed. 2, 1152 (1962).

subsp. **ferronii** (Mabille) Philip Smith, **comb nov.**

B. ferronii Mabille, *Act. Soc. Linn. Bord.*, **25**, 612 (1864).

B. LEPIDUS Holmberg, *Bot. Notiser*, **1924**, 326 (1924).

B. gracilis Krösche, *Feddes Rep.* **19**, 329 (1924) non Leysser, *Fl. Hal.* 16 (1761).

B. britannicus I. A. Williams, *J. Bot. Lond.*, **67**, 65 (1929).

Bromus × **pseudothominii** Philip Smith, **hybr. nov.**

B. mollis L. var. *leiostachys* Hartman, *Handb. Skand. Fl.* ed. 2, 33 (1832) pro parte.

B. gracilis Krösche, var. *micromollis* Krösche, *Feddes Rep.* **19**, 329 (1924) pro parte.

B. lepidus Holmberg, f. *lasiolepis* Holmberg, *Bot. Notiser* **1924**, 326 (1924) pro parte.

B. thominii sensu Tutin in Clapham *et al.*, *Flora of the British Isles* ed. 2, 1152 (1962) non Hardouin, *Congrès Sc. Fr.*, **1**, 56 (1833).

Annum vel bienne. Culmi graciles, erecti, 20–70 cm alti, vaginis foliisque pubescentibus. Panicula laxa vel contracta, erecta, 1–10 cm longa. Spiculae lanceolatae, glabrae vel pubescentes, 10–15 mm longae, breviter pedicellatae. Glumae inaequales, prominenter nervosae, inferior lanceolata, superior ovato-lanceolata. Lemma chartaceum, ovato-lanceolatum, 6·5–8 mm longum, palea longius, prominenter nervosum, marginibus angustis hyalinis plerumque obtuse angulosum. Arista recta, 3–7 mm longa. Palea bicarinata, nervis ciliatis. Antherae 0·2–1·5 mm longae. Caryopsis palea aequilonga.

A *B. hordeaceo* subsp. *hordeaceo* lemmate brevior saepe marginibus acutius angulosis differt.

A *B. hordeaceo* subsp. *thominii* culmo altiore erecto panícula majore laxiore, plurispiculataque differt.

A *B. lepidus* lemmate longiore marginibus obtusius angulosis, parte hyalina angustiore, palea caryopsis aequante differt.

Holotypus: Roadside near Queen Elizabeth Hospital, Birmingham, England. Coll. 1962, P. Smith 458. In Herbarium of the Royal Botanic Garden, Edinburgh (E).

Key to taxa

1. Awns stout, recurved in fruit. Lemmas 6·5–8·5 mm long, bluntly angled. Spikelets densely hairy, in a dense panicle. (Coastal cliffs).

2. *B. hordeaceus* subsp. *ferronii*

Awns straight, or if weakly divaricate then the culms prostrate or procumbent.

Lemmas 4·5–11 mm long, sharply or bluntly angled. Spikelets hairy or glabrous 2

2. Lemmas 4·5–6·5 mm long, margins sharply angled with a broad hyaline margin. Awns weak. Grain exceeding palea.

4. *B. lepidus*

Lemmas 6·5–11 mm long.

3

3. Culms 1–8 (–12) cm, prostrate or procumbent to ascending. Lemmas 6·5–7·5 mm long. Awns sometimes divaricate in fruit. Grain shorter than palea. (Sand dunes).

3. *B. hordeaceus* subsp. *thominii*

Culms 3–80 cm, normally erect. Lemmas 6·5–11 mm long. Awns straight, erect.

Grain shorter than or equalling the palea.

4

4. Lemmas 6·5–8 mm long, usually glabrous, with broad or narrow, normally bluntly angled, hyaline margins. Grain usually equalling the palea.

5. *B. × pseudothominii*

Lemmas 8–11 mm long, usually hairy, with narrow, bluntly angled hyaline margins

Grain shorter than the palea.

1. *B. hordeaceus* subsp. *hordeaceus*

Descriptions

1. **B. HORDEACEUS** L.

subsp. **HORDEACEUS**

Annual or biennial, 3–80 cm. Culms erect or rarely ascending, usually stout, but

slender in depauperate material. Panicles 5–10 cm, erect, lax or rather dense, or reduced to a single spikelet. Spikelets $12-25 \times 4-6$ mm, usually hairy, lanceolate. Glumes unequal, lower lanceolate, upper ovate. Lemmas 8–11 mm, ovate, bluntly angled, with a narrow hyaline margin. Awn stout, straight, erect, 4–11 mm long. Palea shorter than lemma. Anthers 0.2–2.0 mm. Grain shorter than palea. ($2n=28$).

Europe, W. Asia, N. Africa. Introduced and naturalized in many parts of the world.

2. B. HORDEACEUS L.

subsp. **ferronii** (Mabille) Philip Smith

Annual or biennial, 2–15 (–20) cm. Culms erect or ascending, usually stout. Panicles 2–5 cm, erect, dense, often simple, sometimes reduced to a single spikelet. Spikelets $8-18 \times 3-6$ mm, densely hairy, ovate-oblong. Glumes unequal, lower lanceolate, upper broadly ovate. Lemmas 6.5–8.5 mm, rather broad, bluntly angled, with a narrow hyaline margin. Awn stout, flattened at base, recurved in fruit, 2–5.5 mm long. Palea shorter than lemma. Anthers 0.2–1.5 mm. Grain shorter than palea. ($2n=28$).

W. Europe. Cliff-tops.

3. B. HORDEACEUS L.

subsp. **thominii** (Hardouin) Hylander.

Annual, 1–8 (–12) cm. Culms prostrate, procumbent or ascending. Panicles 1–3 cm, erect, dense, often simple, or reduced to a single spikelet. Spikelets $8-12 \times 2-3$ mm, hairy or glabrous, lanceolate. Glumes unequal, lower lanceolate, upper ovate. Lemmas 6.5–7.5 mm, ovate, bluntly angled, with a narrow hyaline margin. Awn weakly divaricate in fruit, 3–7 mm long. Palea shorter than lemma. Anthers ca. 1.0 mm. Grain shorter than palea. ($2n=28$).

W. Europe, probably elsewhere. On coastal dunes and similar habitats inland.

4. B. LEPIDUS Holmberg.

Annual or biennial, 4–70 cm. Culms erect, often rather slender. Panicles 2–10 cm, erect, rather narrow, lax or dense, or reduced to a single spikelet. Spikelets $5-15 \times 2-4$ mm, usually glabrous and glossy, lanceolate. Florets tightly imbricate at first and giving a green and white striped appearance to the spikelet, later slightly divaricate. Glumes unequal, ovate with broad hyaline margins. Lemmas (4.5–) 5.5–6.5 mm, ovate or broadly ovate, sharply angled, with a broad hyaline margin. Awn straight, erect, weak, setaceous, 2–5.5 mm long. Palea shorter than lemma. Anthers 0.5–2 mm. Grain exceeding palea, rarely exceeding lemma. ($2n=28$).

Introduced in Britain in ruderal habitats, perhaps also introduced in W. Europe. Native distribution unknown.

5. B. $\times$ **pseudothominii** Philip Smith (*Bromus hordeaceus* L. $\times$ *Bromus lepidus* Holmberg)

Annual or biennial, 20–70 cm. Culms erect. Panicles 1–10 cm, erect, lax or dense, sometimes reduced to a single spikelet. Spikelets $10-15 \times 3-4$ mm, hairy or glabrous, lanceolate. Glumes unequal, lower lanceolate, upper ovate-lanceolate. Lemmas 6.5–8 mm, usually bluntly angled, with a narrow hyaline margin. Awn straight, erect, 3–7 mm long. Anthers 0.2–1.5 mm. Grain usually equalling the palea. ($2n=28$).

Europe, probably elsewhere.

MATERIALS AND METHODS

(i) Seed sources

The accessions of *Bromus* species used in this work originate from a wide geographical area. British material used in serological and genetic experiments is listed in an Appendix. Morphological studies were made on plants from many parts of the world, but especially

from Britain. The Flora of Warwickshire *Bromus* collection was placed at my disposal, and I am indebted to Messrs. Anton Nielsens, of Vejle, Denmark, for samples of Danish-produced forage grass seeds. All accessions used in experiments are being maintained in a living condition, together with voucher specimens, in the author's *Bromus* collection at the Department of Botany, University of Edinburgh.

(ii) *Morphological studies*

The herbaria of the Department of Botany, University of Birmingham (BIRM), of the Birmingham Natural History Society (Midland Institute, Birmingham), and of the Royal Botanic Gardens, Kew (K), have been extensively consulted to determine the limits of natural variation. The Birmingham collections included the recent Flora of Warwickshire material, so that an up-to-date idea of field variation was obtained. Specimens have been received on loan from the herbaria of Oregon State University, Corvallis (OSC), the Naturhistorisches Museum, Vienna (W), and the Muséum National d'Histoire Naturelle, Paris (P). I am indebted to the Curators of these institutions for their co-operation.

Data from herbarium material was used to construct scatter diagrams to demonstrate the extent of variation in some selected morphological features. Owing to the paucity of collections of *B. ferronii*, there has been a deficiency in the amount of *B. ferronii* material available for scoring.

(iii) *Karyological and Genetic Studies*

The chromosome numbers of cultivated accessions were determined. Attempts at hybridization were made using a variety of techniques. Crossing technique proved to be an obstacle to progress and most success was achieved using the laborious method of hand pollination described by Beddows & Davies (1938). Since the plants are all self-compatible, as was evident from good seed-setting in enclosed panicles, emasculation was essential. Maternal panicles were enclosed in pergamene bags.

(iv) *Ecological Studies*

Enquiries were restricted to observations of the various habitats in which the taxa were commonly found, and how they were associated with one another. Further information was supplied by analysis of the ecological records of the Flora of Warwickshire survey.

(v) *Serological Studies*

Serological techniques have been used in an attempt to determine the relationships between the taxa principally involved in this account. Although it has not yet been possible to apply these methods to *B. hordeaceus* L., *B. lepidus* and *B. × pseudothominii* as comprehensively as is desirable, the preliminary results seem to contribute valuable corroboration to my hypothesis of the evolution of this group of species developed from other criteria. Serological methods applied to many other bromes in this section of the genus (Smith 1965) have proved to be a valuable adjunct to morphological and cytological methods in determining patristic relationships. Hence the present data are presented with confidence.

The serological techniques adopted were basically those of Gell, Hawkes & Wright (1960), involving the use of double diffusion and immuno-electrophoretic analysis of the plant proteins, in agar gels. In their work on *Solanum*, tuber proteins were used, but in the present work the seed proteins were employed. Storage proteins seem to offer the best material for serological comparison, since greater inter-specific differences may be expected in them than in proteins concerned with activities such as photosynthesis, which are perhaps fundamentally similar in all green plants. Klotz (1960) has demonstrated the greater inter-specific differentiation of the storage proteins in a study of *Phaseolus* species. Klotz surmises that the reasons for this may be that the storage proteins are phylogenetically older, but it is hard to find evidence for this view. It seems more likely that storage proteins in seeds

are under particularly severe selective pressure from the environment because during the critical establishment phase when the survival capacity of a plant is most searchingly tested, variation in the composition, size and shape of stored protein molecules might well affect the success or failure of a plant competing with others. Since storage protein acts largely as an amino-acid reserve, the precise sequence of the residues may not be so rigidly fixed as in enzymes carrying out specific tasks in green tissues. So it may be that selective forces have a wider range of viable mutant molecules to operate on, and hence produce a comparatively rapid divergence between species.

Storage proteins seem therefore to be the plant serologists' material of choice, and have the merit of being available in high concentration at a particular stage in the life of the organism. Klotz (1960) was working with globulins, whereas the storage protein of grasses comprises the prolamine and glutelin fractions of the seeds.

Unfortunately, the solvents of prolamine and glutelin proteins (ethanol and alkaline solutions respectively) cause non-specific precipitation of the serum proteins in the antisera used to determine interspecific differences in protein precipitation. Therefore in the present work it was necessary to restrict the serological analysis to the water and saline soluble fractions, i.e. the albumins and globulins. It must be borne in mind that serological differences which may be demonstrated in these are likely to be smaller than the differences which exist in the prolamine and glutelin fractions.

0.8 per cent. saline extracts of finely ground, dehusked seeds of *Bromus* species were compared by raising antisera to them in rabbits. Courses of up to nine injections of the extracts were administered over a period of about six weeks. The earlier injections were of a 1:1 mixture of a 1 per cent. protein solution (the antigen solution) and Freund's adjuvant (Freund & Bonanto 1944) and were intramuscular. Later injections were of unadulterated saline extract into the marginal veins of the ears, or into the muscle of the thighs. 100–150 mg. of plant protein was injected during the course of the immunization.

The blood serum, containing antibodies to *Bromus* proteins, was used to analyse the antigen content of extracts of the seeds. The antiserum and the antigens were allowed to diffuse towards one another in 0.6 per cent. agar gel, buffered at pH 8.6 by barbital-HCl buffer (Michaelis 1930). Lines of precipitated protein ('precipitin') representing the reaction of the antibodies with antigens were developed after 24 hour incubation at 30°C. The differences in pattern produced by the reaction of antigen preparations from different species were regarded as taxonomic criteria. For immuno-electrophoresis, the seed extracts were electrophoresed in agar buffered at pH 9.4 (barbital-HCl) for eight hours (1.2V/cm, 20mA). After this time the antiserum was allowed to diffuse towards the now separated antigenic proteins, to produce an immuno-electropherogram. After 24 hour incubation, the precipitin lines, each representing an antigen-antibody complex, were sufficiently well-developed to be observed and drawn. After a further three days' development, the buffer salts and soluble proteins were washed out of the agar, and the agar itself was dried on a glass plate, protected by a piece of filter paper. When drying was complete the paper was removed and the pattern of lines was stained in 0.2 per cent. Ponceau S in 30 per cent. trichloroacetic acid. After further drying, contact prints or photographs could be made from the finished preparations.

RESULTS

(i) Morphological

The distinguishing features of the taxa in the *B. mollis* agg. sensu Tutin (1962) and of the related species *B. lepidus* are listed in Table 1. Plate 14b shows the gross differences in floret size and shape between *B. hordeaceus*, *B. lepidus* and '*B. thominii*' sensu Tutin (*B. × pseudothominii*). Herbarium material was scored for these features and the results are presented on a scatter diagram (Fig. 1). Recent Warwickshire material is plotted separately in Fig. 2. Floret characters were measured on the lowest floret in the uppermost spikelet of the panicle. Some of the features showed no consistent pattern of variation, and have

thus been omitted from the scatter diagrams. Anther-length varied widely within each taxon, as did stem-width. Spikelet-width and -length appeared very strongly correlated with lemma-length, while awn-length showed a lower correlation. As suggested by Tutin (1962) *B. hordeaceus* subsp. *ferronii* has quite wide spikelets, but my measurements showed that they were no wider than the spikelets of some specimens of *B. hordeaceus* subsp. *hordeaceus*.

TABLE 1. Distinguishing features of *B. hordeaceus* subsp. *hordeaceus*, subsp. *thominii*, subsp. *ferronii*, *B. × pseudothominii* and *B. lepidus*
(All measurements are in millimetres. Stem width was measured 1.5 cm below the first node of the inflorescence.)

Character	<i>B. hordeaceus</i>			<i>B. × pseudo-</i> <i>thominii</i>	<i>B. lepidus</i>
	subsp. <i>hordeaceus</i>	subsp. <i>thominii</i>	subsp. <i>ferronii</i>		
1. lemma-length	8-11	6.5-7.5	6.5-8.5	6.5-8	(4.5-)5.5-6.5
2. awn-length	4-11	3-7 weakly divaricate	2-5.5	3-7	2-5.5
3. spikelet-length	12-25	8-12	8-18	10-15	5-15
4. spikelet-width	4-6	2-3	3-6	3-4	2-4
5. anther-length	0.2-2	ca. 1.0	0.2-1.5	0.2-1.5	0.5-2
6. stem-width	0.5-1.5	0.5-1	0.5-1.25	0.5-1.25	0.5-1
7. spikelet indumentum	usually hairy	hairy or glabrous	densely hairy	hairy or glabrous	hairy or glabrous
8. hyaline lemma- margin	narrow	narrow	narrow	usually narrow	broad
9. lemma shoulder	bluntly angled	bluntly angled	bluntly angled	bluntly angled	sharply angled
10. length of grain relative to palea	grain shorter	grain shorter	grain shorter	grain about equal to palea	grain longer

In both scatter diagrams it will be seen that the spread of points exceeds the variation range quoted by Tutin (1962) and by Hubbard (1954) for these features, emphasizing the extreme morphological variability of the group as a whole. Though few plants of subsp. *ferronii* were scored (none, of course, from Warwickshire) they probably fall into quite a distinct group with dense panicles, recurved awns and densely hairy lemmas. They do not appear to be as distinct from *B. hordeaceus* subsp. *hordeaceus* as is *B. lepidus*, though both subsp. *hordeaceus* and *B. lepidus* are connected by a whole range of variants which approach the Tutin definition of '*B. thominii*', but which intergrade into both the former taxa. The indicated distribution of spikelet pubescence is consistent—a gradual increase of hairiness with increasing lemma size. The existence of names for hairy and glabrous variants of all the taxa concerned, except subsp. *ferronii*, accords with this finding.

It seems reasonable to postulate from these scatter diagrams that some hybridization may be occurring between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*, which is either obscuring a discrete taxon '*B. thominii*', or which may be the sole source of bromes so named. The consistent spread of spikelet hairiness from *B. hordeaceus* subsp. *hordeaceus* to *B. lepidus* may indicate introgression of genes for hairiness from subsp. *hordeaceus* into *B. lepidus*, and factors for glabrosity in the reverse direction.

(ii) Ecological

Field collecting has indicated that pure stands of both *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* can be found but that mixed populations of both these taxa and '*B. thominii*' are more frequent. Often the herbarium sheets examined proved to bear mixed gatherings

of two or three of these taxa. *B. hordeaceus* subsp. *hordeaceus* collections often included material with shorter lemmas, referable to '*B. thominii*' sensu Tutin. Pure stands of *B. hordeaceus* subsp. *hordeaceus* were found in woods, in hayfields and occasionally on roadsides. Pure stands of *B. lepidus* were almost invariably associated with sown grassland of one sort or another, for example, sown sheep pasture, lawns, and newly sown roadside verges and embankments. In these latter habitats, *B. lepidus* was quite commonly found mixed with '*B. thominii*' and sometimes with *B. hordeaceus* subsp. *hordeaceus* as a third component of the brome flora. A mixed population of *B. lepidus* and '*B. thominii*'-type variants grows on an area of the Knocking Hoe National Nature Reserve in Bedfordshire, parts of which were sown after the war (J. G. Dony, personal communication).

A curious population growing in disturbed soil on a cereal field margin at Ufton, Warwickshire, was scored for various morphological features, and the results are plotted in Fig. 3. Variation in lemma-size, sharpness of lemma shoulder, and spikelet hairiness place the plants of this population in a position intermediate between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. No *B. lepidus* could be found nearby at the time of sampling, but several large patches of *B. hordeaceus* subsp. *hordeaceus* grew within thirty metres of this population. According to the key in Tutin (1962) such plants would be referable to '*B. thominii*', but the recognition of such intermediate populations as a separate species requires some experimental validation.

Material of '*B. thominii*' accession 121 was found to segregate slightly in experimental cultivation, producing some plants with shorter lemmas in the second experimental generation. Such segregation supports the idea that '*B. thominii*' populations are composed of plants of hybrid origin. Most samples of '*B. thominii*' came true from seed, however, and showed no variation between generations which could be attributed to segregation.

Further insight into the ecological position of the taxa in Britain comes from an analysis of the copious ecological records of the new Flora of Warwickshire survey (Hawkes & Readett 1963). Fig. 4 represents the distribution of the three taxa, *B. hordeaceus* subsp. *hordeaceus*, *B. lepidus* and '*B. thominii*' sensu Tutin, in the sixteen habitats in which they have so far been recorded. It can be seen that while all three taxa are commonest on roadsides, in the other habitats their distribution appears most interesting. In cultivated land *B. lepidus* is commonest, followed by '*B. thominii*', with *B. hordeaceus* subsp. *hordeaceus* a poor third. *B. lepidus* and '*B. thominii*' are much commoner in pasture land than is *B. hordeaceus* subsp. *hordeaceus*, while in rough grassland *B. lepidus* is much less common than '*B. thominii*' and *B. hordeaceus*. *B. lepidus* is commonest on waste ground, and, where *B. lepidus* is not recorded from a ruderal habitat, '*B. thominii*' is commoner than *B. hordeaceus* subsp. *hordeaceus*. It is perhaps worth emphasizing that the identifications on which these ecological records are founded were all supported by specimens from the various collectors, and were confirmed by the author, in collaboration with the Flora Identification Panel.

From these data it appears that both *B. lepidus* and '*B. thominii*' are associated with artificially sown grassland. Both are poor pasture grasses which are never deliberately sown in Britain, so that the most likely reason for their distribution seems to be that they occur as contaminants in the seeds which are deliberately sown. To investigate this hypothesis, samples of commercial grass seeds have been inspected for contamination by bromes. These samples were purchased from seed firms in Britain, and a valuable collection of Danish strains, both cleaned and uncleaned samples, was made available by the firm of Anton Nielsens, Vejle. *Bromus* seeds found in imported cleaned seed of Danish *Festuca pratensis* Huds. were referable to *B. lepidus* and '*B. thominii*', while in an uncleaned sample of *F. pratensis* from another producer, *B. hordeaceus* subsp. *hordeaceus* seed was seen. Clearly this shows that the seed size and shape of *B. lepidus* and '*B. thominii*' are so similar to those of meadow fescue that seed cleaning methods do not remove them, though the larger seeds of *B. hordeaceus* subsp. *hordeaceus* are removed with less difficulty. *B. lepidus* has also been found in uncleaned seed of Chewings Fescue (*Festuca rubra* subsp. *commutata* Gaud.), and in cheap, cleaned lawn grass seed consisting largely of *Lolium perenne* L. One

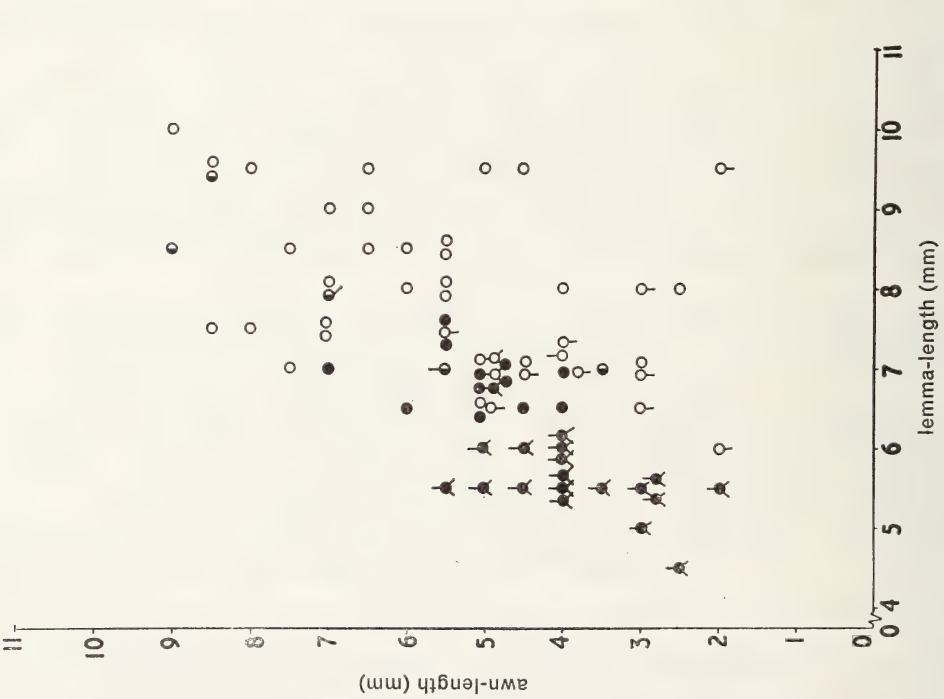


Fig. 1. Scatter diagram of the *B. mollis* agg. sensu Tutin, and *B. lepidus*, compiled from herbarium material.

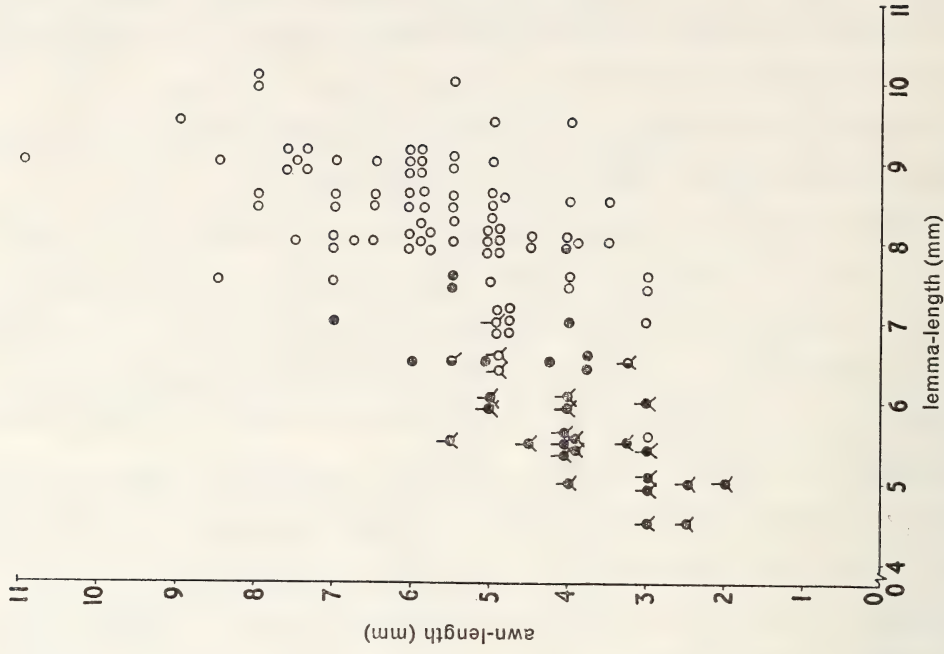


Fig. 2. Scatter diagram of recent Warwickshire collections of the *B. mollis* agg. sensu Tutin, and *B. lepidus*.

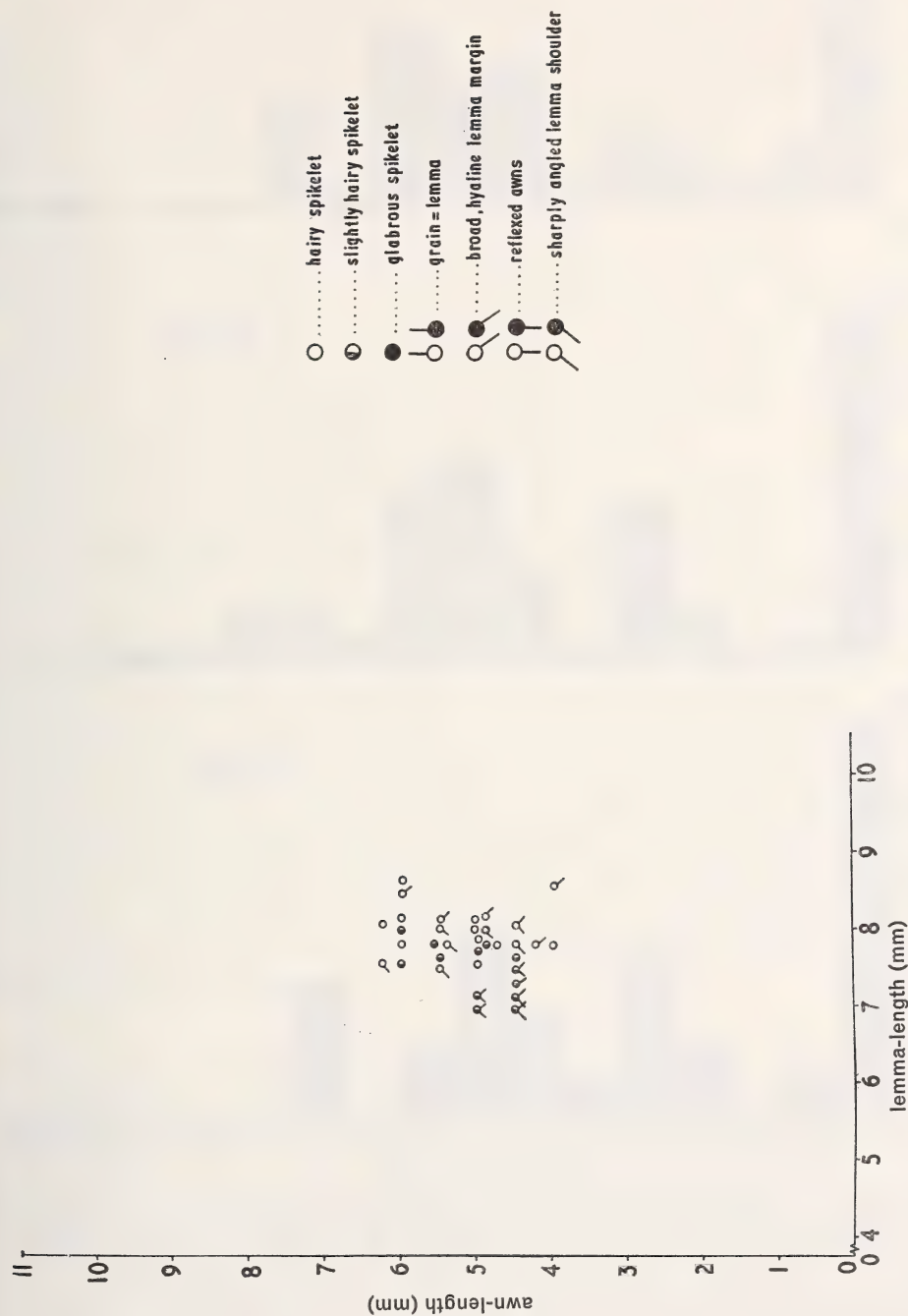


Fig. 3. Scatter diagram of *B. mollis* agg. population from Ufton, Warwickshire.

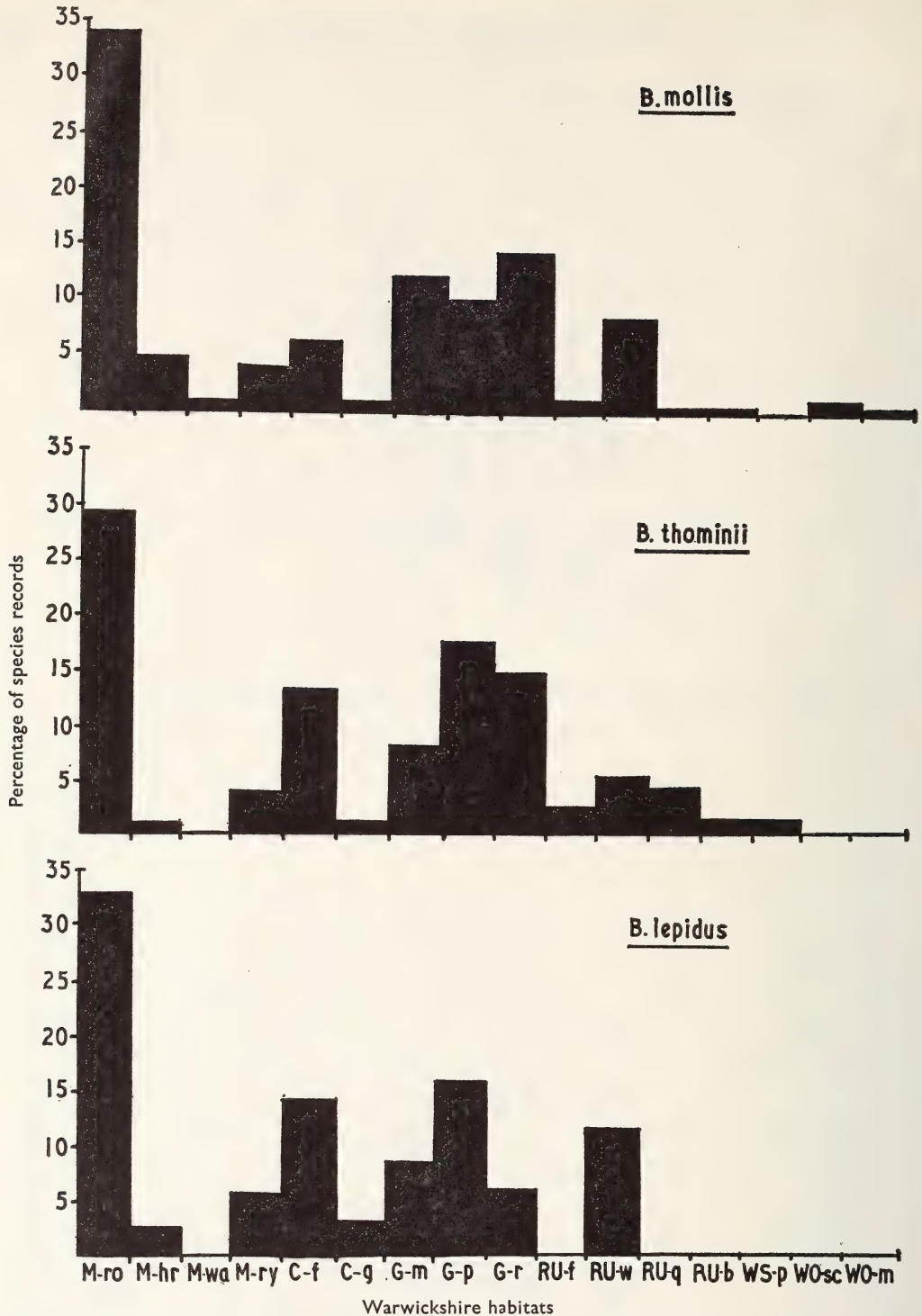


Fig. 4. Histogram of distribution of *B. hordeaceus* subsp. *hordeaceus*, *B. thominii* sensu Tutin and *B. lepidus* in all Warwickshire habitats in which they have been recorded. The percentages are of the total number of records of each taxon in the Flora of Warwickshire Survey. Key to abbreviations:

M-ro—roadside	G-m—meadow	RU-q—quarry
M-hr—hedgerow	G-p—pasture	RU-b—brick or marl pit
M-wa—wall	G-r—rough grassland	WS-p—pondside
M-ry—railway embankment or cutting	RU-f—farmyard	WO-sc—scrub or derelict wood
C-f—cultivated field	RU-w—waste ground	WO-m—mixed wood
C-g—garden		

landscaped site in the University of Birmingham grounds, which bore a rich brome flora of three taxa, *B. lepidus*, *B. hordeaceus* subsp. *hordeaceus* and '*B. thominii*', with all spikelet indumentum variants, was found to have originated from a sown mixture including an impure source of *Festuca longifolia* Thuill. Investigation of other samples of cleaned *F. longifolia* revealed *B. lepidus* as a contaminant.

Beddows (1953) shows that large-scale importations of rye-grass and other grass seed into Britain date from about 1831, so that *B. lepidus* and '*B. thominii*' may have entered Britain in quantity from about this time. The earliest British collection of *B. lepidus* is dated 1836. Early agricultural literature on grass husbandry (e.g. Sturrock 1865; Everitt 1897) indicates that imported grass seed was very impure and needed considerable cleaning. Britain is now a major producer of grass seed, and advice on this very specialized trade is given to farmers by the National Institute of Agricultural Botany, Cambridge. A series of *Herbage Seed Growers' Leaflets* has been produced and additionally a series of *Seed Notes*. *Seed Notes* No. 72 shows that *Bromus* is a recognized weed in rye-grass and fescue crops, and the *Herbage Seed Growers' Leaflet* No. 2 advises farmers to remove from the field and field margins any rogue grasses whose seed may be difficult to remove from the crop.

It seems clear that *B. lepidus* and '*B. thominii*' owe much of their British distribution to the practice of sowing grass seeds in pastures and on roadsides. British Certified Seed, or its foreign equivalent, of very high purity is commonly used, and in this brome contamination is at a minimum, though still present. However, much cheap seed is used by roadside contractors and local councils, and this is often impure.

Methods of seed cleaning by screening for seed size will explain the strong tendency for small-seeded bromes to occur on cultivated ground among sown grasses of similar seed size. *B. hordeaceus* subsp. *hordeaceus* can more easily be removed, and this species seems more commonly established on old roadsides and hayfields than either *B. lepidus* or '*B. thominii*'. Some seed contamination by *B. hordeaceus* subsp. *hordeaceus* is rendered possible by the occasional maturation of smaller seeds in the upper part of the spikelet.

The above discussion relates only to the inland members of this aggregate of species, but it is a common observation that '*B. thominii*' occurs, often abundantly, on coastal dunes where there is no likelihood of artificial sowing. *B. lepidus* is uncommon here, moreover. *B. hordeaceus* subsp. *hordeaceus* occurs on coastal cliffs and on some dunes. It is sometimes depauperate and occasionally has procumbent culms, but these characters have not been found to persist in cultivation (Wilson 1956). '*B. thominii*' from sand dunes has a rather distinct morphology not manifested in the scatter diagrams owing to lack of material. These plants, which are here regarded as *B. hordeaceus* subsp. *thominii*, are usually very small and often prostrate or procumbent, with small, dense paucispiculate panicles. The awns often become divaricate. Experiments revealed that these features were maintained in cultivation, recalling the similar experience of Nilsson (1937) and Wilson (1956). The dune material used came from the Ynys-Las dune system in Cardiganshire and from Burry Port, Carmarthenshire.

(iii) Serological

Using antisera raised to two accessions of *B. hordeaceus* subsp. *hordeaceus* (Nos. 13 and 21 in appendix), the albumin and globulin fractions of the seed proteins of taxa within the *B. mollis* aggregate (sensu Tutin) and *B. lepidus* were studied and compared. Both double diffusion and immunoelectrophoretic analysis of the antigen components in the saline extracts gave compatible results. The precipitin spectra obtained are illustrated in Pl. 15*b* and *c*.

The homologous reaction of *B. hordeaceus* subsp. *hordeaceus* with its own antiserum cannot be distinguished from that of *B. lepidus* nor from inland accessions of '*B. thominii*'. Other *Bromus* species tested, most of which do not form part of the present investigation, gave reactions varying from similar to very different from the homologous reaction, with the exception of *B. interruptus* which resembled *B. hordeaceus* subsp. *hordeaceus* completely in its serological behaviour. *B. hordeaceus* subsp. *ferronii* and subsp. *thominii* from dunes

both showed slight though persistent differences from the homologous reaction. In both these taxa, one antigen line is lacking and the main antigen moves more slowly in electrophoresis than that of the homologous reaction, and that of *B. lepidus* and inland '*B. thominii*'.

These immunological differences were detected by the antibody-forming mechanisms of four adult rabbits.

(iv) Karyological and Genetic

B. hordeaceus (all subspecies), *B. lepidus* and '*B. thominii*' were found to have a somatic chromosome number of $2n=28$ and are tetraploid. Using the technique described by Beddows & Davies (1938) it was possible to establish a number of hybrids of *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. These hybrids resembled '*B. thominii*' sensu Tutin in all their morphological features, and were almost completely fertile. A typical hybrid panicle is shown in Pl. 15a. The F_2 generation, raised from the seeds of the hybrids, proved to be highly variable and to include types which would be referable to *B. hordeaceus* subsp. *hordeaceus*, *B. lepidus* and '*B. thominii*'. Plate 14c illustrates some of the variations in floret size which were produced. Hairy and glabrous spikelets occurred throughout the range of variation.

A fully fertile hybrid of *B. hordeaceus* subsp. *hordeaceus* and subsp. *ferronii* was also obtained, which was morphologically intermediate between the parents.

DISCUSSION AND CONCLUSIONS

Morphological studies suggested that plants referable to *B. thominii* sensu Tutin might be the result of hybridization between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. Field observations showed the common occurrence of mixed populations of all three taxa in fields and on roadsides. *B. hordeaceus* subsp. *ferronii* and '*B. thominii*' from coastal dunes seemed rather more distinct, but inland '*B. thominii*' and *B. lepidus* were shown to be associated with sown grassland. Examination of grass seed samples revealed that both occurred as contaminants in the sown seed of various species of pasture grass. Their seed-size so closely matches that of a number of rye-grasses and fescues that they cannot readily be separated by normal mechanical methods. A similar situation has been reported in the weed *Camelina* by Tedin (1925). Contamination of the seed must occur in the production field, though examination of the uncleaned seed purity records at the National Institute of Agricultural Botany failed to demonstrate the expected high contamination. This may readily be explained. Firstly, the sample sizes used by the N.I.A.B. testers may be too small to reveal the comparatively small number of brome seeds required to initiate substantial contaminating populations. Secondly, it seems likely that the records of contamination by '*Bromus mollis*' (*B. hordeaceus* subsp. *hordeaceus*), of which there are a good many, actually refer also to the smaller seeded bromes. Thirdly, the incidence of contamination may be a regional or climatic variable depending on methods of cultivation and cleaning and on the amount of effort expended in certifying the seed. In the present work it was obvious that seed of Danish origin and seed from southern Britain were frequently significantly contaminated with small-seeded bromes. Gooch (1963) shows from an analysis of purity records of imported Danish meadow fescue grass that 69.8 per cent. of samples were contaminated with '*Bromus mollis*' (*B. hordeaceus* subsp. *hordeaceus*), while 40.7 per cent. of creeping red fescue samples were contaminated. A contaminated sample was one which contained at least one contaminant seed in the portion analysed (though the size of this sample is not defined). Contamination of rye-grass by *B. hordeaceus* subsp. *hordeaceus* was found in only 7.8 per cent. of Danish samples. In samples of English origin, Gooch found *B. hordeaceus* subsp. *hordeaceus* contamination in 17.1 per cent. of samples of *Lolium perenne*, and 20.4 per cent. of samples of *Festuca pratensis*. *B. hordeaceus* contamination was almost twice as frequent in samples from western counties of England as in those from eastern areas. Astonishingly high incidence of contamination—76.4 per cent. and 96.5 per cent. respectively—was recorded in Irish samples of Italian and perennial rye-grass.

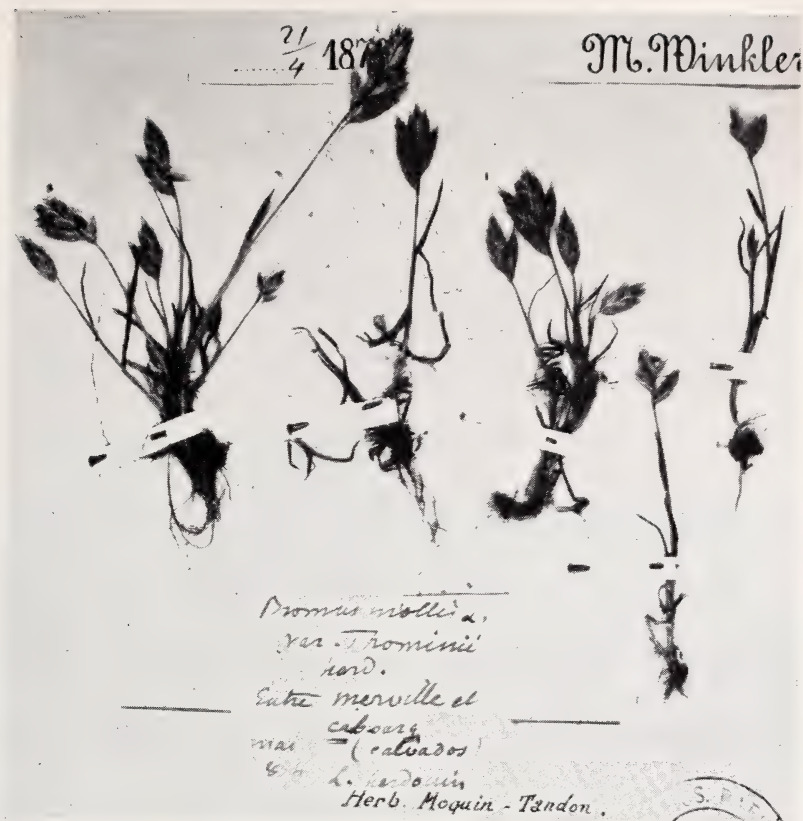


PLATE 14a—Authentic material of *B. thominii* Hardouin (collected and named by Hardouin), in herb. Muséum National d'Histoire Naturelle, Paris (P).

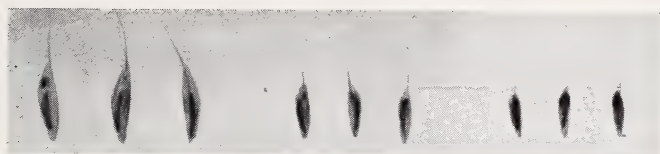


PLATE 14b—Florets of *B. hordeaceus* subsp. *hordeaceus* (left); *B. thominii* sensu Tutin (centre); and *B. lepidus* (right).

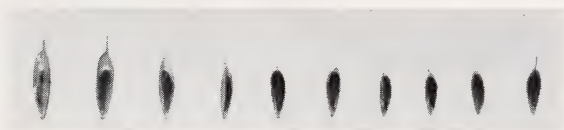


PLATE 14c—Range of variation in florets of the F_2 generation of the cross *B. hordeaceus* subsp. *hordeaceus* $\times$ *B. lepidus*.



PLATE 15a—Panicle of artificial F_1 hybrid of *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*.

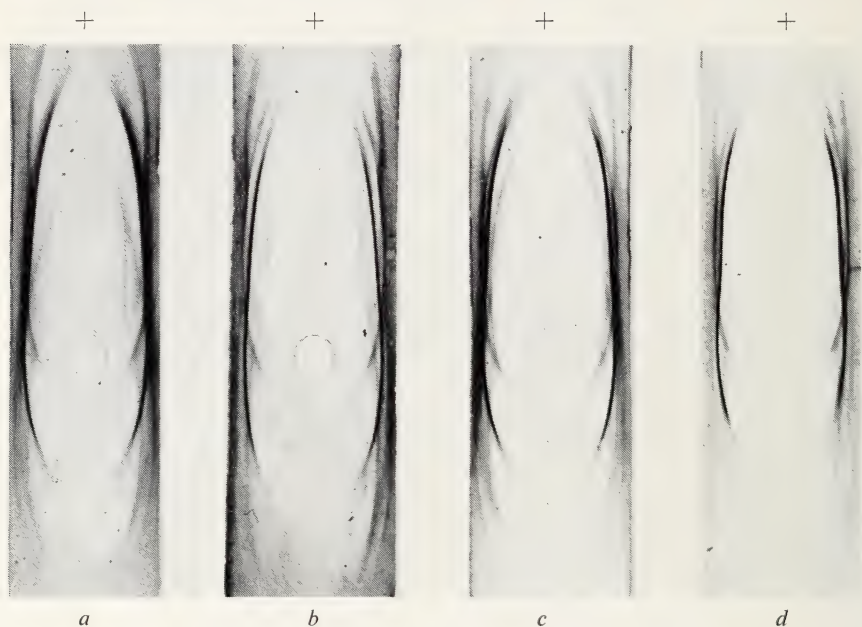


PLATE 15b—Immunoelectropherograms of seed protein extracts of: (a) *B. hordeaceus* subsp. *hordeaceus*; (b) *B. thominii* sensu Tutin; (c) *B. lepidus*; (d) *B. hordeaceus* subsp. *thominii* (Hard.) Hylander.

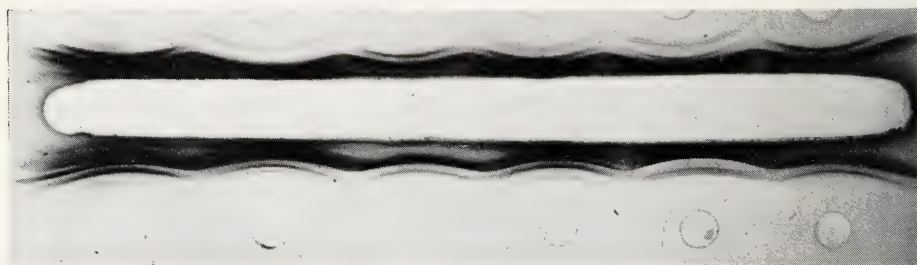


PLATE 15c—Double diffusion spectra of seed protein extracts of: TOP (left to right) *B. thominii* sensu Tutin; *B. hordeaceus* subsp. *hordeaceus*; *B. hordeaceus* subsp. *thominii* (Hard.) Hylander; *B. thominii* sensu Tutin; *B. interruptus*; *B. hordeaceus* subsp. *thominii*. BOTTOM (left to right) *B. thominii* sensu Tutin; *B. lepidus*; *B. hordeaceus* subsp. *thominii*; *B. thominii* sensu Tutin; *B. hordeaceus* subsp. *ferronii*; *B. hordeaceus* subsp. *thominii*. Note missing inner lines from *B. hordeaceus* subsp. *thominii* and *ferronii*.

Thus there seems to be abundant evidence of the origin of the small-seeded annual brome populations from contaminated seed in sown grassland.

Serological evidence showed that *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* were indistinguishable in terms of their seed albumins and globulins, implying therefore a very close patristic relationship. Inland '*B. thominii*' was also indistinguishable, thus supporting the idea that it may result from hybridization, and possibly introgression, between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. *B. hordeaceus* subsp. *ferronii* and subsp. *thominii* sensu stricto were slightly different, which agrees with their morphological and ecological distinctness from the typically inland forms.

Genetic evidence showed that *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* were interfertile tetraploids, thus genetically closely related, and that they could hybridize to produce highly fertile progeny indistinguishable in morphology from inland material of '*B. thominii*'.

It is therefore suggested that inland '*B. thominii*' in Britain results from the hybridization of *B. hordeaceus* subsp. *hordeaceus* with *B. lepidus*. It seems highly likely that such hybridization has been followed by back-crossing of the hybrids to the parents to some extent, a process which would contribute a further range of intermediates to the initial hybrid populations. This introgression hypothesis is supported by the distribution of hairy-spikelet variants in *B. lepidus*, and of glabrous-spikelet variants in *B. hordeaceus* subsp. *hordeaceus*. In each case the spikelet- and lemma-size of these variants is at the extreme end of the variation range which approaches the other taxon. Only rarely are glabrous-spikelet variants of *B. hordeaceus* subsp. *hordeaceus* found with lemma-length in the upper end of the species range. Small-lemma, hairy-spikelet variants of *B. lepidus* have not been seen during this investigation. The hybridization may not have taken place originally in Britain, but wherever in Eurasia *B. lepidus* is native and is sympatric with *B. hordeaceus*. Certainly neither *B. lepidus* nor '*B. thominii*' give the appearance of being native in Britain, since they are not well-established in any natural community. Their populations are ephemeral and they are quickly ousted from the sown grassland in which they are most commonly found by the intended components of the seed mixtures applied. *B. hordeaceus* subsp. *hordeaceus* on the other hand, while also a ruderal plant, seems much more persistent wherever it grows, and tends to spread rather than to disappear. In old hayfields it often seems to be a permanent feature of the flora. Although both *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus* are predominantly self-fertilizing in Britain, Beddows (1936) concluded that the wide variation exhibited by the former could be explained only on the basis of some degree of outbreeding. Observations during the present work indicated that both species sometimes shed pollen, and it is possible that elsewhere both species may normally be outcrossing. The variation generated by hybridization would produce a range of types which would eventually become stabilized by a resumption of selfing (Stebbins 1950). This would explain the wide variation range which exists between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*. The success of the hybrid derivatives, at least in Britain and probably elsewhere where agricultural practices are similar, appears to be a result of the ease with which they contaminate grass seed crops, and so persist with the intended harvest. This type of adaptation in response to 'artificial natural selection' has been frequent in *Bromus*, as witnessed by the cereal field contaminants *B. secalinus* and *B. arduennensis* Dumort., as well as by other species yet to be considered. These are all examples of the effectiveness of the facultative inbreeding system in changing environments, and of the unconscious selection by Man of weed as well as crop plants.

With the coastal populations of *B. hordeaceus* subsp. *thominii*, the explanation of origin by hybridization and possible introgression from *B. lepidus* is not satisfactory. They are well-established in natural communities, and have been, in many cases, observed for over 150 years, and are clearly not established by artificial sowing. The persistence of their morphological peculiarities in cultivation and their serological distinctness from the rest of the *B. hordeaceus* subsp. *hordeaceus*-*B. lepidus*-'*B. thominii*' complex indicates that they have a different evolutionary history. Genetic evidence of their distinctness has been

reported by Holmberg (1924) who described a naturally occurring plant as a hybrid of *B. hordeaceus* subsp. *thominii* and *B. hordeaceus* subsp. *hordeaceus*. The plant was only 50 per cent. fertile. Nilsson (1931; 1937) produced artificial hybrids of the same parentage and found that fertility increased very markedly after comparatively few generations. Presumed hybrids of these taxa appear regularly in the literature and they have been named *B. × jansenii* A. Camus (Camus 1957) in another report indicating partial sterility. Wilson (1956), in an attempted artificial hybridization, failed to get any seed in a small trial. Spatial isolation, and possibly disruptive and stabilizing selection, are the presumed causes of the ecological and genetical peculiarities of these dune plants. Because of these distinctions it seems best to regard them as ecotypes of *B. hordeaceus*. On dunes, the course of genecotypic adaptation, if this is in fact the explanation, has been in the direction of small size of plants, with prostrate or procumbent culms, a tendency to broad short lemmas and small seeds, and rather dense small panicles. The prostrate or procumbent habit is a familiar development in seaside plants, while the broad lemmas may perhaps be a photosynthetic compensating mechanism since the leaves are short-lived. It is the small lemma and seed size which is of particular systematic interest. Perhaps the genetically fixed 'depauperation' was initially disadvantageous in terms of the number of seeds maturing, but was followed by selection of variants with a larger number of smaller seeds. As well as making most use of possibly limiting nutrient supplies, biotypes with smaller more numerous seeds might have the developmental advantage of faster maturation in conditions of imminent drought. The isolation of these gene-pools on dunes would naturally offer the opportunity for divergence in seed protein complement such as has been demonstrated.

Some ecotypic adaptation may have occurred in the bromes inhabiting areas used for grass seed production, but owing to the rarity of variants of *B. hordeaceus* subsp. *hordeaceus* with sufficiently small seeds, and the inconstancy of the selection pressure on any particular gene complement, it has probably been insignificant. Where the crop and weed seed sizes are more closely similar at the outset, genecotypic adaptation is probably the major means of evolutionary change towards the size and shape of the crop seed. Such adaptation is presumably the cause underlying the contamination of rye fields by *B. secalinus* and of *Triticum spelta* L. by *B. arduennensis*. In the present instance, where the seed sizes of *B. hordeaceus* subsp. *hordeaceus* and the crop grasses are rather different, only hybrids combining the characters of a very small-seeded brome could have exploited this niche. A further factor promoting genecotypic adaptation in cereal field contaminants is the regular harvesting of seed with resowing of some fraction of it. The cereal field ecotypes were common enough to persist through these generations of crops and so progressively become better and better adapted. The incidence of subsp. *hordeaceus* variants with seeds small enough to escape removal in the normal seed cleaning techniques is very low, if they exist at all, and so the chance of their reappearing in another generation of the crop plant grown for seed multiplication is minimal. Probably they would be dispersed in the part of the crop sold commercially, and so not be subject to further selection.

Bromus hordeaceus subsp. *ferronii* appears to have serological and ecological peculiarities and its morphological features were found to persist in cultivation. It is interfertile with subsp. *hordeaceus* and most of its characteristics—dense hairiness, short, stout culms and recurved awns—can be interpreted as ecotypic adaptations to the cliff-top environment. Awn recurvature in bromes seems to be xeromorphic feature, and the hairiness may also be so explained, or else be of some protection against grazing.

For an ecotype it may seem to have a rather restricted geographical distribution. There is no reason, however, why an ecotype need be present in all the possible places where its particular environment occurs. Baker (1953) has cited an excellent example of the restriction of morphologically striking apomicts of *Limonium binervosum* (G.E.Sm.) C. E. Salmon to particular localities in south-west England and West Wales. The habitat is similar but the particular apomict in each one differs in morphology sufficiently to have been recognized as distinct species by some taxonomists. *B. hordeaceus* subsp. *ferronii* may illustrate a similar phenomenon in an autogamously reproducing group.

The close morphological resemblance of material of *B. hordeaceus* subsp. *hordeaceus*, *thominii* and *ferronii*, supported by the nature of their serological and genetical resemblances appears to expose them as subspecific variants within a single species. Accordingly this is the course which has been followed in the taxonomic treatment given earlier. The material formerly named '*B. thominii*', which has been shown above to be a hybrid complex between *B. hordeaceus* subsp. *hordeaceus* and *B. lepidus*, is so common and conspicuous that some reference name seems desirable. The name *B. × pseudothominii* Philip Smith has therefore been proposed for it. Though *B. lepidus* is shown to be interfertile with *B. hordeaceus*, and to have an indistinguishable serological spectrum, its specific status is maintained since it contributes to the hybridization as an independent and distinct source of genes, and has a very characteristic morphology, which suggests that at least one of its diploid ancestors is not shared by *B. hordeaceus*.

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APPENDIX

Accessions of *Bromus* mentioned in the account. Voucher material at Dept. of Botany, University of Edinburgh. Flora of Warwickshire material at **BIRM**.

Species	Acc. no.	Origin
<i>Bromus hordeaceus</i> subsp. <i>hordeaceus</i>	13	England, Warwickshire; Edgbaston, Birmingham 15. Vincent Drive roadside. P. Smith 457, 1962.
„	21	England, Worcestershire; Queensway, Halesowen, Old allotment. P. Smith 503, 1962.
„	26	England, Warwickshire; Quinton, Birmingham. Roadside. P. Smith 494, 1962.
„	474	Flora of Warwickshire accession. Myton Farm, near Warwick. On a roadside. 1963.
<i>Bromus hordeaceus</i> subsp. <i>thominii</i>	429	Wales, Cardiganshire; Ynys-Las, sand dunes on the Dyfi estuary. P. Smith 671, 1963.
„	510	Wales, Carmarthenshire; Burry Port. Sand dunes near the Old Harbour. P. Smith 813, 1965.
<i>Bromus hordeaceus</i> subsp. <i>ferronii</i>	462b	Wales, Anglesey; South Stack, on a wall top. Coll. J. B. Phipps. 1963.
<i>B. lepidus</i>	31	England, Worcestershire; Halesowen by-pass. Roadside embankment. P. Smith 502, 1962.
	92	Flora of Warwickshire accession. S.E. of Willoughby. Railway embankment. 1959.
<i>B. $\times$ pseudothominii</i>	116	Flora of Warwickshire accession. S.E. of Barford. Farmyard. 1962.
	121	Flora of Warwickshire accession. Green Lane, E. of Cloudesley Bush. Farmyard. 1962.

The panicle illustrated (Plate 15a) is from a hybrid between *B. hordeaceus* subsp. *hordeaceus* 26 and *B. lepidus* 31.

CHROMOSOME NUMBERS OF *ORNITHOGALUM UMBELLATUM* L. FROM THREE LOCALITIES IN ENGLAND

By R. CZAPIK

*Institute of Plant Anatomy and Cytology, Jagellonian University, Cracow, Poland**

ABSTRACT

The karyological examination of 49 specimens of *Ornithogalum umbellatum* L. from three localities in England showed the occurrence of two euploid cytotypes, a triploid ($2n = 27$) and a hexaploid ($2n = 54$). In one locality two aneuploid plants ($2n = 28$) were found among the triploids. A few cases of mixoploidy (polysomaty and aneusomaty) and some karyotype aberrations are described. The origin of cytological diversity within the population is briefly discussed.

INTRODUCTION

Ornithogalum umbellatum L. shows a high degree of cytological differentiation. Euploid ($2n = 18, 27, 36, 45, 54, 72$) and aneuploid cytotypes ($2n = 19, 20, 21, 22, 23, 28, 43, 52$) as well as plants with B-chromosomes occur within this species according to the data given by several research workers (Table 1). In addition some other aneuploid chromosome numbers unknown for adult plants were found by the author in young seedlings in the progeny of triploids (Czapik 1966).

It should also be emphasized that the cytotypes with 54 and 72 chromosomes have been reported chiefly for cultivated plants and that aneuploid specimens have been found more frequently in wild populations than in garden samples. In view of this, it seemed advisable to study a large amount of material of various origins. In this way the rôle of wild populations and cultivated material in the process of cytological differentiation within the species could be investigated.

MATERIAL AND METHODS

Origin of Plants

O. umbellatum is native in some parts of the British Isles (Warburg 1962) and occurs in natural habitats. It is also in cultivation and it may be a garden escape in many places (Perring, Sell & Walters 1964). The bulbs examined originated from three localities in England (Table 2). The plants growing on the heath near Icklingham (Suffolk, Grid. ref. TL 7673) were probably native. The specimens from two other colonies, viz. a very small one on the roadside near Fleam Dyke (Cambridgeshire, Grid ref. TL 549542) and a large one in the pasture near the church in Hitcham (Suffolk, Grid ref. TL 983512) might be considered as garden escapes of unknown age.

The plants from Icklingham were collected by Mrs. M. Southwell. Since 1951 they have been cultivated in the University Botanic Garden, Cambridge. Six bulbs were dug out from various places of the bed but their clonal origin cannot be excluded.

Two adult plants and 6 young bulbs which belonged probably to two clones were collected by the present author in the locality near Fleam Dyke.

The material collected in Hitcham was more ample. The bulbs were taken from 7 well-separated groups of plants. According to the number of plants in each group only 2–10 bulbs of various size were taken for the karyological examination, and the remaining plants were left in situ.

Cytological Technique

This was the same as used in the author's previous studies on *Ornithogalum* (Czapik 1965, 1966). Single bulbs were grown in jars with tap water. Root growth began after

* The material was collected during the stay of the author at the Botany School, University of Cambridge, in May 1966.

TABLE 1. Karyological differentiation within *Ornithogalum umbellatum* L.

$2n$	Authors
<i>Euploid chromosome numbers:</i>	
18*	Neves (1952, 1956), Giménez-Martín (1958), Czapik (1965)
27*	Heitz (1926; $n=12-14$), Sprumont (1928), Nakajima (1936), Satô (1942), Pólya (1950), Neves (1952), Gadella & Kliphuis (1963), Czapik (1961, 1965)
36*	Neves (1952), Czapik (1965)
45	Sprumont (1928), Neves (1952)
54	Matsuura & Sutô (1935), Holzer (1952), Neves (1952)
72	Neves (1952)
<i>Aneuploid chromosome numbers in adult plants:</i>	
19*	Neves (1952), Giménez-Martín (1958), Czapik (1965)
20*	Neves (1952), Giménez-Martín (1958), Mesquita (1964)
21*	Neves (1952), Giménez-Martín (1958)
22*, 23*	Neves (1952)
28*	Neves (1952), Czapik (1965)
43, 52	Neves (1952)
<i>Aneuploid chromosome numbers in young seedlings and embryos only:*</i>	
24, 25, 26, 29, 30, 32	Czapik (1966)
<i>B-chromosomes (adult plants):</i>	
18+1	Neves (1952), Mesquita (1964-65)
18+3, 19+1, 19+2, 20+1	Neves (1952)
21+1	Neves (1952), Giménez-Martín (1958)
23+1, 27+1	Neves (1952)

* Found in the progeny of triploid plants (Czapik 1966)

approximately two months and was more abundant in darkness. Root-tips were fixed in a mixture of ethyl alcohol, chloroform and acetic acid (6:3:1) after pre-treatment with 8-hydroxyquinoline (0.002 mol./l. aqueous solution) and stained in bulk in alcoholic hydrochloric acid carmine (Snow 1963). Squashes were prepared separately from each root-tip in order to avoid the difficulties of interpretation in case of mixoploidy within a bulb or particular roots. The cellophane method was used to make the squashes permanent (Murin 1960).

RESULTS

The main results of cytological examination are summarized in Table 2. Three cytotypes were found in the material studied ($2n = 27, 28, 54$). In two localities triploid plants were prevalent ($2n = 27$, Plate 16a); in the third one near Fleam Dyke hexaploid cytotypes occurred ($2n = 54$, Plate 16d). The population in Hitcham showed some degree of cytological differentiation. The examination of 35 bulbs from 7 well separated groups of

TABLE 2. Chromosome numbers of investigated plants

Localities	$2n$	Number of bulbs
1. Heath of Seven Tree Road, Icklingham, Suffolk	27	6
2. Pasture, behind the churchyard, Hitcham, Suffolk	27	33
	28	2
3. Roadside near Fleam Dyke, Cambridgeshire	54	8

plants revealed that 33 bulbs belonged to triploid plants, while two others had 28 chromosomes (Plate 16b). The aneuploid number was found in single plants in two different groups. No group of plants consisted of aneuploids exclusively.

The same types of chromosomes were easy to identify in the karyotypes of the British plants as those of the plants originating from Poland (Czapik 1965). The haploid set consisted of one SAT-chromosome of medium size (chromosome VI), three large chromosomes with submedian centromeres characterized by various proportions of their arms (chromosomes I, II, III), two chromosomes of medium size with submedian centromeres (chromosomes IV and V) and three small chromosomes with submedian centromeres (chromosomes VII, VIII and IX).

The hexaploid and most of the triploid plants had normal karyotypes, and no distinct structural changes of chromosomes could be detected. It should be noted, however, that in the triploid plants only one of the chromosomes VI had a visible satellite. Two satellites could be discerned only in root-tip squashes of two plants from Hitcham. The numbers of satellites in the metaphase plates and their size, as well as the length of the constriction between the satellite and the arm, also showed some degree of variability in plants of *O. umbellatum* studied previously (Sprumont 1928, Czapik 1965). No special examination was done, however, to test the cause of this variation.

Only one triploid plant originating from Hitcham showed a change in the composition of its chromosome complement. It had two chromosomes VII while the chromosome IX was represented four times; the other types of chromosomes were present in the normal number.

In plants with 28 chromosomes a strictly triploid complement was increased by the additional occurrence of the chromosome IX, the smallest one in the karyotype. It is very remarkable that variation in the number of these particular chromosomes seems repeatedly to be responsible for the aneuploid differentiation in *O. umbellatum* (Neves 1952, Giménez-Martín 1958, Mesquita 1964, Czapik 1966).

Mixoploid root-tips were detected in one aneuploid and in two triploid plants from Hitcham. Polysomaty was observed in one triploid plant which had a hexaploid sector in one root-tip. One metaphase (Plate 16c), one anaphase and three prophase with 54 chromosomes formed an island among the triploid cells of the root meristem. This type of mixoploidy in *O. umbellatum* was described also by Neves (1952).

One of the aneuploid plants appeared to show a tendency to reversion to triploidy. Eight root-tips were examined: in six roots 28 chromosomes were counted consistently; by contrast in a single root triploid metaphases ($2n = 27$) occurred side by side with plates having 28 chromosomes and in the last root only triploid plates were found.

In a further plant three metaphases with 26 chromosomes were found among the normal triploid plates. In the same root-tip early telophases with bridges were visible. Such abnormalities might lead to numerical differences of the chromosome complements in adjacent cells (Rychlewski 1967). Bridges at anaphase and telophase occurred also in three other roots where no change in karyotypes could be detected.

The case of aneusomaty described above could be interpreted as a result of the influence of external factors on the mitosis; abnormal conditions created by water culture of bulbs before fixation must be also taken into consideration. In the majority of bulbs, however, these disturbances did not greatly affect the normal course of mitosis. The deviating chromosome numbers were also found in some young seedlings of *O. umbellatum* (the progeny of triploids) as well as in some root-tips of adult plants (Czapik 1965, 1966). In seedlings, however, such facts might point to some internal instability caused by aneuploidy.

DISCUSSION

Embryological investigations have shown that triploidy may play a role in the cytological evolution of *O. umbellatum* (Czapik 1966). The progeny of triploids show a wide range of karyological differentiation. Chromosome numbers from $2n = 18$ to 30 were found in seedlings while in embryos $2n = 32$ and 36 also occurred (Table 1). It seems that the

type of karyological differentiation revealed in *O. umbellatum* is similar to that known for *Hyacinthus orientalis*, where the full range of chromosome numbers between $2x$ and $4x$ exists in seedlings and adult specimens of the progeny of triploid plants (Darlington, Hair & Hurcombe 1951; Darlington 1956). However, some of hypo- and hypertriploid numbers ($2n = 24, 25, 26, 29, 30$ and 32) occurring in young plants of *O. umbellatum* have not yet been found in adult plants. The present author supposes that in Polish material the conditions of life in crop-field associations favour vegetative propagation and are disadvantageous for germination of seeds and undisturbed growth of seedlings. In this connection a careful examination of specimens from triploid populations of *O. umbellatum* having more convenient conditions for generative reproduction is needed.

The population of *O. umbellatum* in Hitcham seemed to grow in such a habitat. The cytological diversity observed there was, however, slight. Triploid specimens prevailed and only two from among 33 plants had 28 chromosomes. The aneuploids grew in two separate groups of triploid plants; no group consisted of aneuploids exclusively. According to Lövkvist (1963), in sexually reproducing plants that also reproduce vegetatively e.g. in *Cardamine*, *Sagina nodosa* and *Saxifraga granulata*, aneuploids may have a more pronounced ability to form vegetative diaspores than the euploids. Aneuploid plants of *O. umbellatum* do not seem to belong to this group. They were not found in great numbers nor was the existence of any exclusively aneuploid population reported. As far as the rarity of aneuploid cytotypes within the population is concerned the possibility of the elimination of the additional chromosomes in somatic tissue should be taken into consideration. It is possible that this process is sufficient to prevent the accumulation of aneuploid plants. The case of aneusomaty observed in one bulb of the plant with 28 chromosomes may be considered as an indication of a tendency towards such an elimination.

The vegetative origin of 28-chromosome plants also cannot be excluded. They may be bud sports like some of the garden varieties of *Hyacinthus* whose vegetative origin in cultivation is well documented (Darlington, Hair & Hurcombe 1951). Mixoploidy observed in a few plants from Hitcham seems to be rather common in *O. umbellatum* but the supposition of the vegetative origin of some aneuploids requires further examination.

The cytological differentiation established for *O. umbellatum* in the course of the present investigation does not exceed the limits of the variability hitherto known for this species. Still more material is necessary in order to get a more exact view of the processes contributing to the karyological evolution of the species.

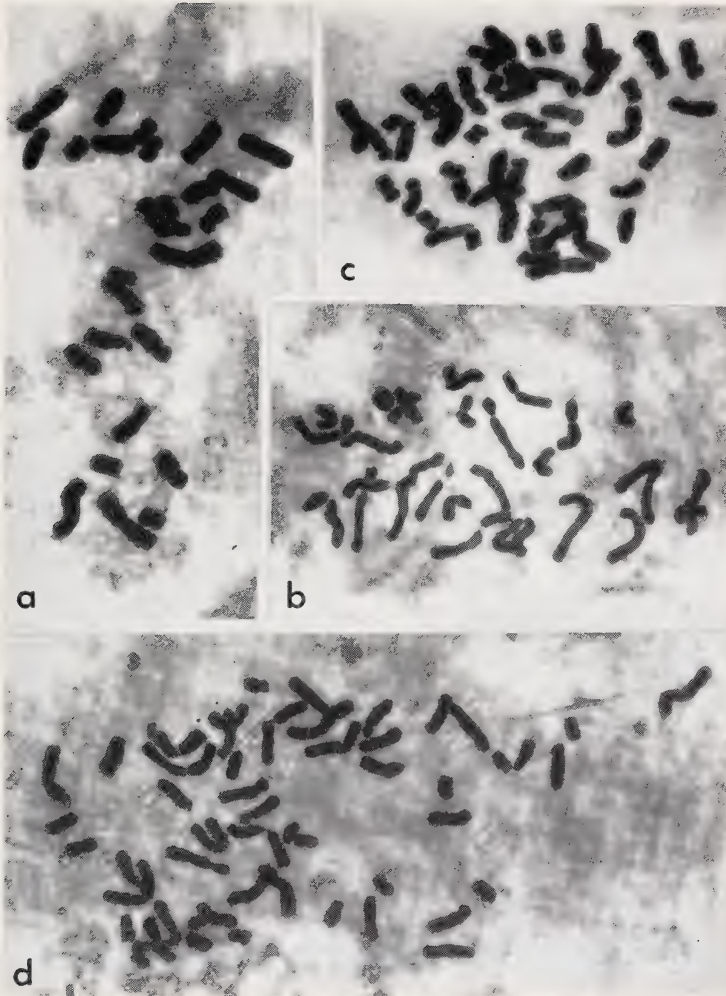
ACKNOWLEDGMENTS

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PLATE 16



Somatic chromosomes of *Ornithogalum umbellatum* L. a—triploid metaphase ($2n=27$, Icklingham); b—prometaphase of an aneuploid plant ($2n=28$, Hitcham); c—metaphase plate from the hexaploid sector of a triploid root tip (54 chromosomes, Hitcham); d—hexaploid metaphase ($2n=54$, roadside near Fleam Dyke). $\times 1000$

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COMPUTER MAPPING OF SPECIES DISTRIBUTION IN A COUNTY FLORA

By J. G. HAWKES

Department of Botany, University of Birmingham

B. L. KERSHAW

Computer Services, University of Birmingham

and R. C. READETT

Birmingham Natural History Society

ABSTRACT

Methods of computer mapping of distribution, habitat and frequency data of vascular plants in Warwickshire are described. A simplified mapping scheme for bryophytes is also outlined.

The primary data for vascular plants are transferred in the form of coded information to punched tape by means of a teleprinter and checked for errors. The data are then processed in the Birmingham University KDF9 computer by means of three separate programs, each taking the data forward to the next stage by means of magnetic tape.

Intermediate print-outs give a preliminary statistical treatment of the data, as well as a simple sketch map, which can be printed on the teleprinter or line printer.

The end product of the final program is a tape designed to give the necessary instructions to an incremental graph plotter. This draws symbols in the correct positions indicative of the habitat or habitats in which the species has been recorded. Two grades of frequency are shown by means of different line thicknesses. The plotted map will be reproduced with an overprinting in another colour, indicating the county boundary and various other features, as well as grid lines and border.

A series of bryophyte maps without habitat and frequency information but with data on fruiting will be printed on the teleprinter.

The wider applications of these mapping techniques are briefly discussed.

INTRODUCTION

The hand plotting of distribution data, whether of plants or of any other class of organisms, can be both tedious and expensive. If the data to be mapped are at all complex, errors may easily occur, which cannot entirely be eliminated, even after the expenditure of even more time and effort.

Within the last decade high speed electronic computers and associated equipment have become generally available and have made it possible for data to be stored with accuracy, and sorted and retrieved in a wide variety of ways. It would seem desirable, therefore, to use such equipment to sort and store distributional data, provided they can be presented to the computer in an appropriate way, and to devise systems by which they can be printed out in map form.

An excellent example of the use of electronic equipment in the production of distribution maps in this country is the B.S.B.I. Distribution Atlas (Perring & Walters 1962). The original maps for this publication were printed on a tabulator from data supplied to it from I.C.T. punched cards. The symbol on the map, which was a filled-in circle (except for some other symbols put in by hand afterwards), was positioned by making use of numerical co-ordinates taken from the National Grid at 10 km intervals.

Soper (1964, 1966) has discussed several methods of mapping the distribution of the vascular plants of Ontario by tabulating machines and digital plotters. The primary data, consisting of a code reference for the species together with geographical co-ordinates and some other information, were put on to punched tape and later transferred to 80-column I.B.M. punched cards. Soper pointed out that both tabulators and digital plotters with a printing head were capable of printing a limited number of symbols in a reasonably

satisfactory manner. On the other hand, a digital plotter with a drawing pen could be made to draw symbols of any shape and size, though it would, of course, need to be 'programmed' for each symbol. He pointed out that the method was not very satisfactory for drawing completely blacked-in symbols, and that smooth curves could not be formed very well because the pen could move only in successive rectilinear steps.

THE FLORA OF WARWICKSHIRE PROJECT

A survey of plant distribution in vice-county 38, Warwickshire, was begun in 1950 as a joint project of the Birmingham Natural History and Philosophical Society and the Birmingham University Department of Botany. This has been a co-operative study, involving a team of amateur and professional botanists in many hours of field work over some 16 years. It was begun by Mr. R. C. Readett and Mr. Peter Green. After the latter's move from Birmingham one of the present authors (J.G.H.) took his place, and the organizing panel now also includes Miss D. A. Cadbury and Mr. M. C. Clark.

The scheme was modified in 1954, when the 'basic square' technique of area recording was introduced (Hawkes & Readett 1954, 1963). This involved the detailed survey of 1 km squares as the unit of recording, one square at random being selected from each block of four, or 'tetrad'. An even survey over the whole county was thus feasible with only one quarter of the effort that would have been involved in recording from every square. There are thus 25 tetrads in each 'major square' of 10×10 km, which was the unit of recording for the B.S.B.I. scheme referred to above. In addition to this, a more conventional method of recording rare plants was carried out, since they would have been likely to have been missed altogether on the random square method.

The records obtained from the basic square surveys were written on to species cards representing a 10×10 km block of 1 km squares, printed at the scale of 1 in. to the mile and hence directly comparable with the Ordnance Survey map of that scale (Hawkes, Readett & Skelding 1955). This method also helped to give an idea of the distribution of the species at any time during the survey, since the records were displayed on a grid system in their correct spatial relationship.

Habitat data and frequency were also recorded on a pre-determined scheme using a system of major habitat groupings (e.g. woodland, waterside, water, cultivated land, etc.); each of these was divided into a number of minor habitats for greater precision (e.g. mixed woodland, oak woodland, conifer woodland, etc.) and suitable lexicographic symbols were devised for each (e.g. WO-m; WO-o; WO-c; for the habitats just given). Frequencies were recorded on the usual simplified system: abundant (a), locally abundant (1a), frequent (f), locally frequent (1f), occasional (o) and rare (r). It was emphasized that the frequencies should refer to each habitat for which the species was recorded, and not to the square as a whole.

From the inception of the scheme it had been hoped that it would be possible to transfer the habitat data in some way on to species distribution maps by means of symbols that would give a general impression of the community or communities in which a species was to be found throughout the county. A number of problems had to be solved here; in the first place, none of the symbols could be of the blacked-in type, since they would need to be presented in various combinations in the same square. Each must therefore be clearly visible, even when combined with several of the others. It was also necessary to devise symbols which would give easily recognizable patterns over the map as a whole. Thus, symbols which relied for their interpretation on their *position within a square* would clearly be valueless, since such a scheme would not enable the reader to obtain a general picture at a glance; each square would have to be examined individually. It was further decided to represent the record from each random square in the complete tetrad in which the random square occurred. This would prevent a false impression of distribution being produced as a result of 'clustering' of the random squares. A reasonably satisfactory series of habitat symbols was devised which conformed to the needs outlined above (see Cadbury, Hawkes & Readett 1957). These have been incorporated into the present scheme

with some modifications. At that stage (prior to 1964) it seemed impossible to devise a scheme for habitat recording which at the same time showed frequencies within habitats, though a general idea of frequencies could of course be obtained by looking at the spread of the species over the county as a whole.

The major habitat categories (woodland, waterside, water, heath, marginal, grassland, cultivated land and ruderal), eight in number, were, as we have already mentioned, divided into minor ones; there were 34 of these minor habitat categories for Warwickshire, and it was clearly impossible to devise a system of symbols to denote all these when each symbol needed at the same time to be distinguishable in a large number of different combinations. It was therefore considered that symbols showing the eight major categories would be all that could be reasonably expected for maps of this sort.

ELECTRONIC DATA PROCESSING

By 1964 a number of problems urgently needed attention. Since it was hoped to draw maps of some 700 species of vascular plants and 200 species of bryophytes a long and expensive period of map drawing seemed to be ahead of us. Although the bryophyte data were fairly simple, the prospect of drawing by hand the habitat symbols on 700 vascular plant distribution maps was one to which we did not look forward with much pleasure. There were somewhere in the region of 1,000 records a species for the more common species, each of which would need to be mentally interpreted into a symbol by the draughtsman and placed accurately on to the base map.

A further difficulty became apparent about that time. The habitat coding scheme, which was devised in 1950 and came into general use in its present form in 1954, was later felt to contain some errors of arrangement of minor into major habitat categories. Thus, the marginal category was found to be rather artificial from an ecological point of view. Whilst retaining the system for recording purposes, it was decided to keep 'hedgerow' in the marginal category and add 'scrub woodland' to it, at the same time removing all the others. 'Roadside' and 'railway' would fit best with the ruderal category (enlarged slightly to include 'viatical' elements); 'walls' and 'quarries' were removed from marginal and ruderal, respectively, and a ninth major category of 'stones, etc.' was created for them. When this was done, clearly an even more complex mental process would be needed to convert the original code letters on the species card into the correct map symbols.

A final point might be considered here. It was planned at a fairly early stage (see Cadbury, Hawkes & Readett 1957) to include habitat analyses in the Flora; these would show for each of the commoner species the range of habitats in which it had been recorded, expressed as the number of records for each habitat and the percentage figure, as well as the apparent 'preference' of the species for a particular habitat. For the second time in a county flora numerical data would be available for statistical analysis, the first being Good's *Geographical Handbook of the Dorset Flora*, 1948. The information available was sorted in one or two cases by counting occurrences in the different habitats and calculating percentages, as the first stage of the process. The data were extremely interesting, but the labour involved was quite considerable and carried with it as many possibilities of error as the drawing of the maps themselves.

Fortunately, at about this time Birmingham University bought an English Electric KDF9 computer, and it was therefore decided to process the whole of our data on this machine and at the same time to explore the possibilities of computer mapping of the distribution data. Clearly, some kind of graph plotter seemed to be the answer to the mapping problem, where X and Y co-ordinates could be used to position the symbols in the correct places on a previously printed map on continuous stationery. Unfortunately, most graph plotters incorporate a printing head with very small standard symbols. These completely obscure each other if overprinted, only one symbol can generally be printed in each position, and the symbols can often only be printed in a fixed sequence. Furthermore, the symbols available seemed to be far too small for our purposes.

The machine we finally adopted, after many exploratory discussions with a variety of firms, is an incremental plotter with a drawing pen, marketed by Benson-Lehner Ltd., of Southampton. Since these instruments are relatively expensive and we should only be needing one for this particular project, we agreed in April, 1965 to buy time on one of Benson-Lehner's own machines. We should like at this point to record our thanks to the representatives of this firm for their valuable help and co-operation in the project.

PREPARING THE DATA FOR THE COMPUTER

Apart from the very necessary programming work,* the first stage in preparing the data for plotting is to put it into a form which can be used by the computer. We had no punched card facilities at Birmingham when this phase of the work started and we therefore decided to use 5-hole punched tape. To this end we bought a Westrex teleprinter, which is in effect an electric typewriter with tape punching and reading facilities.

Punching began in December 1965, and we were fortunate in having the services of a skilled teleprinter operator (Mrs. M. Kershaw) for the whole period, working on a part-time basis, until Easter, 1967. This included not only the punching of the tapes, but also editing them; it must be admitted, in all fairness to the operator, that a lot of the 'editing' was nothing more than adding recently received records to a tape which was in fact a perfect copy of the original data.

The data were taken directly from the species cards, species by species, and in sequence of major square cards, the data being copied exactly and a 'print-out' produced as a by-product of the punching operation (Fig. 1). The print-out was used for checking against the original cards, a tedious exercise carried out by Miss D. Cadbury, Mrs. E. Pickvance, Mrs. Kershaw and others. Thanks are due to them for the dogged way in which they carried out this monotonous but all-important stage of the work.

After punching and checking, the data are ready to be passed to the computer. Three programs are used, but only the first reads the paper tape data. Each in turn operates on the data, taking the work a stage further and passing on partly processed intermediate results to the next stage by means of magnetic tape. The last program produces punched paper tape which is sent to Benson-Lehner and used to control the plotter to draw the final map.

ENTERING THE DATA INTO THE COMPUTER

The computer first checks the format of the data for four types of error:

- (1) Major square number unacceptable.
- (2) Minor square number unacceptable.
- (3) The same 1 km square mentioned twice.
- (4) Observation code unacceptable.

If an error is detected, the computer prints a message to guide the punch operator in correcting the mistake, and switches into a mode of operation in which it does not prepare intermediate results for further processing, but continues to read the data and print messages for any errors detected. In this way all errors in a particular data tape are found in one computer run and can all be corrected before the tape is resubmitted.

If, however, no errors are detected, the computer assembles within its memory an 'electronic image' of the required distribution map. Once this image is obtained, the rest of the computer process is directed to translating it into suitable control signals for the plotter. The first level map image is placed on magnetic tape ready to be further treated by the second program.

The first program, however, does rather more than this. Observations which are accepted and entered on the map image are counted, giving 204 totals, one for each minor habitat/frequency combination. These totals are printed to form the first table in the

* See Appendix, p. 360.

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3
acer campestre 1. 3
04
69.mhrf.
/
05
41.wooo.
43.mbro.
44.mro r.wo sca.
50.mbro.
54.wo sco.mbro.
58.mbro.wo mo.
60.mbro.
62.mhrr.
65.wo mlf.
66.mhrf.
68.mbro.
75.wo mo.mhrf.
76.wo scr.mbro.
82.mbro.
89.cfr.
92.mbro.
94.mhrlf.
96.wo me.
98.mhrr.
/
06
43.mbro.
44.wo sco.
51.mhrf.
54.wo mo.mhrf.
56.mhrr.
60.mbro.
64.mhrf.
65.mhrf.
67.mbro.
70.mbro.
73.mhrf.
75.mbro.
76.mbro.
77.mhrf.
80.mbro.
82.mbro.
84.wo mlf.
87.mbro.
92.mbro.
93.mbro.
94.mbro.wo scr.
98.mbro.
/
07
72.mhrr.
73.wo sco.
82.wo dr.
90.mbro.
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Fig. 1. Part of the data for *Acer campestre*, Field Maple, as typed on the teleprinter, showing major square numbers heading blocks of data, minor square numbers at the start of lines, and letter strings representing individual observations (e.g.: mhrf = hedgerow, frequent; wooo = oak wood, occasional; wo sca = scrub wood, abundant). The figure 3 at the top represents the B.S.B.I. code number for this species.

statistics (Fig. 2). The second table is simply the first recast in terms of nine major habitats and two frequencies, corresponding to the symbols drawn on the maps.

It should be noted that this first program also incorporates a 'random square sieve' which allows habitat and frequency data through for the simple statistics only if they have been recorded for random squares. Data for non-random squares are therefore suppressed, thus rendering what remains more statistically reliable. Many records have been submitted by collectors for non-random squares as well as for random ones and all these have been used for mapping. However, for showing habitat spread and preference of the species to be mapped it was considered essential not to bias the data in any way towards a preference of a collector for recording in a particular habitat, rather than a preference of a plant for growing in it! This preliminary statistical treatment of the data will not only help us to make useful and meaningful statements on habitat spread and preference in the general text of the Flora; it is also intended to provide a comparative table of habitat records for each of the 700 species that are mapped, giving both actual and percentage records in each of the nine major habitat categories.

Acer campestre L. 3

	A	LA	F	LF	O	R	TOTAL
MHR	2	3	134	24	255	71	489
WOM		1	7	1	43	14	66
MSC			3	1	15	6	25
RURD			5	1	8	1	15
RURY			1		7	3	11
WSR			1		8	1	10
WSC					3	1	4
WSD			1	1	1	1	4
WOO					3	1	4
GP			1		1	1	3
GM			1			1	2
GR						2	2
WSP						2	2
RUG						1	1
STQ						1	1
TOTAL	2	4	154	28	344	107	639

HABITAT	ABUNDANT		OCCASIONAL		TOTAL	
	OBS.	PERCENT	OBS.	PERCENT	OBS.	PERCENT
MARGINAL	167	26.1	347	54.3	514	80.4
WOODLAND	9	1.4	61	9.5	70	11.0
RUDERAL	7	1.1	20	3.1	27	4.2
WATERSIDE	3	0.5	17	2.7	20	3.1
GRASSLAND	2	0.3	5	0.8	7	1.1
STONES ETC.			1	0.2	1	0.2
TOTAL	188	29.4	451	70.6	639	100.0

Fig. 2. Data format check and simple statistics for *Acer campestre*. The input tape for this species contained no errors, so the computer has printed no error messages. In the first block of data the records are listed by minor habitats in one direction and frequencies in the other; general totals are given in the right-hand column and bottom line.

In the second block of data the records are listed in major habitat groups on two grades of frequency (abundant and occasional). Totals and percentages are also shown.

Note: these figures are based on random square data only.

The 'sketch map' (Fig. 3) uses each print position to represent one tetrad. If the species has not been observed in that tetrad, 'space' (blank) is printed; if the only observation(s) are occasional or rare, '+'; and if at least one abundant to frequent observation has been recorded, 'X'. There are 10 print positions to the inch across the page, but only 6 lines to the inch vertically; by inserting 'space' in alternate positions we have 5 symbols to the inch horizontally and 6 to the inch vertically, which is as near as it is possible to get to equalizing the horizontal and vertical scales.

The maps are therefore slightly wider than they should be, but are nevertheless most useful in giving a general impression of the distribution of each species throughout the county. They will not appear in the Flora (but see bryophyte maps, mentioned below) and will be used merely to provide a general indication of species distribution when the textual part is being drafted.

Those tetrads through which the county boundary passes are 'marked' in the computer's memory. When such a tetrad is empty, full stop is printed for it instead of space. These full stops build up a suggestion of the county boundary, assisting the interpretation of the sketch map.

FURTHER TREATMENT OF THE MAP IMAGES

The map images are taken from magnetic tape by the second program and converted into suitable control signals for the plotter, which are placed on a further magnetic tape. The third program transfers from this magnetic tape to paper tape; this is done for the convenience of the computer room staff and need not be discussed further here.

The plotter consists, effectively, of a pen moving over a sheet of paper, capable of drawing any shape required by incremental movements of 0.1 mm (or 0.005 in. on the non-metric model) in any one of the four cardinal directions. Left to right movements are



Fig. 3. Interim 'Sketch Map' for *Acer campestre* L.

Printed on the computer's fast output line printer, this map took only three seconds to produce.

- + Occasional to rare in tetrad.
- X Frequent to abundant in tetrad.
- . Indicates position of county boundary when no record exists in this tetrad.

accomplished by the actual movement of the pen, whilst up and down movements are accomplished by corresponding movements of the paper. Diagonal lines are drawn by combined pen and paper movements, whilst further control signals instruct the pen to begin or to cease marking.

A reasonable solution to the problem of showing frequencies, as well as habitats, on the same map has also been devised, though admittedly not all grades of frequency can be given. This was done by indicating 'rare' to 'occasional' by means of a thin line and 'frequent' to 'abundant' (including 'locally frequent' and 'locally abundant') by a thick one. If these ideas were to be translated into a completely automated system it would clearly be impossible to change pens every time a change of line thickness was required. We therefore decided to use a thin pen throughout and to program it to re-draw the symbol after displacing the pen by two increments if a thick line was required. Since the pen thickness (0.2 mm) is the same as this displacement, the two single thin lines will ideally produce a line twice the thickness of the thin one. In theory there should not be a perfect coincidence of the two lines when diagonals and circles are drawn, but in practice they seem to coincide quite well.

All the symbols (except the circle, which is a special case) are made up of vertical, horizontal or diagonal straight lines (Fig. 4).

Fig. 5 shows how the circles, thick and thin, are built up from short horizontal, vertical and diagonal straight lines. The exact arrangement of these lines was decided by a preliminary computer run to design the best possible circle within the limitations of the plotter.

Two problems arise in preparing the plotter control tape: moving the pen to the required map location for a symbol, and drawing the symbol once the pen is correctly located. The second is easier of solution, since the drawing of a symbol is identical, regardless of its position on the map: 18 standard sets of drawing instructions, one for each symbol, are held in the computer and the correct one is selected after the pen has been positioned.

Positioning the pen to draw a symbol is complicated by the desire to keep pen movement, and therefore plotter time and cost, to a minimum. As each symbol is drawn it is erased from the computer's map image, and the machine then chooses the nearest remaining symbol to the plotter pen's current position to be drawn next.

Besides drawing the symbols, the plotter writes a reference number on each map so that it can be identified and given the correct title in printing; two register or 'fiducial' marks, one at the top left of the map and the other at the bottom right, are made so that the printers can correctly superimpose the plotted symbols on the standard outline of the county which is overprinted on every map (Fig. 6).

PUBLICATION OF THE MAPS

In this paper we cannot go into the plans for printing the Flora as a whole, but shall confine ourselves to the mapping process. Pergamon Press, Ltd., have agreed to publish the Flora, and have, of course, been consulted over the presentation of the maps. They plan to make a map of two printings. One of these, printed in black, will be reproduced from the plot of the symbols for each species, and will have keys and species names added at the time of photographing. The other will be printed from a standard block, in some other colour (probably blue, red or brown) and will comprise the county boundary, the grid lines, some physical features, such as conurbations, roads, railways, etc., and the border and panels. These will be combined, using the fiducial points for exact registration of the two printings. Transparent overlays will also be provided, giving geological and other information of possible interest for an interpretation of distribution patterns.

BRYOPHYTE DISTRIBUTION MAPS

The bryophyte survey, which has been planned and largely carried out by Mr. T. Laffin, is conceived on a slightly different basis from the vascular plant survey. In the bryophyte study, species lists without habitats but with data on 'fruiting' or 'sterile' will be punched

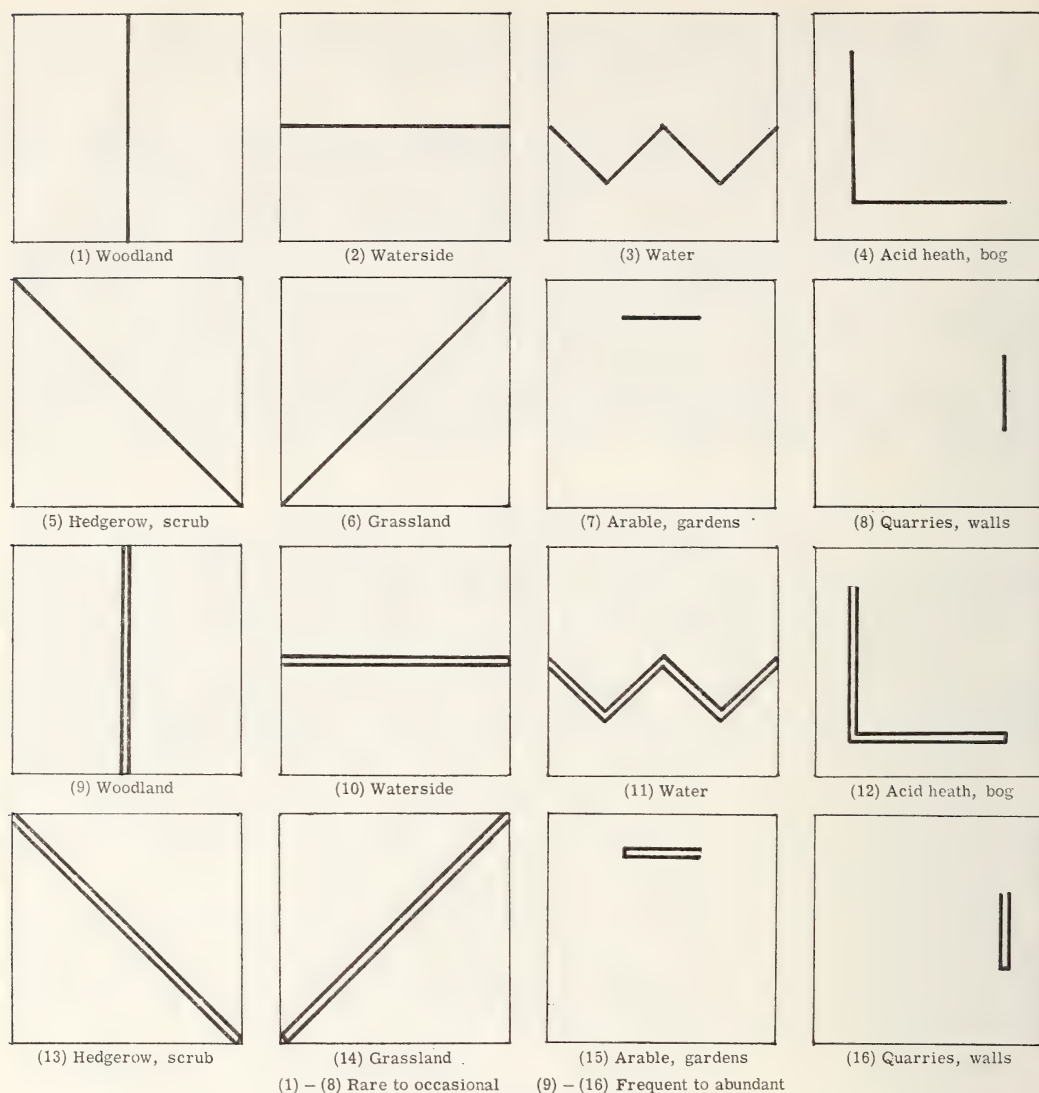


Fig. 4. Enlarged drawings of habitat symbols (other than 'ruderal') showing the track of the pen centre. At the actual size at which these are plotted (in a square of 6 mm sides) the line drawn (0.2 mm) is wide enough to fill completely the space between the lines of a thick symbol.

on the teleprinter. Thus, each record will consist of a species code reference, based on the bryophyte census catalogue number, together with a grid reference and a symbol denoting fruiting or sterile. The tapes will be passed through the computer with a different program, and an output tape produced which will give a map on the teleprinter. This device is used rather than the fast printer, since it is proposed to publish these maps direct, and the print quality of the fast printer is not really good enough for publication. Pilot maps have been produced already but at the moment of writing the primary bryophyte tapes have yet to be punched.

The teleprinter maps will bear two distinct kinds of symbol, for fruiting or sterile, and the records for these will be added up and percentaged as a by-product of the computer program (Fig. 7). These maps will also be overprinted with a standard map in some other colour, as with the flowering plant maps, though they will be reduced in size so that

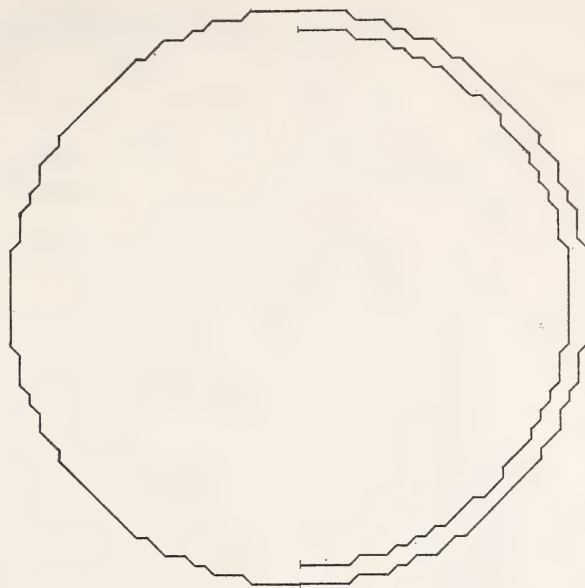


Fig. 5. The circle (Ruderal symbol), not shown in Fig. 4. On the left is the pen track to draw a thin circle. The two tracks on the right, separated by about two steps throughout, combine to form a thick circle.

four maps, instead of two, can be printed on each page. These maps, like those produced on the fast printer, suffer from inequality of vertical and horizontal scales, so the standard overprint map will have to be correspondingly distorted.

FURTHER APPLICATIONS

At the time the Warwickshire Flora survey was begun there was no prospect of a computer becoming available at Birmingham and for this reason the storage of data on punched cards or tape was not envisaged. Our data were therefore rather laboriously written on to species cards and only much later transferred to tape. It would almost certainly have been easier to have put our records on to punched cards in the first instance, as was done for the B.S.B.I. Atlas of the British Isles.

A Fungus Survey of Warwickshire has now been started and a flowering plant survey of the Wyre Forest, near Bewdley, is just beginning. With the card punching, sorting and reading facilities now available to the biology departments at Birmingham it is hoped that the data can be stored directly on punched cards or on tape. In both of these schemes mapping of some kind is envisaged, though the exact details have not yet been decided.

In County Flora work or in recording distribution of plants for even smaller areas one has limited and often specific objectives. For surveys of a wider nature on a national scale, on the other hand, the perspectives are remarkably wide. Such mapping techniques could be used to portray the distribution of any kind of organism, of fungal or other diseases, of genetic variability in cultivated plants or the results of demographic surveys, to name only a few applications. Simple and inexpensive maps of the 'sketch map' type can be produced with great speed, once the basic programs are available, and provided the data are collected in a suitable form. The more sophisticated type of map which is drawn on a graph plotter has an even wider application, limited perhaps only by the capacity of the data collectors to obtain the information desired. What seems quite clear is that computer mapping has an exciting future whose outlines at present we can only indistinctly perceive.

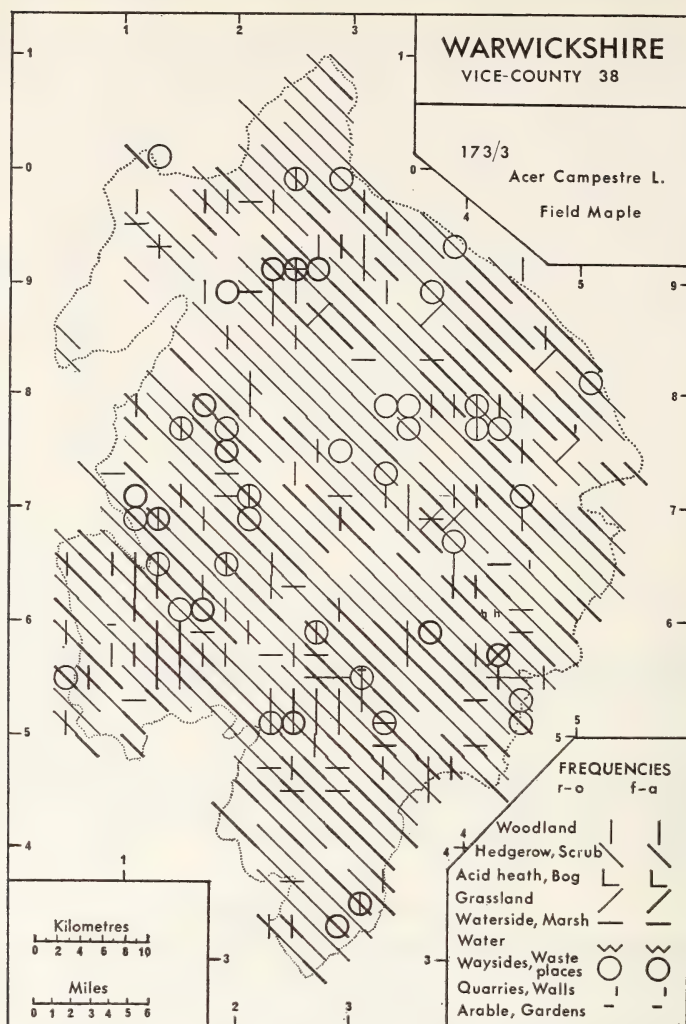


Fig. 6. Plotted map for *Acer campestre*. The county boundary, title, grid references, etc., have been added by hand. In the final publication these and other data will be overprinted in another colour. (Note: This is only a pilot map; symbol connectivity will be improved in the Flora itself.)

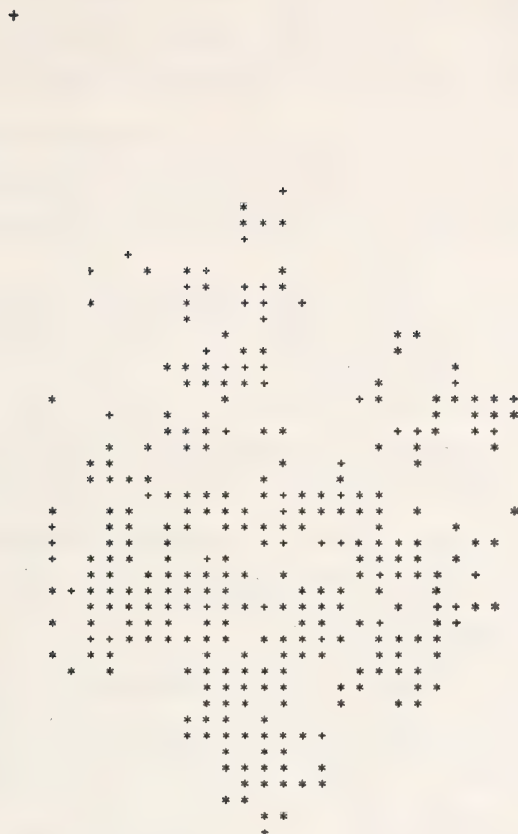
APPENDIX

FURTHER DETAILS OF THE COMPUTER PROGRAMS

Some readers may be interested in a rather more detailed description of the computer programs than was thought admissible in the body of the paper. The language used was K-Code, the KDF9 dialect of Mercury Autocode, except for the final program which was written directly in symbolic assembler. K-Code possesses many sophisticated and useful bit handling and logical operations and allows the easy introduction of patches of assembler in areas of high-level language.

The unit of recording, the minor square, is equated with the computer word. The KDF9 word has 48 bits, of which the least significant 18 are used to represent the presence or absence of the species under consideration in the 18 possible habitats, 9 'abundant' and 9 'occasional'. One other bit indicates whether or not the square is random; this is the sign bit, giving fast discrimination of random/non-random squares by the sign detection hardware.

2129011
Amblystegium serpens (hedw.) b., s. and fr.



471 observations, 375 (79.62 percent) fruiting.

Fig. 7.1A simple moss distribution map (*Amblystegium serpens*), produced on the teleprinter. Borders, grid references, etc., will be printed in another colour in the final publication.

+ Not fruiting, sterile.

* Fruiting.

Records of sterile and fruiting are totalled and percentaged.

If K-Code had facilities for 2-dimensional arrays, one would have been used to represent the map plotted by squares. This facility, however, is missing, so it is necessary to use a 1-dimensional array and calculate unique subscripts from the X- and Y-positions of the square under consideration, themselves calculated from the major and minor square

numbers. If, when first mentioned, a square has any bit other than the sign bit non-zero, an input error, minor square mentioned twice, is signalled. Whenever an error is detected, an appropriate message is output and an error marker is set.

The input letter strings are packed into one word each. The input symbols read by K-Code are of 8 bits each, so the longest possible string, 6 letters (e.g. WOSCLA) just fits into one 48-bit word. Had there been 7-letter input strings the programming would have been considerably more difficult.

An assembled input string is compared word by word with a permanent list of 204 permissible strings. The subscript of the list word which matches the string gives a simple encoding, a number from 0 to 203 inclusive, of the input word. If no match is found the 'code unacceptable' error occurs. After a successful search of the list, the encoded form of the input string is used in three ways:

1. Placed directly onto magnetic tape, so that the input data, encoded, will be available for future work without the necessity of reading the paper tapes again.
2. As subscript to control the adding of 1 to one of 204 counters, thus accumulating the raw material for the statistics.
3. Also as subscript, to select a shift length. A 1 bit, shifted by this amount, becomes a marker for an occurrence in that major habitat/frequency and is combined with the previous contents of the correct work in the map image by the logical 'OR' operation, thus avoiding disturbing any markers already present in that word.

When the map is complete, known by the detection of the character '>' on the input (an arbitrary choice from the unused symbols on the teleprinter keyboard) the error marker is consulted. As messages are output as soon as an error is detected, if the marker is set no further action for that species is needed.

Assuming the error marker clear, however, the next action is to convert the map plotted by squares into the map plotted by tetrads. Suitable indexing selects the four squares forming one tetrad, and they are combined into one word. A slight complication arises here. A species may be both abundant and occasional in the same major habitat—e.g. abundant in oak woodland, occasional in mixed woodland. An abundant symbol blots out an occasional symbol in the plot, but to draw the thin symbol would be a waste of time and money. The routine which combines squares into tetrads therefore erases occasional observations wherever there is an abundant observation in the same tetrad and major habitat. This is achieved by a combination of shifting and logical operations. The tetrad record is placed into the appropriate location of a tetrad array, which is filled up by a suitable scanning process and becomes the final map image. This image is placed on magnetic tape ready to be handed on to program 2.

The statistics are assembled from the 204 counts, suitable totals being taken and the information re-ordered with the most favoured habitat being printed first, then the next most favoured and so on. Zero counts are suppressed.

The sketch map is formed by printing 'space' if a zero word is found during scanning of the tetrad array, 'X' if the value is greater than 511 and '+' if the value is non-zero but not greater than 511. Details of the county boundary are held in preset ('V') stores in which each bit represents a tetrad, being 1 if the boundary passes through that tetrad, zero if not. If the tetrad is empty, the appropriate bit is consulted to decide whether or not to print full stop.

The second program takes the first program's map images from magnetic tape and prepares a new magnetic tape which the final program converts into paper tape for the plotter. Having obtained an image from magnetic tape, program 2 scans it row by row. Each row is 'pre-scanned' from left to right and the positions of the left-most and right-most occupied tetrads compared with the current pen position. The latter is held in two words, one for X and the other for Y, and is assumed to start at the top left corner of every map. If the pen is nearer the left-most symbol the row is plotted with the pen moving generally from left to right, and *vice versa*. This is not a perfect way of choosing the shortest

path to visit every symbol, but it is a reasonable compromise between waste pen movement and program complexity.

Having selected an occupied tetrad, the computer recalculates the current pen position in terms of an origin at the bottom left corner of that tetrad. All plotting uses this 'floating origin' technique; its advantage is that the symbol-drawing routines need not keep track of the varying positions of the symbols relative to a fixed origin. Instead they work relative to an origin which is always in the current tetrad, and a short and fairly simple routine moves the origin from tetrad to tetrad.

The computer now examines all entry points to all symbols in the selected tetrad and picks the nearest one to the current pen position. An entry point is a point at which drawing of a symbol may start; for example, the 'woodland occasional' symbol, a vertical line, may be drawn either by taking the pen to the top centre of the tetrad and moving it down, or by taking it to the bottom centre and moving it up. Top and bottom centre are the two entry points for this symbol. For the thick symbol, a narrow vertical rectangle, there are four entry points, one at each corner. Similar entries exist for all symbols, and having chosen the handiest the computer raises the pen and takes it to that point. No movement may be necessary, as with 'waterside' and 'water' symbols in the same or horizontally adjacent tetrads, in which case the pen is not raised.

Each symbol, including the circle, is built up from straight lines, and each straight line is defined by two items. It is rather easy to split KDF9 words into three 16-bit parts, known as the C, I and M parts. (Exactly why they are given these names would take us too far from our present subject.) Having selected a symbol entry point, the computer refers to a word whose C part specifies how many steps are needed to draw the first line of the symbol. The M part holds a bit pattern which can be interpreted as a step instruction by the plotter, so that between them the C and M parts completely specify the line. The I part is zero if that line completes the symbol, non-zero if at least one more line is needed to complete it. In the latter case, similar details for the next line are in the next word on the list.

This can best be explained by an example. Three lines are needed to draw the 'woodland abundant' symbol starting at its top left corner. The symbol is a rectangle 60 steps high and 2 steps wide, and the relevant control words are:

Word 1 C part	60	(Steps down)
Word 1 I part	Non-zero	(Another line follows)
Word 1 M part	'Down'	(Expressed as a plotter control)
Word 2 C part	2	(Steps across)
Word 2 I part	Non-zero	(Another line follows)
Word 2 M part	'Right'	(As a plotter control)
Word 3 C part	60	(Steps up)
Word 3 I part	Zero	(Symbol complete)
Word 3 M part	'Up'	(As a plotter control)

Compare with this the single word used to draw the 'woodland occasional' symbol (vertical line) from the top:

C part	60	(Steps down)
I part	Zero	(Symbol complete)
M part	'Down'	(As a plotter control)

Similar sets of words are provided for every entry point of every symbol, together with a 'symbol directory' giving details of where they begin in the control word array and of the pen positions before and after drawing them.

Having plotted one symbol the computer removes its marker from the map image and checks if the current tetrad is now empty, *i.e.* all symbols in it have been plotted and their markers removed. If not, the process of finding the nearest entry point to the (new) pen position, going to it, plotting the symbol and removing its marker is repeated until the tetrad is clear, when the next occupied tetrad is found, dealt with and cleared in the same

way. After one row has been plotted the next is examined, the decision to plot from left to right or right to left made afresh and the whole process repeated until the map is complete.

The map area is extended by four rows above and below the county, and the fiducial marks are created by putting dummy 'woodland occasional' and 'waterside occasional' observations into the top left and bottom right tetrads. These plot as vertical and horizontal lines, which combine to form '+' crosses whose centres, always in fixed positions relative to the map grid, are the fiducial points.

On magnetic tape a line is represented by two or four 6-bit characters. In the two character case, the first is the actual control symbol for the plotter, which occupies 5 of the 6 bits. The next 6 bits are a binary number giving the length of the line in terms of plotter steps required to draw it. If the line is longer than 63 steps, the sixth (32) bit of the first character is made 1 and the second character is the quotient on dividing the number of steps required by 64. Any remainder is dealt with by another two characters, the first with its 32 bit zero and the second directly specifying the remainder. This system cannot draw lines longer than

$$(63 \times 64) + 63 = 4,095$$

steps. The longest possible line on a map, right from top to bottom, is 3,180 steps, so this limitation is not important.

The final program simply transfers the information from magnetic tape to paper tape. It takes two 6-bit characters from magnetic tape, examines the 32 bit of the first and if it is 1, clears it and multiplies the second number by 64. The first character is then output to paper tape the specified number of times. This system, which effects a considerable economy of magnetic tape, is to be adapted as part of the on-line plotting system when Birmingham University's plotter is delivered later this year.

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PARIETARIA OFFICINALIS AND P. JUDAICA

By C. C. TOWNSEND

The Royal Botanic Gardens, Kew

ABSTRACT

A full account is given of the nomenclature and typification of the British species of *Parietaria*. It is shown that the type of *P. officinalis* L. is specimen No. 1220.2, and that of *P. judaica* L. specimen No. 1220.3, in the Linnaean Herbarium (LINN). *P. officinalis* is a species found in the Orient and central and northern Europe, but absent from the British Isles. The British species should be called *P. judaica* L., of which *P. ramiflora* Moench and *P. diffusa* Mertens & Koch are synonyms. The diagnostic features of *P. officinalis* and *P. judaica* are given.

Although name-changes in the British flora have been not infrequent in recent years, comparatively few have been based purely on taxonomic conclusions; rather have the majority resulted from the exploration of the very necessary, but to most botanists rather arid, fields of bibliography and nomenclature. It would appear, however, that the name by which British botanists know the common Pellitory-of-the-wall must be changed on purely taxonomic grounds.

In the current authoritative check-list of British plants (Dandy 1958), the Pellitory is listed as *Parietaria diffusa* Mertens & Koch, with *P. officinalis* auctt. and *P. ramiflora* auctt. in synonymy. These synonyms reflect two taxonomic conclusions; firstly, that the names *P. officinalis* L. (1753) and *P. ramiflora* Moench (1794) have been misapplied to our British species, and secondly, that taxa described under these names represent one or more species distinct from *P. diffusa* Mertens & Koch.

The existence of at least two closely related species of *Parietaria*—one erect in habit with larger leaves, the other more decumbent with smaller foliage (to which the degree of accrescence and form of the perianth of the hermaphrodite flowers and various other characters have been added)—has been indicated by three principal authors, viz. Linnaeus (1756), Moench (1794) and Mertens & Koch (1823). Linnaeus, in the dissertation '*Flora Palaestina*', described *Parietaria judaica* L. in the following terms:

Parietaria Judaica accedit ad Parietariam officinalem, sed caule glabro, petiolis brevioribus, florum aceruis ad ramos, vix vero ulli ad caulem.

This diagnosis was based on material collected by his student Hasselquist in Palestine, as the entry here '582 judaica H. Palaestina' indicates.

Moench contrasts his new species *P. ramiflora* with *P. officinalis* in the following manner:

officinalis L., caule erecto: foliis lanceolato-ovatis: subhirsutis: florum glomerulis caulinis pluribus pedunculatis. *Icon Oederi, Tab. 521.*

ramiflora, caule decumbenti: ramis non caule floriferis: glomerulis sessilibus: foliis hirsutis ovatis. *Parietaria judaica* Linn. *Parietaria officinalis* Pollich. *Pal. n.* 940 huc pertinet. Folia minora atro-virentia.

Mertens & Koch simplified the matter (for themselves!) by distinguishing two species of *Parietaria* and, feeling that other names had been confused by previous authors (as reflected in their synonymy), they renamed these species *P. erecta* and *P. diffusa*. The single name *P. officinalis* (of various authors) figures in the synonymy of *P. erecta*, while in the synonymy of *P. diffusa* the names *P. officinalis* 'nach Smith', *P. judaica* Wild. and *P. ramiflora* appear.

From the above facts, and from Mertens & Koch's further observations, it is clear that:

1. In describing *P. ramiflora*, Moench was also superfluously renaming *P. judaica* L.
2. In describing *P. diffusa*, Mertens & Koch believed themselves to be renaming

P. ramiflora Moench, but did not consider that this was in fact true *P. judaica* L. Neither did they know for certain whether their *P. erecta* was true *P. officinalis*.

The first requirement is thus to typify both *Parietaria officinalis* and *P. judaica*. Paclt (1952) has stated that the type of *P. officinalis* is in the *Hortus Cliffortianus* Herbarium at the British Museum, where the species is represented by two specimens, of which Paclt gives photographs. One of these is '*P. erecta*' and is described by Paclt as the holotype; the other is '*P. diffusa*', and is described by Paclt as the paratype. In point of fact, Linnaeus did not cite a holotype and therefore, by definition, there could be no paratype. If the *Hortus Cliffortianus* specimens could be regarded as types at all they would be syntypes, because Paclt selected the specimen resembling '*P. erecta*' as the lectotype of *P. officinalis* L. Clearly, however, neither of these specimens can be regarded as the type of *P. officinalis*. Linnaeus' concept of this species had altered from that which he held when writing the *Hortus Cliffortianus* by the time he wrote the *Species Plantarum*. Two points alone will illustrate this:

1. In the *Hortus Cliffortianus*, '*Parietaria sicula, alsines folio. Bocc. sic. 47, t. 24*' is cited under *P. officinalis*. In the *Species Plantarum* this has been transferred to *P. lusitanica*.

2. In the *Hortus Cliffortianus* the main diagnostic phrase given for *P. officinalis* is '*Parietaria foliis lanceolato-ovatis*', while in the *Species Plantarum* this reads '*Parietaria foliis lanceolato-ovatis alternis*'.

From point (2) it is obvious that, in addition to his changed concept of *P. officinalis*, Linnaeus had before him at the time of writing the *Species Plantarum* (when the *Hortus Cliffortianus* Herbarium was not available to him) a further specimen enabling him to add the word 'alternis' to his diagnosis. Thus there can be no doubt that the true type of *Parietaria officinalis* is the specimen No. 1220.2, in the Linnaean Herbarium housed at the rooms of the Linnean Society of London (LINN). The statement by Scholz (1955) that *P. officinalis* must be rejected as a *nomen ambiguum* is quite incorrect.

At this point, the name *P. officinalis* departs from consideration for the British Pellitory-of-the-Wall. Moench typified this species correctly, for the Linnaean specimen is the plant also known as *P. erecta*, and is not a British species. Dandy is thus correct in calling the British Pellitory '*P. officinalis* auct.' (non L.)

There is in the Linnaean Herbarium one specimen (1220.3) labelled '*judaica*' by Linnaeus in his own handwriting and bearing a sign indicating a western Asiatic origin. This is evidently the plant of the *Flora Palaestina* dissertation, and can be accepted as the holotype of *P. judaica*. Another specimen in the Linnaean Herbarium (1220.4) bears the abbreviation 'H.U.', indicating that it was cultivated in the Uppsala University Botanic Garden, which was under Linnaeus' control; but the epithet *judaica* was added by Smith, the subsequent owner of the Linnaean Herbarium, and not by Linnaeus himself.

The real problem is—are *P. judaica* L. (*P. ramiflora* Moench) and *P. diffusa* Mertens & Koch conspecific, or are they not? Opinions have differed widely, and during the course of naming general collections of plants from the Balkans and south-west Asia the writer has had an opportunity to test the various treatments, and to resolve the matter while preparing an account of the *Urticaceae* for the *Flora of Iraq*. All that can be said is that from the existing accounts one is quite unable to distinguish confidently between *P. diffusa* as represented by British material and *P. judaica* as represented by Oriental material.

The greatest authority on the flora of eastern Europe and western Asia, Edmond Boissier, had no doubts in this matter. In 1875 he reduced *P. diffusa* to synonymy under *P. judaica*, describing at the same time a var. *brevipetiolata*, into which he sank *P. multicaulis* Boiss. & Heldr. Hayek (1924) took up the name *P. vulgaris* Hill, *Brit. Herb.* 491 (1757), for the decumbent Pellitory, and cited *P. diffusa*, *P. ramiflora* and *P. judaica* Hal. (non. L.) in his synonymy, with reference to a paper by Vierhapper (1919). *P. vulgaris* Hill, however, is a name which must be rejected under Article 23 of the *International Code of Botanical Nomenclature*, as an incidental binomial published in a work which did not consistently employ binomial nomenclature. Vierhapper appears to have attempted to separate *P. judaica* and *P. 'ramiflora'* by means of vegetative characters which become less impressive as one

studies material from various points in the geographical range of the aggregate as a whole.

Hegi (1912) adopted the strange course of using the name *P. ramiflora* Moench, while placing *P. judaica* L. in synonymy, together with *P. diffusa*. This has been rectified by Schreiber (1958) in the second edition of Hegi's *Flora*, who omits *P. judaica* from the synonymy of *P. diffusa* without giving reasons for so doing. Finally, the two European *Floras* which use, probably, the broadest and narrowest views of species were consulted. Fiori (1923) relegated both *P. erecta* and *P. judaica* to varietal rank under *P. officinalis* with *P. ramiflora* and *P. diffusa* in synonymy under *P. officinalis* var. *judaica*. In the *Flora URSS*, Jarmolenko (1936) separated *P. judaica* from '*P. officinalis*' (i.e. *P. 'ramiflora' / diffusa*) and '*P. erecta*' (*P. officinalis*), on the grounds that in *P. judaica* all the flowers are hermaphrodite, while in the other two species the lower flowers of the inflorescence are pistillate. Examination of the Linnaean type, and general material of *P. judaica* in herbaria, did not bear out this distinction; though the female flowers of *P. judaica* are always harder to see than those of *P. officinalis* L., at least one can be seen on the type specimen without dissection of the cymes.

While examining the Kew herbarium (K) material of *Parietaria* an interesting feature arose from this distinction brought to light by Jarmolenko. This is the gradual reduction eastwards in the number of female flowers to be found in the decumbent *Parietaria*. In the extreme west of its range (e.g., in Great Britain), female flowers are plentiful. On reaching Greece these are still readily found but are considerably fewer in number. A specimen illustrating this is *Heldreich, Herb. Fl. Hellen. 94*, gathered on the Athens Acropolis. In western Turkey (e.g., *Sinten, Iter Trojanum 486*), female flowers are still frequent, but as one moves eastwards they become progressively harder to find and are often absent. The writer could detect no female flowers, for example, on isotype material of *P. multicaulis* Boiss. & Heldr. (from Pisidia), or on *Davis, Dodds & Ćetik 19045*, gathered at Niğde, C. Anatolia, or on several other recent specimens gathered by Dr. P. H. Davis and his collaborators. On the following specimens: *McNeill 502* (Bitlis), *Davis 16616* (Bozkir) and *Aucher 9794* (Aintab), however, female flowers were scarce but certainly present. Sometimes in the Orient the female flowers are solitary and are found in the axils of the lower leaves—e.g., *Maitland 100* (Baalbek, Syria) and *Post 1015* (Beirut, Lebanon). When female flowers are present, their morphology is similar to those of the British and western European *P. diffusa*. Somewhat strangely, all the Egyptian material seen has plentiful female flowers. In Iraq, female flowers may be present or not in gatherings otherwise taxonomically indistinguishable, and in Iran female flowers are rarely found at all. The pattern of gradual decline makes specific or even infraspecific separation by means of this character impossible. Weddell (1856) attempted to separate *P. judaica* and *P. officinalis* var. *diffusa* (Mertens & Koch) Weddell by stressing the latter part of Linnaeus' diagnosis—'*Florum acerui ad ramos, vix vero ulli ad caulem*', observing: '*Par ces mots: florum acerui, etc., l' auteur de l'espèce a en effet mis en relief un des traits les plus essentiels de la plante, et celui qui la distingue le plus nettement du P. officinalis. En d'autres termes, les tiges cespitueuses du P. judaica sont sous-frutescentes et vivaces, tandis que celles du notre Pariétaire (P. officinalis) commune sont ordinairement herbacées et annuelles*'. A footnote guards us against using plants of *P. judaica* flowering in the first year for this comparison. Weddell also observed in his description of *P. judaica*: '*floribus hermaphroditis quam feminei multo numerosioribus*', but does not go so far as to say that female flowers may be absent. Béguinot (1908) did not find this growth character at all satisfactory, nor does it appear to be so; in the Orient many species become more woody than in Europe, often due to constant grazing by the ubiquitous goats, and all manner of transitional forms occur. Two specimens from the Rowanduz Gorge of Iraq, *Guest 13094* and *Guest 2091*, show respectively a much-branched plant with almost all the flower-clusters on the branches and a less-branched plant with most of the cymes disposed along the stem. The remarks of Mertens & Koch follow much the same pattern as those of Weddell, but it is clear that none of these authors had seen the type specimen of *P. judaica*. No character has come to light by which *P. judaica*

may be separated from *P. diffusa* and *P. 'ramiflora'* or by which two distinct taxa representing the latter two species may be recognized.

Thus, the earliest name available for the British Pellitory-of-the-Wall is *P. judaica* L. It is remarkable that this name has not hitherto been adopted in this country in view of the fact that Villars (1787) used the name *P. judaica* L. for the Western species before either *P. ramiflora* Moench or *P. diffusa* Mertens & Koch was published for which correct decision he was taken to task by Weddell (1856).

Various authors have included the decumbent Pellitory (under one name or another) in *P. officinalis* L. at varietal or subspecific rank, but it is in fact a distinct species. *P. officinalis* has a much more restricted range, being chiefly found in central and northern Europe, reaching westwards to the Iberian Peninsula (where it is rare) and eastwards to northern Iran. *P. judaica*, on the other hand, extends further west to the British Isles and Macaronesia, east to Tian Shan and Pakistan and south to N.W. Africa, Egypt, Palestine and Iraq. The differences between the two species are dealt with in detail by Mertens & Koch; much of the difficulty in separating them has been caused by undue emphasis being placed on characters of foliage and habit, in both of which *P. judaica* in particular is very variable. Table 1 summarizes the characters found most useful by the present writer.

TABLE 1. Comparative characters of *Parietaria officinalis* L. and *P. judaica* L.

	<i>P. officinalis</i> L.	<i>P. judaica</i> L.
<i>Female flower</i>	Length in fruit 2.75–3 mm, much exceeding the bracts, very conspicuous. Segments more broadly lanceolate, midrib and margins confluent only at the tip.	Length in fruit 2.0–2.25 mm, not much exceeding the bracts, rather inconspicuous. Segments narrowly lanceolate, subaristate with the confluence of the midrib and margins.
<i>Hermaphrodite flower</i>	Petianth remaining campanulate in fruit, not exceeding 3 mm.	Petianth in fruit tubular, accrescent to 3–3.5 mm.
<i>Achene</i>	More narrowly ovoid, 1.5–1.8 mm long, frequently distinctly asymmetrical.	Shortly ovoid, 1.0–1.2 mm long.

The following is a limited synonymy, omitting the numerous infraspecific taxa based mostly on leaf characters.

PARIETARIA OFFICINALIS L., *Sp. Pl.* 1052 (1753).

P. erecta Mertens & Koch, *Röhlings Deutschlands Flora* ed. 3, 1, 825 (1823).

P. officinalis L. var. *erecta* (Mertens & Koch) Weddell, *Archs. Mus. natn. Hist. nat.*, Paris 9, 507 (1857).

P. officinalis subsp. *erecta* (Mertens & Koch) Béguinot, *Nuov. G. bot. ital.* 15, 341 (1908).

PARIETARIA JUDAICA L., *Fl. Palaest.* 32 (1756); *Amoen. Acad.* 4, 466 (1759).

P. vulgaris Hill, *British Herbal* 491 (1757), nomen nonrite binom.

P. ramiflora Moench, *Meth.* 327 (1794), nomen superfluum illegitimum.

P. assurgens Poir., *Encycl. Méth.* 5, 15 (1804).

P. punctata Willd., *Sp. Pl.* ed. 4, 4, 953 (1805).

P. diffusa Mertens & Koch, *Röhlings Deutschlands Flora* ed. 3, 1, 827 (1823).

P. maderensis Reichb., *Flora (Regensburg)* 13, 131 (1830).

P. officinalis L. var. *diffusa* (Mertens & Koch) Weddell, *Archs. Mus. natn. Hist. nat.* Paris 9, 507 (1857).

P. officinalis L. var. *ramiflora* Aschers., *Fl. Brandenb.* 610 (1864).

P. officinalis L. var. *judaica* (L.) Gort., *Fl. Friul.* 2, 140 (1906).

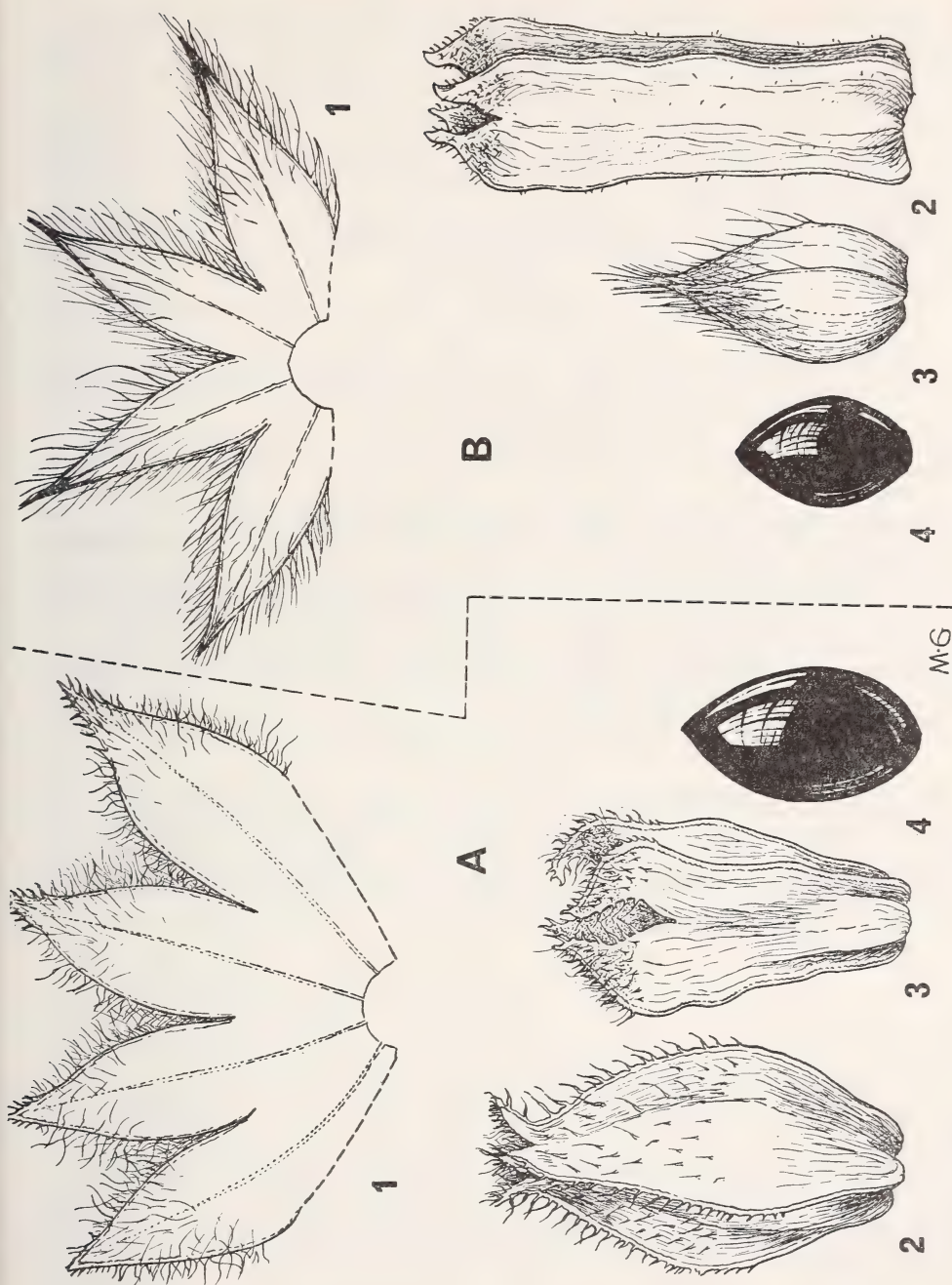


Fig. 1. A. *Parietaria officinalis* L., 1, female perianth opened; 2, female perianth; 3, hermaphrodite perianth; 4, achene (from Kmet 3868, Hungarian material). B. *P. judaica* L., 1, female perianth, opened; 2, hermaphrodite perianth; 3, female perianth; 4, achene (from Rawi in National Herbarium of Iraq 23686, Iraqi material). All $\times 14$.

P. officinalis L. subsp. *judaica* (L.) Béguinot, *Nuov. G. bot. ital.* **15**, 342 (1908).

P. officinalis L. 'Rasse' *ramiflora* Aschers. & Graebn., *Syn. Mitteleurop. Fl.* **4**, 623 (1911).

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Since this paper was submitted for publication, J. Mennema (Leiden) & S. Segal (Amsterdam) have published two papers on 'Het geslacht *Parietaria* in Nederland', in *Gorteria* **3** (7), 96–102 (1967) and **3** (8) : 109–118 (1967). Working primarily from a Western European viewpoint, they reach the same conclusions as the present author; unfortunately, Dr. Mennema and I each heard of our interest in this problem at too late a stage for a co-operative effort to be produced.

THE HYBRIDS OF *MIMULUS CUPREUS*

By R. H. ROBERTS

51 Belmont Road, Bangor

ABSTRACT

The hybrid *M. ♀ guttatus* × *♂ cupreus* has been synthesized and found to be completely sterile. All attempts to obtain the reciprocal cross have failed. Naturalized plants from several northern British localities are identical with plants of the synthesized hybrid, with one exception. This is a double-flowered plant from Scalloway, Shetland, v.c. 112. The results presented here suggest that this plant is also a hybrid of the same parentage. *M. cupreus* and *M. luteus* have been found to be completely interfertile, and it is suggested that *M. cupreus* may not merit specific rank. The hybrid *M. ♀ guttatus* × *♂ (M. luteus* × *cupreus)* has also been produced and is also completely sterile.

INTRODUCTION

In a previous note (Roberts 1964) it was suggested that certain plants of naturalized *Mimulus* from Scotland and Shetland might be the hybrid of the North American species *M. guttatus* DC. and the Chilean *M. cupreus* Dombrain.* A similar plant has also been seen from Cumberland, v.c. 70. Like the hybrid between *M. guttatus* and *M. luteus* L., all of these have highly sterile pollen and a short pubescence on the calyx, pedicels and upper parts of the flowering stem. They differ from *M. guttatus* × *luteus* mainly in their smaller size and in having a more or less uniformly copper-coloured corolla, marked only with small spots in the throat. In the *M. guttatus* × *luteus* hybrid the corolla is yellow and usually has some larger reddish spots on the lobes, in addition to numerous small dots down the throat. An additional feature of the Shetland plant is that it has a petaloid calyx, coloured like the corolla, but spotted with somewhat larger and more deeply coloured spots. The pollen of this plant also has a higher percentage of fully-formed grains (Table 1), but in all other respects it is indistinguishable from the single-flowered putative hybrid.

TABLE 1. Percentage pollen fertility in the naturalized hybrid *M. guttatus* × *cupreus*.

Locality	Flower no.			
	1	2	3	4
Single-flowered plants:				
Vale of St. John	3.5	7	15	10.5
Rhunahaorine	3	0	1.5	2
Double-flowered plants:				
Scalloway	24	35	30	26
River Whiteadder	24			

The artificial synthesis of this hybrid was undertaken and the results are summarized below.

Although the differences between *M. guttatus* and *M. luteus* were first pointed out as early as 1813 by de Candolle (quoted by Grant 1924), other botanists believed them to be conspecific. It was not until some years later, when seeds had been sent from South America by various collectors, that it became possible to distinguish *M. luteus* from its North American relative.

M. guttatus is a more or less pubescent perennial, often glandular-pubescent above and glabrous below. It is highly variable; in North America some local races of the aggregate are said to be annual, and a few races are entirely glabrous. It can generally be separated

* *M. cupreus* Dombrain, *Floral Mag.*, 2, t.70 (1862).

from other members of the genus by its stout, fistulous stems, and ovate or orbicular leaf-blades, which grade into small bracts at the top of the racemose inflorescence. It has a bilabiate, yellow corolla, with the lower lip much longer than the upper, and the throat nearly closed by two densely hairy ridges, marked with small red or brown spots. It is a native of western North America, where it is the commonest and also the most polymorphic species of the genus, occurring along streams and in wet places from Alaska to northern Mexico (Grant 1924; Pennell 1951; Vickery 1959).

M. luteus, on the other hand, is a completely glabrous, more slender plant, with decumbent flowering stems and smaller, acute leaves. The inflorescence also has fewer flowers and longer pedicels than *M. guttatus*. The corolla tube is relatively narrow, but the throat is open and red-spotted, while the lips of the corolla are nearly equal, with spreading lobes. Corolla colour is more variable than in *M. guttatus*, ranging from pale to deep yellow, and either unspotted, as in *M. guttatus*, or with large reddish-brown spots on one or more of the lobes. It is native only in Chile, where it is common along streams and in moist places (Grant 1924).

M. cupreus is similar in many respects to *M. luteus*, but differs in being usually annual and sometimes puberulent. It is a smaller plant, with a compact habit and smaller, subrhombic-ovate or elliptical leaves. The corolla is also like that of *M. luteus*, with a wide throat, nearly equal lips and spreading lobes; it differs only in its smaller size and in its colour: golden-yellow at first, changing to a brilliant copper colour at maturity. This species is restricted as a native plant to southern Chile (Grant 1924).

Since *M. luteus* and *M. cupreus* occupy the same geographical region, their crossability has also been investigated and the results are discussed below.

RESULTS

M. cupreus has been reported as an escape in the Lake District by McClintock (1957). However, all the specimens of naturalized *Mimulus* with copper-coloured flowers which have been examined, including one from the Vale of St. John, Cumberland (collected by Mrs. E. M. Satow), were found to have highly sterile pollen. Seeds of two horticultural strains of *M. cupreus* were obtained, and the plants raised from them were used for crossing with *M. guttatus*. The same material of *M. guttatus* was used as in previous hybridizations with *M. luteus*: one plant from the River Ogwen, Caernarvonshire, v.c. 49, and another from Dolgellau, Merioneth, v.c. 48.

Thirty cross-pollinations were made in both directions, the usual precautions being taken of emasculating the flowers in bud, and covering with a cellophane bag after pollen transfer had been effected. In the following account the name of the female parent is given first.

The cross *M. guttatus* $\times$ *cupreus* produced a fairly good seed set. Eight of the resulting capsules were opened before dehiscence and gave the following seed counts: 315, 430, 286, 210, 324, 184, 452 and 416. But these seeds were smaller and more variable in size than those of the parent species, and their germination was much lower: around 20 per cent to 35 per cent compared with 87 per cent to 100 per cent in the parents. The reciprocal cross *M. cupreus* $\times$ *guttatus* produced an average of approximately 340 empty testae per capsule. Since many of these looked deceptively like good seeds, the contents of all the capsules were kept on damp blotting paper for ten weeks to test for any germination. Only one fully-developed and two poorly-developed seeds were seen, and even these failed to germinate.

These results were almost identical with those obtained when *M. guttatus* was crossed with *M. luteus*, the only difference being that one seed of the cross *M. luteus* $\times$ *guttatus* germinated and grew into a robust plant (Roberts 1964).

As might be expected from the poor quality of the seeds, the seedlings of *M. guttatus* $\times$ *cupreus* were generally smaller and weaker than those of the parent species; several had only one cotyledon and died 3 or 4 days after germinating. Fifty seedlings were transplanted

into sterilized soil, but three of them proved to be severely stunted and malformed. In one of these the leaves bore hardly any resemblance to those of normal *Mimulus*; they were smoothly elliptical with no trace of serrations, and the mid-vein was continued as a projection from the lower surface of the leaf a short distance from the tip. The second had minute, alternate leaves, and produced root initials from the leaf axils, as well as from various points between the nodes. These two survived for over 3 months, but remained extremely dwarfed and slender. They were both under 2 cm high when they became chlorotic and died. The third showed similar anomalies, but was so minute and weak that it only reached a stature of 0.7 cm before dying. The remainder of the transplanted seedlings soon overcame their initial disadvantage and grew into vigorous plants. The majority of them were taller and more robust, and produced more flowers per plant than either of the parent species. Hybrid vigour was also shown in the larger size of the flowers, which were uniformly copper coloured with small spots only in the throat of the corolla. All of these plants were puberulent, mostly on the calyces, pedicels and upper parts of the flowering stems. There was, however, considerable variation in the density of the puberulence, and those plants in which it was very sparse could easily be mistaken in the field for *M. cupreus*.

Pollen from a few flowers of each of these plants was examined in a few drops of aceto-carmin, when the fully-formed grains took up the stain and were easily counted. As the results from all the F1 progeny were so similar, those from only ten plants are given (Table 2). Thirty-five flowers of these hybrids were either selfed or intercrossed with other

TABLE 2. Percentage pollen-fertility in ten plants of the synthesized hybrid
M. guttatus × *cupreus*.

Plant reference no.	Flower no.			
	1	2	3	4
C1	3	2.5	3	2
C2	0	4.5	2	0.5
C3	3.5	5.5	5	—
C4	10	9.5	4.5	13
C5	2	4	3	4
C6	0.5	5	2.5	2
C7	5.5	6	3.5	6
C8	3	4.5	7	—
C9	8.5	6	11	7.5
C10	0.5	3	2	1.5

F1 individuals; twenty-five flowers were pollinated with *M. guttatus* and another twenty-five with *M. cupreus* pollen. Pollen of the F1 plants was also used on the stigmas of ten flowers of each of the parents. In no case was any seed obtained.

Selfing and back-crossing were also tried with two plants of the naturalized putative hybrid which had been brought into cultivation. These were the single-flowered plant from the Vale of St. John, Cumberland, and the double-flowered plant from Scalloway, Shetland. In the case of the Cumberland plant the results were exactly the same as with the synthesized hybrid: six of its flowers were selfed, and another six pollinated with *M. guttatus* and six with *M. cupreus* pollen. Again not a single seed was obtained. This plant was morphologically identical with the synthesized F1, and its pollen was similarly highly sterile (Table 1). It is therefore presumed to be a hybrid of the same parentage.

In addition to having a double flower, the Shetland plant differed in two other respects: its pollen had a higher percentage of well-formed grains, and it produced a very low number of seeds, both after selfing and after pollination with *M. guttatus*. During 1963 and 1964 a total of eighteen flowers were selfed, ten others were pollinated with *M. guttatus* and another ten with *M. cupreus* pollen. The selfed flowers produced from 0 to 3 seeds per

capsule; only twenty-three seeds were obtained in the course of two seasons. Seventeen of these germinated, but several of them had small, malformed cotyledons, and others lacked the normal green colour. Although they were transplanted into sterilized soil none of them made any growth beyond the cotyledon stage, and all of them died within a fortnight of germination. From the capsules which had been fertilized with pollen of *M. guttatus* a total of twelve seeds was obtained. Seven of these germinated readily and the resulting progeny are discussed below. Pollination with the pollen of *M. cupreus* gave no seeds at all, neither were any seeds set when pollen of the Shetland plant was placed on the stigmas of *M. guttatus* or *M. cupreus*.

The back-cross progeny of the Shetland plant with *M. guttatus* showed many peculiarities. They were all densely covered with long, viscid, glandular hairs, and exhibited various flower abnormalities, the commonest being severe malformation of the stigma, style (often trifid) and ovary. In some of these plants the flowers were small (corolla less than 1.5 cm long), malformed, and failed to open; later flowers on the same plants, however, were less severely stunted and opened normally. Curiously, all of them had petaloid calyces like the Shetland plant, and flower colour was more or less intermediate between that of the parents.

The pollen of these back-crossed plants had a higher fertility than that of the seed parent (Table 3), and it was anticipated that seed production would show a corresponding

TABLE 3. Percentage pollen fertility in three plants each of the first and second back-cross of the Shetland plant with *M. guttatus*.
B1, B2, B3: (*M. guttatus* × *cupreus*) × *guttatus*
BG1, BG2, BG3: [(*M. gutt.* × *cupr.*) × *gutt.*] × *guttatus*.

Plant reference no.	Flower no.			
	1	2	3	4
B1	64.5	72	54	69
B2	66	58	60	52
B3	42	30	34	34
BG1	19.5	22	26	20
BG2	62	55	58	64
BG3	23	32	28	25

increase. Selfing and inter-crossing of the back-crossed individuals gave only a slightly higher seed-set than was seen in the Shetland plant (from three to seven seeds per capsule in eight capsules), but none of them germinated. Ten capsules which had been fertilized with pollen of *M. guttatus* gave a closely similar result: only thirty-four seeds were obtained altogether. But these were better developed and germinated in 3 to 5 days.

The plants of this second back-cross to *M. guttatus*, i.e. (Shetland plant × *guttatus*) × *guttatus*, grown in 1966, showed much the same abnormalities as the first back-cross. Some of them had greatly reduced vigour and minute corollas which did not open, but withered on the plant without dropping. One or two of the more vigorous plants had flowers which were closer in shape and colour to those of *M. guttatus*. But it was remarkable that all of them possessed petaloid calyces, even when the corolla itself was severely reduced. Seed production in these plants was no greater than in the seed parents, while pollen fertility showed a slight downward trend (Table 3).

The plants of both back-cross generations appeared to be less vigorous than the putative F1 Shetland plant, and it seems extremely doubtful whether any of them would have survived in the wild. All the available evidence therefore supports the view that the Shetland plant is the hybrid *M. guttatus* × *cupreus*, and that its petaloid calyx is the result of a simple mutation which may also be responsible for its higher pollen fertility and its ability to set a few viable seeds. It is difficult otherwise to account for the appearance of

the double-flowered character in every individual of successive back-cross generations. Among the plants of *M. cupreus* raised from seed, several were found with one or more of the calyx-lobes enlarged and coloured like the corolla. It seems possible therefore that the petaloid-calyx character in the Shetland plant has been inherited from its *M. cupreus* parent. Nevertheless, the appearance of gross morphological abnormalities in the first and second back-cross generations indicates a severe genetic disharmony between *M. guttatus* and *M. cupreus* despite the ease with which the F1 is formed.

The plants of the two horticultural strains of *M. cupreus* were crossed in both directions with *M. luteus* (progeny of a naturalized plant found in Caithness by D. P. Young in 1959). The hybrids were easily obtained, and there was a full set of well-developed seed, equal in every respect to those of the parents. There was no difference in their quality whichever species was the seed parent, and germination in both crosses was very high: from 94 per cent to 100 per cent. The resulting seedlings were very vigorous, and showed no morphological abnormalities. Hybrid vigour in these crosses was displayed in their larger size, bigger flowers (with various combinations of the corolla colour and markings of the parent species), and greater number of flowers and capsules. Pollen fertility was unimpaired, and seed production showed no diminution either on selfing or back-crossing to the parents. The F2 progeny similarly suffered no reduction in either pollen fertility or seed production, and it is evident that *M. cupreus* and *M. luteus* are completely interfertile.

These fertile hybrids were cross-pollinated in both directions with *M. guttatus*. The results were identical with those obtained when *M. luteus* and *M. cupreus* were crossed with *M. guttatus*: hybrids were only produced when the latter was used as the female parent, and they all proved to be completely sterile.

DISCUSSION

These observations strongly suggest that the coppery-flowered *Mimulus* naturalized in several northern localities in Britain are mostly hybrids of *M. guttatus* and *M. cupreus*, the former being the seed parent. They are easily mistaken in the field for *M. cupreus*. They can, however, be distinguished from it by the presence of a minute pubescence on the calyx, pedicels and upper parts of the flowering stems, particularly the leaf-bases and nodes, and by the complete absence of normally-developed capsules. Confirmation of their hybrid nature can be obtained from microscopic examination of the pollen, which, as has been seen, consists mostly of empty and shrivelled grains. Even in the double-flowered Shetland plant, whose pollen fertility is somewhat higher than that of the single-flowered hybrid, the full grains constitute only 20 per cent to 35 per cent of the total. These figures, based on larger samples of pollen, are somewhat lower than the provisional estimates formerly given (Roberts 1964). A specimen recently collected in Berwickshire, where it has been 'known for about 40 years in the River Whiteadder and its tributaries' (D. McClintock, personal communication, 1966), is practically identical with the Shetland plant. The only flower available for examination had a pollen fertility of 24 per cent, and there is little doubt that this plant is also the same hybrid.

The ability of the double-flowered hybrid *M. guttatus* × *cupreus* to produce a few seeds after selfing implies that some of its pollen is functional. The production of viable seeds after fertilization with the pollen of *M. guttatus* lends further support to the view that the latter is one of the parents of the double-flowered hybrid. This low seed set also seems to contrast sharply with the complete failure to obtain seed from the single-flowered hybrid—both naturalized and synthesized—and to conflict with the conclusion that the double-flowered hybrid is an F1 of the same parentage. But this difference between the two forms of the hybrid may not be as significant as it appears, and, in fact, may be only a matter of degree. Stebbins (1950) quotes an instance of hybrids in the genus *Paeonia* which, though almost completely sterile, produce one seed in perhaps one thousand or ten thousand, or even one in a million.

There is, so far, no authentic record of *M. cupreus* as a naturalized plant in the British

Isles. The most likely origin of its hybrid with *M. guttatus* is from a deliberate garden cross, at the time when *Mimulus* was popular in gardens around the middle of the 19th century. The persistence of the hybrid as a naturalized alien has no doubt been facilitated by the ease with which it propagates and spreads vegetatively, as well as by its hardiness which enables it to survive the winter in Britain. In this respect it is like *M. guttatus*.

The complete interfertility of *M. cupreus* and *M. luteus* seems to lend support to the view (e.g. Bailey 1927) that their morphological differences are hardly sufficient to maintain them as separate species. The analogous behaviour of both species when crossed with *M. guttatus* also implies that the genetic differences between them are small. Reference to the horticultural literature indicates that it is these two species which have been crossed to produce the vigorous, large-flowered, fertile hybrids which were once popular as garden plants. It is probable that some of the sterile naturalized plants, recently shown to be widespread in Britain, are the trihybrid *M. guttatus* $\times$ (*luteus* $\times$ *cupreus*). Artificially produced plants of this hybrid were so variable that it was found impossible to distinguish many of them from the hybrid *M. guttatus* $\times$ *luteus*.

LOCALITIES FROM WHICH THE HYBRID *M. GUTTATUS* $\times$ *CUPREUS* HAS BEEN SEEN

- v.c. 70, Cumberland: Vale of St. John, *Mrs. E. M. Satow*.
 v.c. 81, Berwick: River Whiteadder and its tributaries, 1966, *Miss E. Logan Home*.
 v.c. 89, North Perth: River Tay, near Dunkeld, 1958, *D. P. Young* (herb. D. P. Young).
 v.c. 90, Angus: Tarfside, Glen Esk, 1960, *Miss U. K. Duncan* (herb. U. K. Duncan).
 v.c. 91, Kincardine: near Fettercairn, 1960, *Miss U. K. Duncan* (herb. U. K. Duncan).
 v.c. 101, Kintyre: Rhunahaorine area, south of Gigha Ferry, 1964, *A. G. Kenneth* (herb. R. H. Roberts).
 v.c. 103, Mid Ebuies: Coll, 1966, *Miss U. K. Duncan* (herb. R. H. Roberts).
 v.c. 108, West Sutherland: near Inverkirkaig, 1961, *Miss V. Gordon* (herb. V. Gordon).
 v.c. 112, Shetland: near Scalloway, 1962, *R. C. Palmer & Walter Scott* (herb. R. H. Roberts).

Specimens of the synthesized hybrid have been deposited in the herbarium of the National Museum of Wales, Cardiff (NMW).

ACKNOWLEDGMENTS

The living material of the naturalized hybrid was kindly supplied by Mrs. E. M. Satow, of Great Langdale, and Mr. Walter Scott, of Scalloway, to both of whom I wish to express my thanks. I am also indebted to all those who sent the herbarium specimens without which these observations could not have been made.

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THE INTERSPECIFIC RELATIONSHIPS OF *JUNCUS EFFUSUS* AND *J. CONGLOMERATUS* IN BRITAIN

By A. D. Q. AGNEW

Botany Department, University College Nairobi, P.O. Box 30197, Nairobi, Kenya

ABSTRACT

Juncus effusus and *J. conglomeratus* appear to be specifically distinct in the British Isles; *J. conglomeratus* is the rarer species. Their principal diagnostic features are given.

Evidence is presented to show that the two species hybridize at higher altitudes in Britain, probably because the overlap of their flowering periods is longer in these regions than at low altitudes.

Evidence is also found for gene flow within *J. effusus* populations from *J. conglomeratus* and the reasons for the continuing specific distinctness of these two species is discussed.

INTRODUCTION

Juncus effusus has long been known as an extremely variable species. This is reflected at once both in its wide range of ecological tolerance (Agnew 1961) and in its morphological variability, and it is clear that, since both these features are simultaneous expressions of the inherent variability, no full appreciation of the species can be made without considering its variation with respect to its taxonomy.

From the start the species in its relation to *J. conglomeratus* has been a puzzle to taxonomists. Thus, although the species is known under its Linnaean name, Linnaeus himself seems to have had no clear idea of the differences delimiting it from *J. conglomeratus* or *J. inflexus*, two closely related species, although he evinced some interest in them, as his annotated copy of the *Species Plantarum* (1753) shows. The position may be summarized thus: in the Linnaean Herbarium (LINN) the specimens annotated by Linnaeus as *J. conglomeratus* (Savage 1945, no. 449.2) are in fact *J. effusus* var. *compactus* as we know it, while those annotated as *J. effusus* (Nos. 449.4 and 449.5) are *J. inflexus* as we know it. Due to the extraction of some parts of the original description of *J. effusus* for inclusion in other later species (this has been summarized by Tweed and Woodhead 1947) and subsequent further doubt concerning the delimitations of the two species, they were both included under the one specific name *J. communis* by Meyer (1819).

Krisa (1962) has drawn attention to this confusion in Czechoslovakia, and has concluded that the two species are only recognizable as end points in a continuously variable series of forms, which are regarded as introgressive hybrid populations. The whole series of forms including both species is regarded by Krisa as a 'conspecies'. It will be noted that the conclusions of the present author, who upholds the complete validity of the two species, based on examination of material from the British Isles, differ from those of Krisa. It is due to this discrepancy in views that the following account of work undertaken between 1952 and 1955 is presented. The present author has examined some stands of the two species in Czechoslovakia and feels that the situation there may not be very different from that in Britain, once the restricted nature of the much rarer *J. conglomeratus* is recognized.

Table 1 is a list of the specific differences which have been found most constant in Britain.

CHARACTERS FOR BIOMETRIC ANALYSIS

Work on the variation of both species was done at Edinburgh (Scotland) in 1952 and in 1953–55 at Bangor (North Wales).

To make comparisons between *J. effusus* and *J. conglomeratus*, characters must be used which show a difference between the two species; the form of the inflorescence is such

TABLE 1. Diagnostic features of *J. effusus* and *J. conglomeratus*.

Character	<i>J. effusus</i> L.	<i>J. conglomeratus</i> L.
Stem sheathing scales	Black to red-brown at base	Red-brown to olive at base
Stem-ridges at inflorescence	30–60	15–24
Spathe-length	Usually 15–30 cm	Usually 5–15 cm
Bract of second cyme	Not as long or as long as split in spathe	Longer than split in spathe
Inflorescence	Diffuse or compact	Almost invariably compacted into globose head
Perianth	Outer whorl of three segments about 0.5 mm longer than inner whorl Perianth segments olive with green or light brown centres	Outer whorl as long as inner whorl Perianth segments with dark red—brown edges, lighter centres
Stamens	Anthers oval, shorter than filaments	Anthers strap-shaped, longer than filaments
Style	Very short or absent	One third as long as ovary
Fruit	Retuse or truncate, not apiculate	Truncate, apiculate

a character. The other two chosen were ridge-number and the length of the spathe above the inflorescence. These will be dealt with in turn.

Since the varietal classification of both *J. effusus* and *J. conglomeratus* depends on the condensed or diffuse nature of the inflorescence, this is an obvious character to choose; however there are some difficulties in its measurement. The method chosen has been to measure three axes of the inflorescence at right angles to one another, taking the first measurement parallel to the stem and spathe. The product of the three lengths is then calculated and from this and a count of the total number of flowers in the inflorescence a figure is obtained of the number of flowers per unit volume (ml) of inflorescence ('condensation'). It will be seen that this is in many ways an arbitrary figure since the product of the axes does not give the true volume of inflorescence. However, sufficiently comparable figures can be obtained in this way.

The axes were measured to the nearest millimetre and commonly were less than 10 mm in length. Clearly, this introduces an error in the figure obtained for 'condensation' which increases as length decreases; thus the variance of figures obtained for condensation should increase as the mean condensation increases. This has proved a drawback to the treatment of *J. conglomeratus* by this character, and it has been necessary to transform all figures of condensation logarithmically before statistical treatment.

Spathe length is short (5–15 cm) in *J. conglomeratus* and long (15–25 cm) in *J. effusus*. However it is not a very good character since there are many intermediates. It is very quick to measure and does give a separation of the two species on the scatter diagrams mentioned below.

Ridge-number on the stem below the inflorescence has been found to be very useful indeed. Not only is it easy to observe, especially when the stems have been left to dry for a period, but it gives effective separation between *J. effusus* and *J. conglomeratus* with no overlap and takes an intermediate value for hybrids.

An experiment was carried out to test the plasticity of these characters. Two adjacent populations of *J. effusus* differed in their growth form, i.e. clumped and unclumped (diffusely growing), and occupied distal ends of a soil and vegetation catena from very wet conditions (the unclumped form) to drier grassland (the clumped form). Twenty individuals of each population were transplanted and grown under similar conditions; the results are summarized in Table 2. The previously significant difference in the spathe-length disappeared

TABLE 2. Transplant experiment of *J. effusus* plants from Braint, Anglesey.

	Mean spathe- length	Significance of difference	Mean ridge no.	Significance of difference	Mean no. 'flowers per ml'	Significance of difference
Before cultivation:						
Clumped population	15.48	++	43.9	N.S.	43.05	+++
Unclumped population	19.90		42.9		20.28	
After cultivation:						
Clumped population	16.12	N.S.	34.60	N.S.	72.53	++
Unclumped population	14.13		36.20		44.88	

't' test probabilities given as: + = 5 per cent. $\geq p > 1$ per cent., ++ = 1 per cent. $\geq p > 0.1$ per cent., +++ = $p \leq 0.1$ per cent.

under cultivation, but the difference in inflorescence condensation remained, indicating that this character at least is genotypically controlled.

The value of this experiment is enhanced by the seed-size measurements. The mean seed-size of these two populations was almost identical so that it was not expected that a significant difference in any other character would remain after cultivation. At the same time these results do not invalidate the continued use of ridge-number and spathe-length as population parameters when comparing *J. effusus* and *J. conglomeratus*, although spathe-length is of doubtful use when *J. effusus* alone is dealt with.

POPULATION ANALYSES

The population analyses initially carried out were those of mixed *J. effusus* and *J. conglomeratus* populations. A scatter diagram of such an analysis is shown in Fig. 1. It can be seen that there is a good separation of the two species on ridge-number, spathe-length,

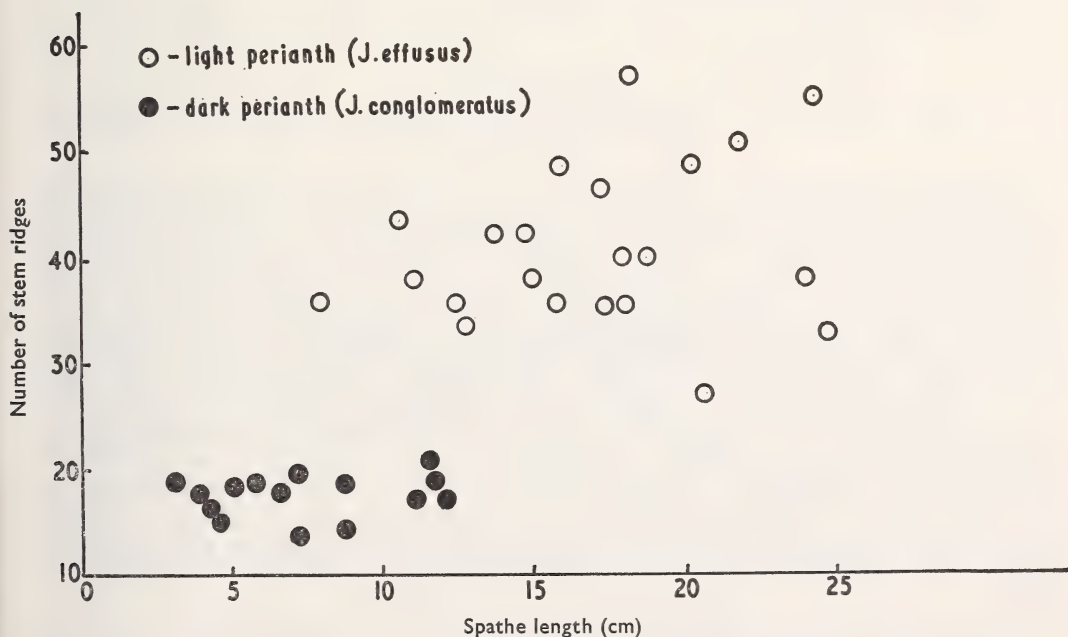


Fig. 1. Scatter diagram of a community containing *J. effusus* and *J. conglomeratus*. The scatters of the two species are easily separated.

and a qualitative character, that of perianth-colour. There are no complications in this diagram.

Two populations have been found, one near Edinburgh (Fig. 2) and one near Glasgow, which do not show such a clear separation of the two species. Here there are individuals which have some characteristics of each species. These plants have been found to be easily separable from both *J. effusus* and *J. conglomeratus* by their intermediate number of stem ridges, the dark perianth segments (the latter typical of *J. conglomeratus*) and the intermediate character of the inflorescence.

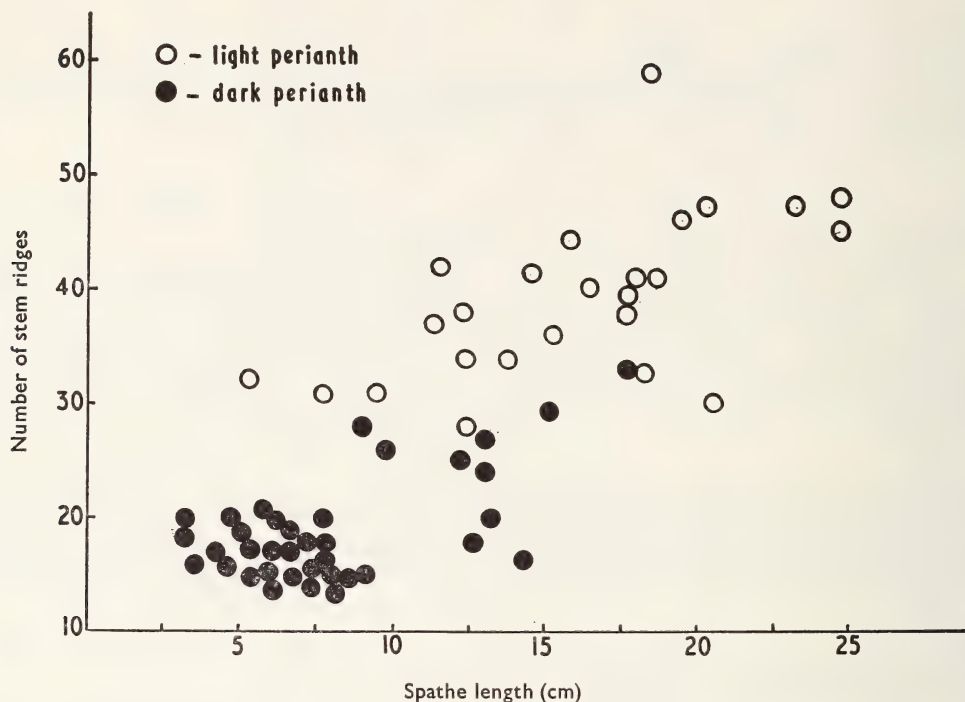


Fig. 2. Scatter diagram showing an intermediate between *J. effusus* and *J. conglomeratus*, from a population at Penicuik, Midlothian.

In North Wales this type of complex has been found on two occasions. The analysis of one of these populations (Fig. 3) shows as before a group of plants intermediate between *J. effusus* and *J. conglomeratus*. In this case there were enough plants of all groups to attempt a statistical analysis, when a positive correlation was found between ridge-number and spathe-length only in the intermediate group. This shows, in my opinion, that the intermediate type is a hybrid, since one would expect a hybrid to show correlations between the characters which distinguish its parents. It has been supposed in this case that these intermediates are groups of F_1 or subsequent generation hybrids, with a little back-crossing.

Populations showing introgression have however been found at Edinburgh and on the Snowdon massif. Scatter diagrams of the former are shown in Figs. 4 and 5. They can be seen to include characters of both species in a complex which shows recombinations of many types. These populations show also introgression only with *J. effusus*, the scatter being between the position of the supposed hybrid and that of *J. effusus*. The correlation of these two characters, ridge-number and spathe-length, is significantly positive in both cases.

That hybrids can occur between the two species has been recognized for some time (Buchenau 1906; Richards & Clapham 1941). The two species were artificially crossed in the garden in 1955. Seeds set in normal numbers in all the flowers crossed and germinated

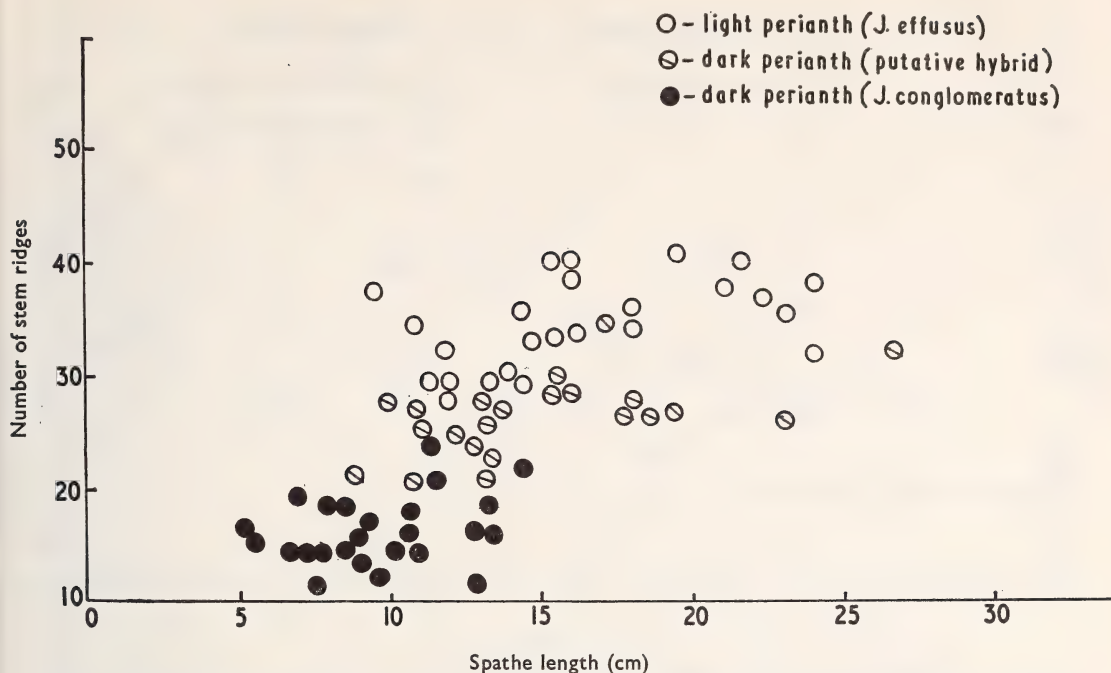


Fig. 3. Combined scatter diagram of three populations, distinguished on this diagram by the use of three symbols. The intermediate grew spatially between the others and in an intermediate habitat. All were from within 100 m of each other at Llyn Idwal, Caernarvonshire.

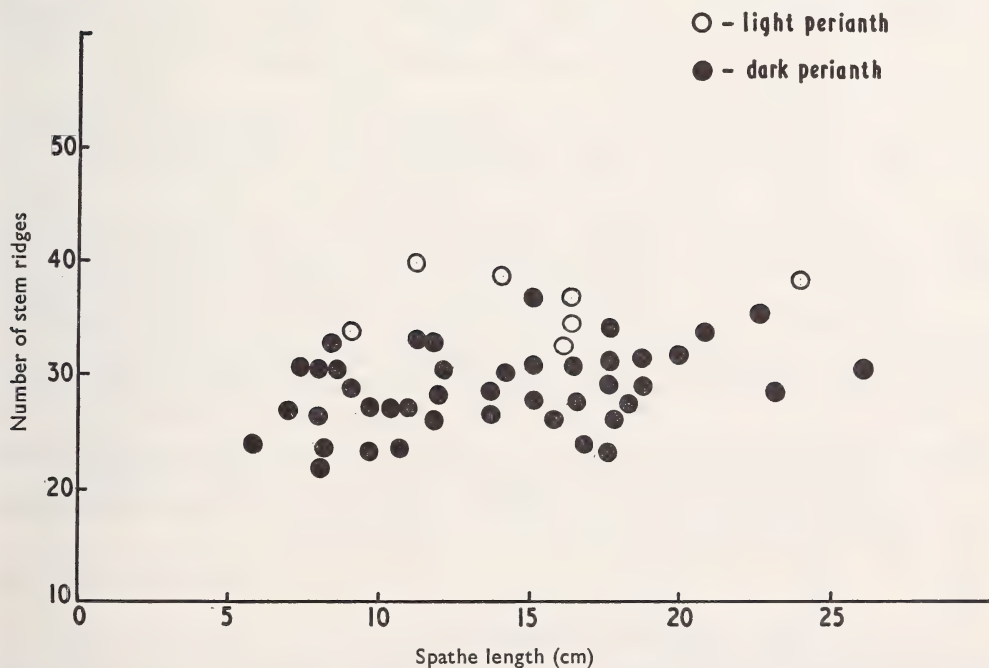


Fig. 4. Scatter diagram of a population from West Linton, Midlothian. The intermediate introgressive nature of the population can be seen by comparison with Fig. 1.

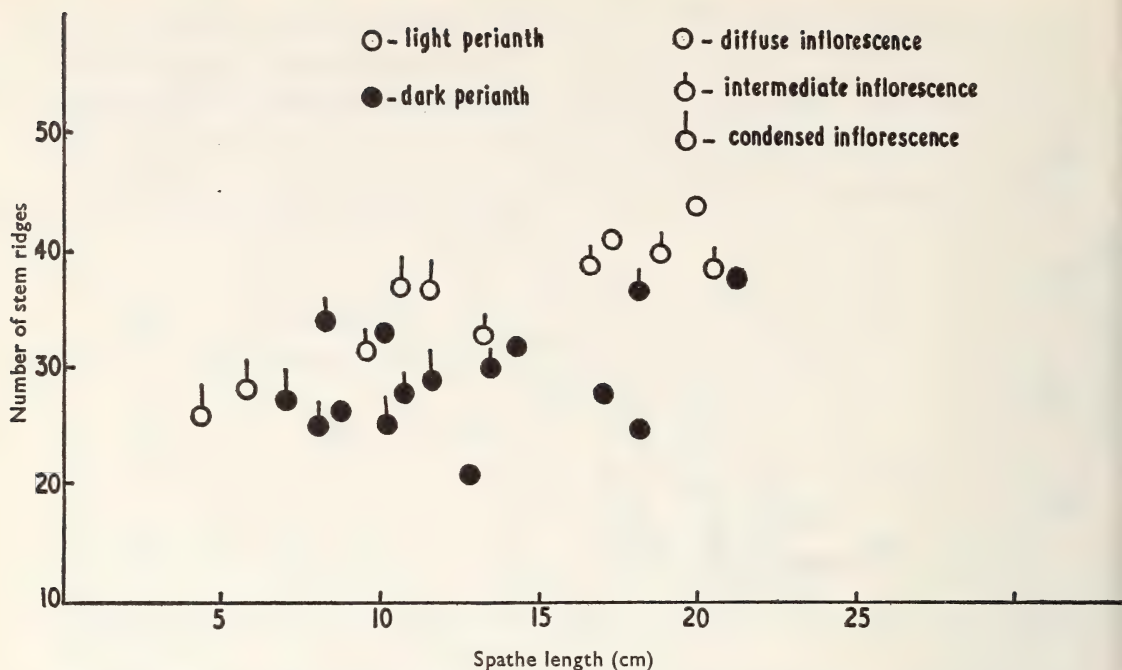


Fig. 5. A further population from West Linton, Midlothian, where inflorescence condensation is also represented.

normally, the seedlings unfortunately being killed by damping off before reaching the 4-leaf stage. There seems no reason to suppose that they could not have developed into mature plants. The hybrids observed in the field moreover appeared fully fertile. This is in contrast to the statements made by Buchenau (1906, p. 137) that he considers the hybrids to be highly sterile and rare. Richards & Clapham (1941, p. 378) state that the presence of hybrids needs confirmation in Britain.

It seems, then, that hybrids exist both as populations of hybrids and as populations introgressing with *J. effusus*. No signs of introgression with *J. conglomeratus* have been found in any population. This may be due to the type of crossing available to the species. As has been repeatedly noted (Richards & Clapham 1941; Buchenau 1906; Krisa 1962) the flowering times of the two species differ and are perhaps responsible for the lack of hybrids. *J. conglomeratus* flowers before *J. effusus* and the flowers of both are protogynous. This means that most crossing between species will be between the pollen of the earlier and the ovules of the later flowering species and this should hold true for hybrids as well. Thus all crossing, introgressive or otherwise, would be in the direction of *J. effusus* as seed parent. This will lead to the seeds being deposited around the plant genetically nearest to *J. effusus* giving an increased likelihood of the progeny being themselves crossed with *J. effusus*. Since the two species usually grow in slightly different habitats, *J. conglomeratus* preferring the drier areas, it can be seen that this effect could have great significance.

Having shown the evidence for hybridization, I propose now to deal with the analyses of the variation within *J. effusus* itself.

VARIATION OF *J. EFFUSUS*

The figures for the variation of populations of *J. effusus* were obtained at Edinburgh with the exception of those analysed for the experimental investigation into the amount of phenotypic variation to be expected. A scatter diagram, made up of four populations, of condensation of inflorescence against ridge-number is shown in Fig. 6. The means of the

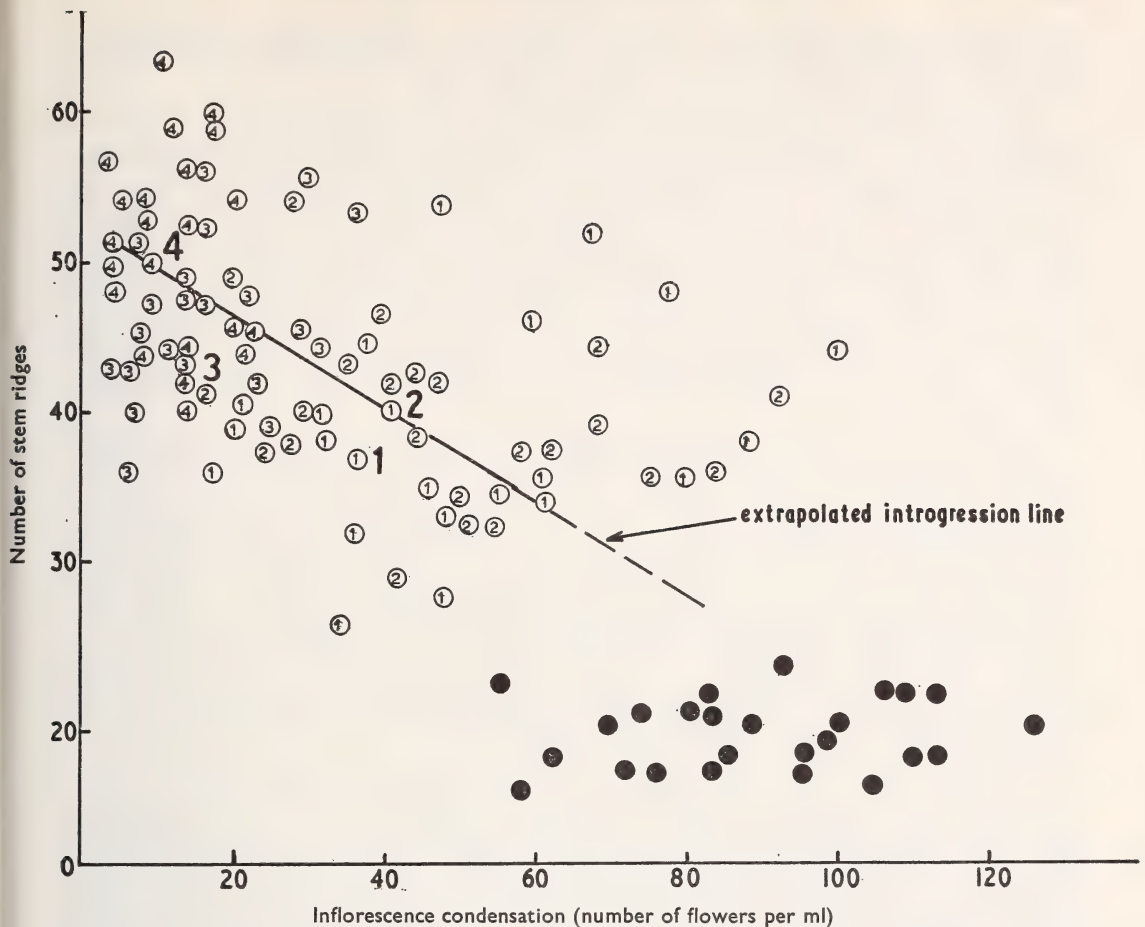


Fig. 6. Scatter diagram of four populations of *J. effusus* where the individuals are numbered according to their population and the mean for each population is plotted as a large, uncircled figure. A population of *J. conglomeratus* (solid dots) is given so that it can be seen to lie on the extrapolated regression line of the four *J. effusus* populations.

populations are shown within the diagram. It is evident that there is some correlation between these two characters, and that the correlation is in the general direction of the position that *J. conglomeratus* occupies in this diagram.

With this in mind the four populations were analysed for correlations between the three parameters measured. The significance of any correlation observed is shown in Table 3. It can be seen that only one population shows significant correlations within

TABLE 3. Correlations between and within four populations of *J. effusus*. Correlations determined between spathe length (A), number of ridges (B), condensation of inflorescence (C). Significance of correlation coefficient gives as: N.S., not significant; + = 5 per cent. $\geq p > 2$ per cent.; ++ = 2 per cent. $\geq p \geq 1$ per cent.; +++ = $p \leq 0.1$ per cent.

Analysis of each population:		A/B	A/C	C/B
	1	N.S.	N.S.	N.S.
	2	N.S.	N.S.	N.S.
	3	++	+	N.S.
	4	N.S.	N.S.	N.S.
Combined analysis of all populations:		++	N.S.	+++

itself and that both of these are positive correlations. The populations taken together show two significant correlations—between spathe-length and ridge-number (positive) and between ridge-number and condensation (negative).

Anderson (1953, p. 287) has suggested that when a scatter diagram shows a correlation of characters there is evidence for gene flow from some other species, and that the characters of the species responsible for this may be found roughly by extrapolation—that is, by producing the line of the correlation until it enters the region in the diagram which would be occupied by a known species were it present. That species is suggested as the one responsible, by hybridization and subsequent backcrossing, for the gene-flow responsible for the correlation. In the present instance, it can be seen from Fig. 6 that the correlation line would in fact produce through the area representing *J. conglomeratus* on the diagram; that is, the area of high inflorescence-condensation and low ridge-number. In the same way the correlation of spathe-length against ridge-number also is in the direction of *J. conglomeratus*.

The lack of correlations within populations shows that the correlation between these characters is not due to genetic linkage. The correlation between spathe-length and ridge-number is possibly not very important; as noted above spathe length is very plastic, and there is a correlation within one of the populations of the group. The correlation between ridge-number and condensation however appears to be very important. Not only are no correlations between these two characters shown within the population, but also these two characters seem to be the most environmentally stable of those used.

The explanation, in the author's opinion, is that gene flow is occurring from *J. conglomeratus* into *J. effusus* populations. This would fit all the facts of variation within and between populations and explain why the correlations between populations are in the direction of the *J. effusus*—*J. conglomeratus* regression.

Another line of evidence, from the mean seed-size of populations of *J. effusus*, confirms this hypothesis. Seed-size was taken as the product of length and breadth. Fifty seeds were taken from each population by taking at random 50 stems from each, shaking these over paper, and taking a small sample of the seeds so gathered. The size of samples was checked several times by measuring a further 50 seeds when it was invariably found that the means approached each other very closely. The means observed differed significantly from population to population and this was found to correlate with the altitude at which the sample was taken, the mean seed-size increasing with altitude. The means of seed-size are shown in Fig. 7. Analysis gives the regression as highly significant ($p < 0.1$ per cent).

Now *J. conglomeratus* has a larger mean seed size than *J. effusus* (0.13–0.15 sq. mm in the scale given in Fig. 7). Gene flow from hybridization at high altitudes could give a series of this sort with the genes of *J. conglomeratus* becoming progressively diluted with those of *J. effusus* as lower altitudes are reached. This hypothesis implies greater hybridization at high altitudes; there is evidence for this and for its cause.

The hybrids and introgressive hybrid swarms so far found in Scotland and North Wales have been at altitudes exceeding 150 m although both species occur, in non-hybridizing populations, down to sea level. There follows a list of the hybrids found, with their altitudes.

Type of hybrid	Place	Altitude
Probable F ₁	Penicuik, Midlothian (Scotland)	183 m
Probable F ₁	Rutherglen Park, Glasgow	152 m
Probable F ₁	Llyn Idwal, Caerns. (Wales)	366 m
Probable F ₁	Cwm Glas, Caerns. (Wales)	381 m
Introgressive hybrid	West Linton, Midlothian (Scotland)	305 m
Introgressive hybrid	West Linton, Midlothian (Scotland)	305 m
Introgressive hybrid	Llyn Llydau, Caerns. (Wales)	457 m

Taking the latitude into account, it can be seen that the hybrids so far found have been at the higher altitudes. This was realized some time ago and a search has been made in

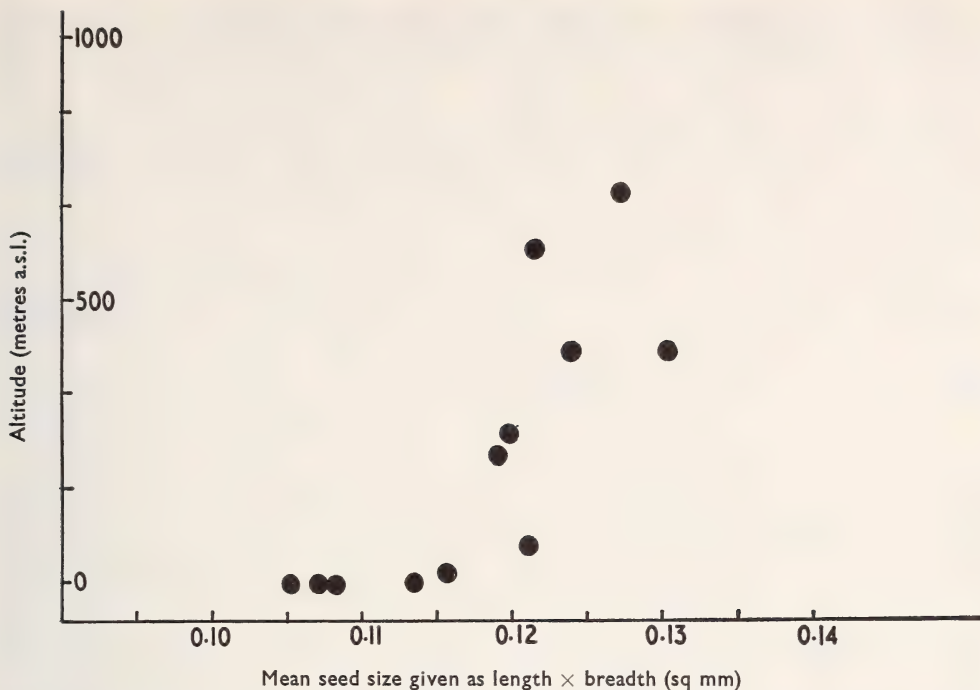


Fig. 7. Mean seed size of twelve *J. effusus* populations from North Wales plotted against altitude of occurrence.

lowland *Junceta* for the hybrids, as yet with no result. It is not intended to show that there are no hybrids at low altitudes, but that they are much more frequent on high ground. Since *J. effusus* is tolerant of the acid conditions so prevalent on British mountains of high rainfall, whereas *J. conglomeratus* is not, it follows that the number of habitats available to *J. conglomeratus* in the mountains are few. *J. conglomeratus* does however occur to 450 m on the Pentland Hills, Midlothian, and to 630 m on the Tarmachan crags above Killin (Scotland). It can be seen therefore that altitude is no barrier to this species in Britain.

In view of the sympatry of the species it is surprising that hybrids do not occur more often. Anderson (1948) has postulated the existence of 'hybrid habitats' as accounting for many of the hybrids observed between sympatric but not concomitant species. In the present case, of course, the species are almost always concomitant. Possible 'hybridity' of the habitat occurs often through human interference, but although search has been made for hybrids in those types of community with agricultural disturbance, none has been found. The hybrids observed were only in one case found to occupy an intermediate type of habitat which was recognizable as such. This was at Llyn Idwal (Wales).

FLOWERING PHENOLOGY

One difficulty attendant on a comparative study of flowering times is that a large distance must be covered during the flowering season to observe sample localities. It has thus been found possible to sample only four localities, ranging from sea level to 381 m. It is unfortunate that the information provided by the analysis of seed size was obtained, initially, somewhat fortuitously and no effort was made in previous years to study the phenology of the two species. Thus a record of flowering times has been made for only one year in North Wales.

Difficulties have also been experienced in the measurement of flowering. The method finally employed was to take five random stems from the stand under consideration and dissect flowers from them. If both dehiscent and undehiscent anthers were present on any stem the stand was considered to be in flower.

The data obtained are represented in Fig. 8. The altitude has been placed on a logarithmic scale for convenience only. With the few samples taken it cannot be said to be significant

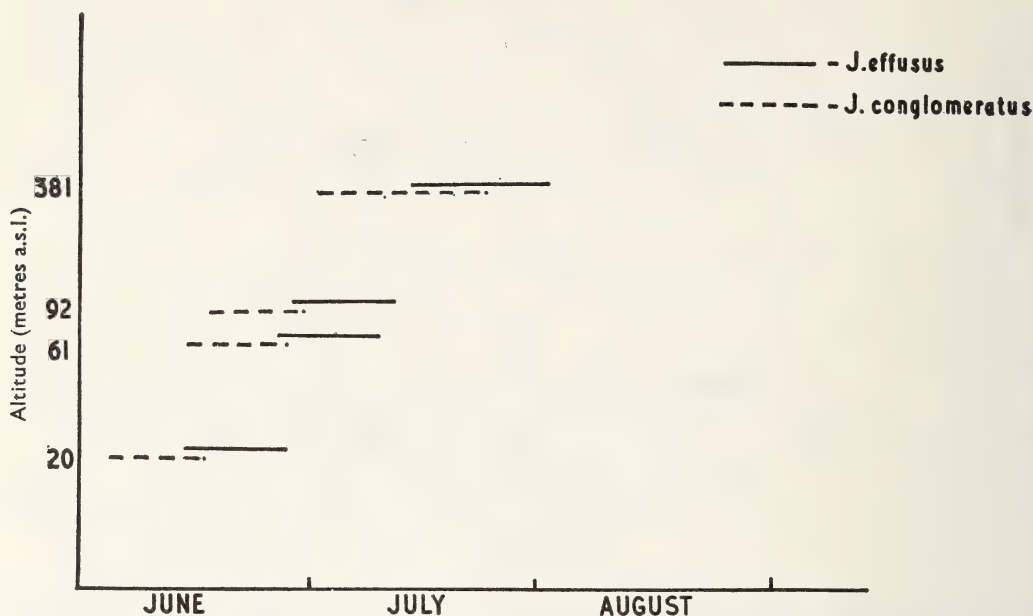


Fig. 8. Variation in flowering periods of *J. effusus* and *J. conglomeratus* with altitude in North Wales, in 1956.

that this allows a straight line to join the starting points of flowering for each species. Due to the preference of *J. conglomeratus* for the more base-rich habitats there are no intermediate stations between 121 and 366 m at which both species may be found close enough together to be influenced by the same environmental conditions. Thus in this area of North Wales, at least, it is unavoidable that there should be a gap here. For reasons of transport and time it was impossible to visit continuously more than one site above 366 m.

Fig. 8 shows that there is some overlap in flowering times at all altitudes. This has also been found in Midlothian. The high altitude population however shows the same difference in the start of flowering times between the two species but a much greater overlap between them. These few results are somewhat inadequate, but indicate that flowering times of the two species may show greater overlap and thus allow a greater chance of hybridization at high altitudes.

No cause, phenological or otherwise, has been found for the apparent lack of hybrids over part of the range of the two species in Britain.

DISCUSSION

It has been shown that hybrids and particularly introgressive hybrids do occur between *J. effusus* and *J. conglomeratus*. Back-crossing does appear to take place, but only with *J. effusus*, and there is thus a possibility of gene flow from *J. conglomeratus* into *J. effusus*. That this occurs is shown by two lines of evidence: (i) correlations between characters which separate the two species in four populations of *J. effusus* taken together, but not within each population, and (ii) increasing seed-size with altitude. The latter corresponds

to the increased hybridization at high altitudes, allowing, so to speak, *J. conglomeratus* genes into the populations there, from whence they 'percolate' in increasing dilution to sea level. The greater overlap of flowering times observed at high altitudes is responsible for greater frequency of hybrids there.

From the foregoing some tentative conclusions may be drawn as to the nature of *J. effusus* variation.

It has already been stated that the species is extremely variable both ecologically and morphologically. This variation may be due in part to the possible genetic amplitude available to the species due to gene flow with *J. conglomeratus*. Thus *J. conglomeratus* has the more condensed inflorescence of the two species. If gene flow is occurring predominantly in the direction of high to low altitude, one would expect the more compact forms of *J. effusus* at higher altitudes. This is found to be generally the case in the writer's experience, and in that of Tweed and Woodhead (1946) who state that the variety (*J. effusus* var. *compactus*) is the dominant one on high ground. In fact no truly effuse forms have been found by the writer in high or exposed habitats.

However, this does not altogether fit the pattern of the ecological variation of *J. effusus* (Agnew 1961). *J. conglomeratus* is associated with the more basic type of habitat. Thus in North Wales at least it is associated with the basic rock outcrops of the mountains, and with the boulder clay and limestone regions of Caernarvonshire and Anglesey. The only site in my experience where it is dominant to the exclusion of *J. effusus* is on the Carboniferous Limestone at Penmon Point, Anglesey. No pH values of lower than 4.3 have been recorded for it by the present author, and Pearsall is quoted by Richards & Clapham (1941) as considering it more basicole than *J. effusus*. The flow of *J. conglomeratus* genes through *J. effusus* should confer a basicole tendency and, since the compact form of *J. effusus* presumably contains more of these genes than the effuse form, one would expect the latter to be the more acidicole variety. In fact the reverse is the case in North Wales at least. This is one of the problems that might be solved by further transplant experiments.

There is also the problem of interspecific barriers between *J. effusus* and *J. conglomeratus*. A hypothesis has been put forward in this paper to explain the apparent lack of introgression and gene-flow into *J. conglomeratus*, the latter species acting as a 'gene reservoir' to *J. effusus*. It is curious that *J. effusus* has remained distinct from *J. conglomeratus*, since it cannot be envisaged that this gene flow is a recent process; the factors acting in favour of *J. effusus* cannot include a sterility barrier, and the effect of phenology has been discussed. There remains therefore selection pressure.

Only one possible example of this has been found. It has been noted that the *J. effusus* plants of North Wales are prone to a fungal infection of the capsules. This was first investigated during the comparatively wet summer of 1954 when many samples taken from a marsh area showed no uninfected capsules at all. The infection allows the carpel wall to reach maturity but it contains no seed, only a mass of fungal hyphae. This fungus was not identified. It was noted that the compact variety of *J. effusus* was very much more heavily attacked than the effuse form, probably owing to contagion between capsules. In one pair of populations, one compact, the other effuse, of 5,000 capsules examined from each, 2,560 in the former and 606 in the latter were infected.

This is the only quantitative evidence obtained for selection against *J. conglomeratus* characters in *J. effusus*. It is interesting to note that this fungal infection was never observed by the present author on *J. conglomeratus*. In any case it seems likely that this is one of the factors operating in favour of the effuse *J. effusus* form, thus preventing the species from drifting wholly towards *J. conglomeratus*.

ACKNOWLEDGMENTS

Dr. P. H. Davis initiated and guided this study while I was an undergraduate, and it gives me pleasure to acknowledge my debt to him. I am also grateful to Professor P. W. Richards under whose supervision this work was continued in North Wales.

APPENDIX

Locations and habitats of populations of *J. effusus* and *J. conglomeratus* cited in text figures.

	Population	Location and Habitat
Fig. 1	All	Marshy grassland at edge of Threipmuir reservoir, Balerno, Midlothian, with <i>Deschampsia caespitosa</i> and <i>Molinia caerulea</i> .
Fig. 2	All	Flush area on hillside, with <i>Agrostis</i> spp. at Penicuik, Midlothian.
Fig. 3	All	Flush area and adjacent hillside, with consequently varying associated species, at Llyn Idwal, Caernarvonshire.
Fig. 4	All	Grassland (rough pasture) with <i>Nardus stricta</i> and <i>Deschampsia flexuosa</i> adjacent to streamsides with <i>Agrostis tenuis</i> and <i>Holcus lanatus</i> $\frac{3}{4}$ km west of West Linton, Midlothian.
Fig. 5	All	As for Fig. 4.
Fig. 6	1	Threipmuir reservoir, Balerno, Midlothian, as in Fig. 1.
	2	Penicuik, Midlothian, as in Fig. 2.
	3	Wet open woodland with <i>Holcus lanatus</i> at Penicuik, Midlothian.
	4	In <i>Salix</i> carr bordering Threipmuir reservoir, Balerno, Midlothian.
Fig. 7	All	These were spot samples and no record remains of their detailed provenance.
Fig. 8	Lowest	<i>Agrostis tenuis</i> grassland at Bangor, Caernarvonshire.
	next	<i>Agrostis tenuis</i> grassland 1 km south-west of Bangor.
	next	Coarse wet grassland with <i>Deschampsia caespitosa</i> at Llandegfan, Anglesey.
	highest	As for Fig. 3 at Llyn Idwal, Caernarvonshire.

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NOMENCLATURAL NOTES ON THE GENUS *ANTHYLLIS* L.

By J. CULLEN

University of Liverpool Botanic Gardens

The following new combinations, etc., have been made necessary by the preparation of an account of the genus for *Flora Europaea*.

ANTHYLLIS MONTANA L.

subsp. **hispanica** (Degen & Hervier) Cullen, comb. nov.

A. montana var. *hispanica* Degen & Hervier, Bull. Acad. Int. Géogr. Bot. 15: 68 (1905).

ANTHYLLIS VULNERARIA L.

subsp. **bulgarica** (Sagorski) Cullen, comb. nov.

A. dillenii Schult. 'Unterrasse' *A. spruneri* Boiss. var. *bulgarica* Sagorski, Allg. Bot. Zeitschr. 14: 173 (1908).

subsp. **argyrophylla** (Rothm.) Cullen, comb. nov.

A. argyrophylla Rothm., Feddes Repert. 50: 190 (1941).

A. webbiana auct. mult. non Hooker, Bot. Mag. t.3284 (1833).

subsp. **reuteri** Cullen, nom. nov.

A. hispida Boiss. & Reuter, Pug. Pl. Nov. 36 (1852) non *A. vulneraria* var. *hispida* Boiss., Fl. Or. 2: 158 (1872).

subsp. **forondae** (Sennen) Cullen, comb. nov.

A. forondae Sennen, Sched, ad Pl. d'Esp. 5695 (1926).

subsp. **pindicola** Cullen, subsp. nov.

A subsp. *maura* (G. Beck) Lindb. foliis solum in parte inferiore caulis insertis, foliis inferioribus equifoliatis, foliolis (7-) 9-13 (-15), ellipticis vel orbiculatis, calyce concolore, sparse hirsuta differt.

Holotype: Greece, Epiros, inter Vriskos et Joannina, 8. vii. 1958, *Rechinger* 20721 (W—Herb. Rechinger).

subsp. **weldeniana** (Reichenb.) Cullen, comb. nov.

A. weldeniana Reichenb., Fl. Germ. Excurs. 515 (1832).

subsp. **hispidissima** (Sagorski) Cullen, comb. nov.

A. hispidissima Sagorski, Allg. Bot. Zeitschr. 14: 174 (1908).

BOOK REVIEWS

Flora of Iraq, Volume 1. Evan Guest (editor). Pp. xvi +207, with 9 plates (2 in colour), 36 figures (including 2 coloured maps) and 6 tables in the text. Ministry of Agriculture, Baghdad, Iraq, 1966. Obtainable from R. Maclehose & Co., Glasgow. Price £1 10s.

Turkey and Iran border Iraq, and form with it one of the most fascinating botanical areas in the world, particularly with regard to plant geography and plant domestication. The floras of all three countries are at present being covered by exhaustive treatments, Iran's by K. H. Rechinger, Turkey's by P. H. Davis and Iraq's in the work being reviewed here. The area has not been covered since Boissier's *Flora Orientalis* (1867–1888) and so this is a timely renewal of interest in it. The flora of Iraq has many of the easterly extensions of Mediterranean weeds, as well as many British and European casuals; this Flora will therefore be of value to British botanists. Volume 1, however, requires special consideration if its context is to be understood. It is a general treatise on vegetation and environment in Iraq, and includes diverse matter such as a gazetteer which will be of real value only to those attempting to elucidate the labels and field notes of herbarium sheets, and a 49-page illustrated glossary aimed at Arabic-speaking users of the Flora. There are only 55 pages on vegetation. The book is written as an adjunct to school and University texts within Iraq as well as a scientific work. Thus its scope is wide, and criticism comes easily to the specialist in any field, but this should not detract from the achievement that it represents.

No one who has not worked in Iraq can envisage the delays and red tape attached to any project there. The gaps between impulse, action and completion of any work are wide, and Mr. Guest is to be looked on with awe as someone who has surmounted innumerable obstacles. He is an Arabist whose contribution to the proper understanding of local plant names will shine throughout all the volumes of this work. But it is due to the special conditions in Iraq that this volume is dated 1966 while little new material has been incorporated since 1961.

My criticisms are confined to the treatment of vegetation except for two items: the useful rainfall records of the Hydrological Survey of Iraq (1959) are not mentioned in the section on the climate of Iraq, and in the bibliography (which incorporates material to 1964) it would have been better to use the World List for abbreviations of periodicals—'Journ. Ecol.' is clumsy.

Except for the list of plant 'associations', apparently no new material has been incorporated into the section on the vegetation of the country. This is a pity, for Mr. Guest must have made many original observations which, backed by research at Kew where this volume was written, could have added to the value of the section. Thus in the treatment of the Irano-Turanian region he quotes Drude (1890) for endemism rates, as cited by Eig (1931). Surely more up-to-date estimates would have been possible? This comment also applies to the uncritical acceptance of Zohary's (1950) figures for the proportions of Iraq species in each biogeographic region.

The special nature of Saharo-Sindian vegetation is dismissed in a few words, without considering Murbeck's (1920) old but thought-provoking work; and surely some groups of plants do show special development in this area, such as *Neurada procumbens* (in its own subfamily of the Rosaceae), *Gymnarrhena micrantha*, and *Launaea* spp.

The list of plant communities in Iraq is given in terms of 'associations' which are assigned binomials without published relevés and without any mention of the availability of the data for future phytosociologists. The desert area is covered as far as the major vegetation types are concerned (though I would not imagine *Pulicarietum guestii* to be anything but a local facies of *Artemisietum herbae-albae*, not necessarily degraded), but the other areas of Iraq are very cursorily covered.

The quality of the printing is good, and the work as a whole is relatively free from errors, but the standard of photographic reproduction is poor in the examples that I have seen.

Flora of Iraq, Volume 2. C. C. Townsend and Evan Guest (editors). Pp. viii +184, with 32 plates, 1 coloured frontispiece and 3 text figures, 1966. Price £1 10s.

This Flora will, I suspect, remain as one of the curiosities of botanical literature since it is arranged on the basis of Hutchinson's 1959 treatment of the Families of Flowering Plants, a fact for which neither Mr. Townsend nor Mr. Guest can be held responsible.

In this volume only *Equisetum*, ferns, gymnosperms and Rosaceae are covered. There is a key to the families of Iraqi Angiosperms which is stated to have been modified from Hutchinson's key. A little more modification with the Iraq flora in mind would have made the key much shorter. Most families are keyed out in the present work just as many times as in Hutchinson's original, although the Iraq flora is poor in genera of some families. For instance the Sterculiaceae is keyed out eight times but, as far as I know, apart from ornamental cultivands only one species (*Glossostemon bruguieri* DC.) grows in Iraq.

Throughout the work little reference has been made to collections in the Baghdad University Herbarium. I appreciate that in the past it has been difficult to procure specimens on loan from the University authorities, but I hope that renewed efforts will be made to do so in the future. In the present volume *Agri monia eupatoria* L. is not recorded for the Baghdad district although it grows there near the site of the old Rustam Herbarium and is represented by specimens in BUH.

R. D. Meikle has given a fine treatment of the Rosaceae, and I enjoy the broad view of the genus *Prunus* taken here, sinking *Amygdalus* and *Cerasus*. J. B. Gillett has revised the late R. A. Blakelock's account of *Ephedra*, which has left the genus in an easily understandable order.

The plates are excellent and show the high standard of draughtsmanship that we associate with Kew productions.

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A. D. Q. AGNEW

Botanical Latin. W. T. Stearn. Pp. xiv+566 and 42 illustrations. Nelson & Sons, Edinburgh. 1966. Price £5 5s. 0d.

Systematic botany is one of the very few surviving strongholds of the Latin language as a *lingua franca*. This may seem to many people a curiosity, worth preserving, perhaps, for its historical associations, but of no significance in the modern world of science-based technology. Yet to any systematist who has experienced the very real relief of finding, for example, a new species in the Bulgarian Flora described in Latin in a special appendix—or even to the forester who uses Latin binomials with confidence as an international nomenclature—botanical Latin is very much more than a 'freak'. It was, therefore, all the more surprising that no comprehensive book in English existed which attempted to teach this language before William Stearn's masterly opus. Reviewers often say, with varying degrees of conviction, that a book 'fills a long-felt want'. The phrase can be sincerely used to commend this remarkable work.

'Botanical Latin', in the words of the author (in a preface entitled '*Apologia pro Libro meo*'), 'aims to provide a working guide to the special kind of Latin internationally used by botanists for the description and naming of plants.' It is a reasonable claim; after a fascinating historical and introductory Part I, the author devotes Part II to basic grammar, and some old friends appear ('*amo, amare*') as well as some less familiar, more technically useful ones ('*florere*' to flower). The idea is excellent, and the book is completely self-contained. Part III, somewhat uninformatively entitled 'Syntax and Other Matters', provides the systematic botanist with everything he needs to write his own Latin diagnosis or description. Part IV is an extraordinarily complete vocabulary working both ways. Characteristically the author says 'it does not claim to list every word which has ever been used in descriptive botany', but few will criticise it on the score of inadequacy.

An excellent work, complete and attractively produced, ideal for the student of botanical taxonomy in every respect except one—the price. Perhaps nothing can be done about this problem; but 5 guineas is too much to expect the student to pay for a book which, to be honest, is only one of many which he is going to have drawn to his attention during a three-year University course. How many will persuade a rich parent or relative that this is the ideal Christmas present? It is sad to think that, to very many students for whom this book could be really useful, it will remain yet another work to be consulted hurriedly and inadequately in a Departmental library. Perhaps a shortened version, incorporating the excellent Part II, might be produced at a more modest price? I sincerely hope so.

S. M. WALTERS

A Dictionary of the Flowering Plants and Ferns. J. C. Willis. Seventh Edition, revised by H. K. Airy Shaw. Pp. xxii+1214+liii. Cambridge University Press. 1966. Price £5.

It is good to be able to welcome a new edition of this familiar work which, in one or other of its previous manifestations, has occupied a prominent position on the desks of many botanists. For, indeed, it provides in a handy concise form much information that is otherwise only to be found widely scattered through the literature.

Willis's *Dictionary* first appeared in 1897 in two volumes, of which the first contained articles on

various botanical topics such as Morphology, Classification and Economic Botany, while the second was the dictionary proper. The second (1904) and third (1908) editions were in one volume with, in the latter, an additional 'glossarial index'. In 1919, Willis completely revised the work, omitting the general topics of Part 1. In two further editions (1925, 1931), he rewrote certain pages and added a supplement. The sixth edition was reprinted four times between 1948 and 1960, but no additional material appears to have been added since 1931.

In producing this new edition, Mr. Shaw has adhered mostly to the previous format; but, in order to provide adequate discussion of certain topics and still keep the size of the book within a reasonable and handy compass, he has had to omit certain information that appeared in previous editions. Thus all headings concerned with popular and economic names have been omitted, as well as the articles on morphological topics (e.g. perianth, stipule), so that the alphabetical entries are largely confined to names of genera and families. The reviser's aim has been 'to include every published generic name (whether validly published or not) from 1753 onward, and every published family name from the appearance of the *Genera Plantarum* of Jussieu in 1789'. The only other entries other than genera or families are some supra- and infra-familial taxa and the uninomials of Ehrhardt and Du Petit Thouars. In addition, the family entries have been somewhat altered. Instead of Engler & Prantl and Bentham & Hooker equivalents of each family, the author of the family name is given. This is a very valuable piece of information which could not have been included in previous editions as much of the relevant research had not been done; but it is a pity that space was not available for reference to the two most widely used systems of classification.

Another feature of previous editions that is here conspicuous by its absence is the reference, under each genus of the larger families, to the position of the genus according to the synopsis of 'Classification and Chief Genera' given at the end of the account of the family. At first glance the number of such synopses appears to have been reduced; but this is due to the elevation of several subfamilial taxa to family rank (e.g. in Gentianaceae and Onagraceae). Many of the synopses which remain, however, have been elaborated and revised according to modern treatments (e.g. Ranunculaceae, Ericaceae).

One of the notable features of this edition is the introduction of a completely revised family concept. At a time when workers continue to produce evidence that many of the well-known families are to some extent heterogeneous and that the classification of Angiosperm families into orders has not yet been successfully achieved, it appears wise to avoid strict adherence to any of the published family treatments. Instead, Mr. Shaw has attempted to 'purify' many families by the exclusion of the heterogeneous elements, while being apparently in no hurry to re-allocate these elements to other existing families. This policy has resulted in the recognition of many unfamiliar families, often monogeneric e.g. Sladeniaceae (*Sladenia*; ex Theaceae), Uapacaceae (*Uapaca*; ex Euphorbiaceae), Kingdoniaceae (*Kingdonia*; ex Ranunculaceae), but sometimes quite large (e.g. Alliaceae). These families, including as they do many of the anomalous genera of existing families, usually show features indicative of relationships in several directions. It is therefore very helpful to have, at the end of each family entry, Mr. Shaw's ideas regarding the affinities of that family. Even though not everyone will agree with his suggestions—and some of them are most unexpected—it would be difficult, if not impossible, to find another modern work of comparable scope in which the relationships of families and genera have been considered on such a wide scale.

The treatment of genera is necessarily dependent to an even larger extent on the availability of recent revisions and the author's own opinions. It is not surprising, therefore, to find some large genera subdivided when, in the reviewer's opinion at least, it would be preferable to take a broad view (e.g. *Hippocratea* L.).

Irrespective of these considerations of rank and taxonomic recognition, it is good to note the addition of such a large number of genera omitted from previous editions and the inclusion, under both generic and familial heads, of many references to recently published work. The value of the volume as a research tool is considerably enhanced thereby.

This new edition of 'Willis' has obviously entailed much careful and detailed work, but two points of criticism come to mind. Firstly, the synonymy signs are confined to = (i.e. 'a synonym of . . .') and ~ (i.e. 'sometimes included in . . .'). It would have been helpful to distinguish in addition between nomenclatural and taxonomic synonyms, but the extra work involved would no doubt have been enormous. A more practical criticism concerns the summary of the classification of Bentham & Hooker at the end of the work. This, like the summary of Engler & Prantl's system, has been reprinted unchanged from the previous edition. Willis, however, had added two small families to the numerical sequence adopted by Bentham & Hooker. Since these are both near the beginning (21. *Vochysiaceae* and 48. *Cyrilleae*), most of the numbers of the families differ by one or two from those in the original system as used in Kew, the British Museum and other herbaria. This difference has already proved confusing to herbarium workers and it is a pity that the opportunity to revert to the original enumeration was not taken.

Although now somewhat larger than before, 'Willis' is still convenient for use as a desk-top reference

volume. The differences in type-size and page-headings, small though they are, will also make it easier to use. The only inconvenient feature in this connection is the price which, at £5, renders 'Willis' less easily available than before; but the additional information in this edition makes it well worth the increased cost.

N. K. B. ROBSON

Primary Productivity in Aquatic Environments. C. R. Goldman (editor). Pp. 1-464. University of California Press. 1966. Price £3 10s.

This volume records the proceedings of the first symposium to be held in the International Biological Programme. A total of 27 papers were presented in six sections dealing with various aspects of primary productivity in both freshwaters and the sea.

As with all symposium volumes there is considerable variation in the standard of individual papers. Some are useful surveys of an area of investigation, and others are mere abstracts of work published or about to be published elsewhere. The editor admits that the papers did not lend themselves to rigid organization, so that the book lacks the form that might be achieved by a single author. This is a feature of many symposia, and should not be allowed to detract from the general value of the volume, which covers many topics with greater expertise than could be expected from a single author. Some of the authors also acknowledge that their first drafts have been modified by the discussions which took place at the symposium.

For the non-specialist in primary production this book provides an introduction to the people who are studying this topic in aquatic habitats and provides an idea of the directions in which their lines of research are travelling. Most of the papers deal with primary production by planktonic algae, but some of the papers deal with higher plants; of these the paper by Westlake on the productivity of aquatic macrophytes is the most likely to be of direct interest to readers of this journal.

The volume is well produced, with few printer's errors, and the general usefulness is increased by the addition of indices of water bodies, organisms and subjects.

J. GREEN

Plant Taxonomy. V. H. Heywood. Pp. 60. Studies in Biology, No. 5. Edward Arnold. 1967. Price 12s. 6d. hardback; 7s. 6d. paperback.

This is a clear and closely reasoned exposition of the main aspects of modern taxonomy, and the author is to be congratulated in condensing so much information into some 60 pages of text and diagrams. It touches on most of the newest lines of advance in the subject, relating them where appropriate to the more traditional methods.

The author starts with the need for the classification of organisms and the historical development of taxonomic thought from the classical to the experimental approach. He then sets out to examine the raw materials of taxonomy, populations. This is perhaps arguable: populations may form the raw material of evolutionary development, but individuals could be considered as the raw material of any classificatory system. The various breeding systems which influence the pattern of variability and hence of evolutionary change are next dealt with, followed by a section on patristic similarity, cladistics and homoplasy, which might appeal much less to the average student, but certainly ought to be understood by him. Then comes a chapter on phenotype, genotype and ecotypic differentiation which should, in the reviewer's opinion, have come earlier in the book when the raw material was being discussed.

Taxonomic characters are treated in chapter 6, but seem to include only morphological and anatomical ones, though it must have been the author's intention to lead from these through to the biochemical ones, which are the subject of the following chapter. Cytological characters, however, are not mentioned until much later, in the last chapter. The chapter on biochemical systematics is easily the best in the book, and in the space of a few pages opens up new and exciting vistas to the reader.

The concept of character weighting is discussed in the next chapter, followed by a good, but necessarily simplified exposition of numerical taxonomy in chapter 9.

The final chapter, on chromosomes, taxonomy and evolution, contains a section on karyotypes and chromosome number which should surely have been placed in chapter 6. However, the evolutionary aspects of polyploidy and the significance of isolating mechanisms clearly find their correct place in this final chapter. One would like to have seen the section on isolating mechanisms as well as that on hybridization considerably expanded, and more mention made of Anderson's introgressive hybridization concepts. No doubt, however, the author was strictly limited as to space, so that the extension of one section would have forced him to exclude or shorten another.

This book presents modern taxonomy in a clear and exciting manner in a form likely to appeal to the average modern student who is so often nurtured on a pure diet of molecular biology. The biochemical, numerical and evolutionary sections are particularly interesting and should stimulate the student to read more widely. Here again, the author gives a useful select list for further reading, referring, amongst other

items, to the excellent work by Dr. P. H. Davis and himself, *The Principles of Angiosperm Taxonomy*.

The provision of an index would greatly have enhanced the value of the book, but may have been omitted for reasons of space or because it would not have been consistent with editorial policy. The book is remarkably good value and includes a number of good diagrams and some excellent plates. It should be of interest to many sixth-form pupils and should be required reading for all first and/or second year University students reading Botany and Biology.

J. G. HAWKES

Vergleichende Chorologie der zentraleuropäischen Flora. Pteridophyten—Gymnospermen—Monokotylen—Dikotylen (Salicales—Fabales). H. Meusel, E. Jäger and E. Weinert. Text band: Pp. 583 with 9 plates. Kartenband: Pp. 258 with 992 distribution maps. Format: 34×30 cm. VEB Gustav Fischer Verlag, Jena. 1965. Price: MDN 295,00 (approx. £30).

This work is published in two parts and describes the world-wide distribution of selected plants from the Pteridophytes, Gymnosperms, Monocotyledons and Dicotyledons (Salicales to Fabales). Further parts are to be published later. This is not just a revised version of Professor Meusel's *Vergleichende Arealkunde* (1943) but is completely rewritten and very much enlarged. Stress is placed on the comparative distributions of Central European species but attempts are made, where possible, to plot patristically related species that are not found in Central Europe; in some genera such as *Colchicum*, *Glyceria*, *Larix*, *Oxytropis*, *Picea* and *Pseudostellaria* this is well done but in many other genera no information is given on extra European species.

The first part or 'Textband' is particularly valuable and, at the beginning, reviews the main systems for the classification of distribution patterns and discusses, in detail, the floristic elements that make up the Central European flora.

The next chapter deals with the distribution patterns of whole families and selected sub-families, genera and sections. The amount of detail given for each group varies; some groups are well covered while others merely have short descriptions. It must be borne in mind that gathering information of this nature is very tedious and we must be thankful for any data on this subject. The next part of this volume of text contains a table (running to 179 pages) of the selected species with their distribution in abbreviated form, the floristic element to which they belong and selected references. The next 272 pages contain full descriptions of the distribution of the mapped species and with each species is given a selected synonymy, some information on related species and some relevant references. This volume ends with a bibliography which contains well over 1,000 references but, unfortunately, some of the references cited in the text are not to be found in the bibliography—it is to be hoped that this will be rectified in later volumes.

The second part, which is bound as a separate book, contains 992 distribution maps. The maps are printed four to each page and they are clear and well reproduced. Most distributions are shown by shading but simple outlines and point distributions are also used. Where there is suitable information on the recent spread of species this is often given; good examples are: *Camelina microcarpa* Andr. ex DC., *Sisymbrium altissimum* L. and *S. loeselii* Juslen. Well documented extinctions or contractions of range are indicated and good examples are: *Aceras anthropophora* (L.) Ait., *Ophrys apifera* Huds. and *Batrachium (Ranunculus) hederaceum* (L.) S. F. Gray. Obvious introductions, doubtful records and a few fossil distributions are also given. Most maps illustrate the distribution of two or more species, subspecies or varieties; map 71b, for example, shows the separate distributions of 15 taxa included within the *Carex angarae* Steud. group. Many maps illustrate the distribution pattern of genera and sections. The species densities within these genera and sections are usually given by printing the number of species to be found in selected areas.

It must be admitted that this book does contain some mistakes, but mistakes in a work like this are inevitable where the authors have relied on published literature for nearly all of their records. The mistakes often arise from differences in taxonomic opinion and not just simple misidentifications of plant material. However, these mistakes should not detract from the book as a whole. Professor H. Meusel and his colleagues Diplombiologen E. Jäger and E. Weinert have collected and handled an immense amount of material which has been sorted and published in a readily accessible form. The price of this book is prohibitive and it is to be hoped that libraries, at least, can be persuaded to make the knowledge contained in this book 'readily accessible'.

C. D. K. COOK

Floral Biology. Mary S. Percival. Pp. xv+243, with 67 text figures. Pergamon Press, Oxford, London, Edinburgh, New York, Paris and Frankfurt. 1965. Price 20s.

Floral biology is an attractive subject, dealing as it does with the form, structure and mechanisms of the flower and with associated pollinating agents. It has been out of favour for much of this century, largely

as a reaction against the 'excesses of frequently teleological "adaptationists" ' in the post-Darwinian period who saw function at every turn on the most slender evidence. It is thanks to the work of people such as Baker, Grant, Jaeger, Leppik, van der Pijl and Stebbins that floral biological studies are now on a sound and scientific footing again.

Dr. Percival's account is a brave attempt to present the subject and outline the modern techniques that can be employed, in the hope of attracting new workers into this field. There can be no doubting her enthusiasm, but her book can only be recommended with grave reservations. It is, in fact, riddled with errors, inaccuracies, inconsistencies and stylistic infelicities, and appears to have been badly edited.

After a brief introduction which includes a potted history of floral biology, the first chapter is devoted to 'Sex in flowers'. There is a useful section on terminology in which we are told that 'Species, all individuals of which have the same kinds of flowers, and possessing hermaphrodite and female flowers are *gynomonoecious*'—a baffling statement unless one knows beforehand what the term means. The frequently used term 'polygamous' is not given. Fig. 2 gives an extraordinary illustration of *Begonia* in which the label pointing to 'anthers with line of dehiscence' in fact leads to nothing comprehensible even under a $\times 10$ lens. In figures 4 and 5 the spurious accuracy of the width of the lower lip of the corolla and the length of the tube (3.7 mm, 4 mm, 6.7 mm and 8.5 mm respectively) is misleading. On p. 7 the statement that gynodioecism in *Glechoma hederacea* 'appears to be due to a virus-like particle in the cytoplasm of the female plant, for if the female is grafted on to the hermaphrodite plant, the latter becomes female' surely demands some further explanation. Much more serious is the unpardonable confusion between pollination and fertilization in the definitions of autogamy, allogamy and hybridization.

In Fig. 8, *Helleborus corsicus*, the stigmas are described as 'proterogynous' whereas on p. 8 the term is correctly applied (and differently, although equally correctly spelled) to the flower. The pictures of *Fuchsia* (Figs. 9(a) and (b)) and of *Asclepias* (Fig. 14) are far below the quality one expects in a published work, while Fig. 21 which is said to be '*Momordica balsamina* L. S. flower centre' is a baffling black and white silhouette resembling an ink blot. Both the description and illustrations of the stigma of *Grevillea* are difficult to follow and appear in any case to be contradictory. And so one could go on. Whole pages are undisciplined and rambling such as the account of the features of anemophilous flowers on pp. 55 seq. when the author jumps from group to group with scant regard for subjects, antecedents, paragraphs and so on, not to mention factual errors, misleading generalizations and bizarre notions of taxonomy.

Chapter 3 is concerned with the agencies of pollination. Bat pollination is included but there is no reference to or pictures of bat flowers or the extensive work of Baker and Harris on this topic. Myrmecophily receives no mention. It is interesting to learn that maize pollen is so large ($700,000\mu^3$) and that it falls almost vertically to the ground. Unfortunately, the dimensions, when one has worked out what they mean, are of little help without those of other pollen grains for comparison. The section on hydrophily is difficult to follow and with regard to flowering in the Podostemaceae (p. 61), self-contradictory. Fig. 33 is not of *Zannichellia palustris* as stated, which has quite a different structure from that figured.

Chapters 4 and 5 deal with animal food in flowers and are full of interesting information—'in *Helleborus orientalis* stamens dehisce all round the clock'—and Table 2 gives a useful survey of the rhythm of pollen presentation in a wide range of species though one might be forgiven for wondering how accurate it is.

It would be easy to continue this sad commentary. A last quotation illustrates the kind of passage that induces a feeling of helplessness in this reviewer—'members of the Lobelioid group of the Lobeliaceae lost their only pollinators in areas where the Hawaiian Honey-creepers, Drepanididae, became extinct. The birds had bills of the right proportions to probe the flower tubes. These plants, one is *Cyanea hirtella* Rock, are persisting and setting seed although the birds have gone and have successfully reverted to autogamy.' And who can blame them?

The number of omissions is remarkable—no mention of H. G. Baker's outstanding series of papers and reviews of floral biology and breeding systems, nor of E. J. H. Corner (not even a mention of figs); the fundamental review of reproductive modes in higher plants by Fryxell is not mentioned; van der Pijl's review (1960–61) of flower evolution finds no place (although there is a reference to earlier of his works); Meeuse's *The Story of Pollination* is omitted as is the much earlier volume by Clements and Long, which said much of it all before. Other important omissions are Verne Grant's *Natural History of the Phlox Family* and *The Origin of Adaptations*, both highly relevant works. Other works are misquoted such as 'Principles of Evolution of Genetic Systems by C. A. Darlington', and 'Dr. Hans Kugler's Introduction to Floral Biology' mentioned in the Introduction which is in fact a German work as one can deduce from the Bibliography, and 'Dr. Stefan Vogel's Floral Biological Types as a Factor in Classification (1954)' which is not only not in English, but is not even a book as one is led to expect: it is a review (given in the References, not the Bibliography) published in *Bot. Studien* 1, Jena.

The references (apparently papers cited in the text) and the Bibliography (the books cited) are in thorough need of revision. Both the Darwin references in the Bibliography have the wrong dates and the wrong titles

(correct, however, in the Introduction). The references to Kerner and Knuth contain errors regarding the dates of publication and the number of volumes. There is an index to animals, one for plants and a very brief and incomplete subject index.

The use of common and scientific names is quite haphazard—see pp. 158–59, paragraphs 3–4 for a concentrated example. There are numerous mis-spellings such as *Robinia pseud-acacia*, *Lithospermum purpuro-caeruleum*, and *L. purpurpocaeruleum*, *Myosotis discolor Pers.*, secretary (secretory), D.C. (DC.), rachices, data is, fascicles, Plantage, *Rhododendrom*, *Escholtzia* and *Eschscholtzia*, *Rubus fruticosus* age, Manilla, *Helianthemum chamaecistus*, *C. sinensis*, v: Valencia, apomyxis, *Coleus thyrsoideus*, *C. thrysoides* and *C. thyrsoideus* (none of them correct!), *Cyania hitrella*, *Echium vulare*, *Heracleum spondylium* and *Ranunculus puberulus*. Other errors noted included 'Royal Horticultural Society's Dictionary of Horticulture' and Larsen & Tung (1952) in text, which appears correctly as (1950) in references where the volume number of the Botanical Gazette is wrongly given as 3 instead of 111.

The generally slipshod approach employed in writing the book leaves one apprehensive about its overall value. With so many obvious inaccuracies one simply does not know what pieces of information to trust. And yet there is clearly much of value in the book. I can only suggest to Dr. Percival, her Editors and Publishers that the volume be meticulously revised and republished. There are few enough books in this field which one can recommend for student use and it would be a service to botany if this one could be revised and added to the list.

V. H. HEYWOOD

Hortulus. Walafrid Strabo. Translated by Raef Payne. Commentary by Wilfrid Blunt. Pp. xii + 92. Number 2 of the Hunt Facsimile Series. The Hunt Botanical Library, Pittsburgh, Pa. 1966. Price \$12.

A book about Walafrid Strabo with a commentary by Wilfrid Blunt, text and translation by Raef Payne, and published by the Hunt Botanical Library, must be excellent. This book, both in substance and form, is, in fact, superexcellent. Wilfrid Blunt's account of Strabo—itsself a piece of literature—shows clearly that the widely held opinions about the cross-eyed are not always true. Among other treasures we have here a facsimile of the best-known manuscript *Hortulus* in fine Caroline minuscules. Of those who contributed to the design of the volume, special mention should be made of Wilfrid Blunt, at whose suggestion the pretty green linoleum cuts were spread over the crystal-clear type of the Latin and English texts, which they by no means obscure. When these days are past and gone, this work will remain—an emblem of the civilization we now enjoy.

H. GILBERT-CARTER

Flóra Slovenska. Edited by J. Futák. Vol. 1, Pp. 602, 9½ × 7 in. Bratislava, 1966. Price 40 Czech crowns. Vol. 2, Pp. 345, 9½ × 7 in. Bratislava, 1966. Price 28 Czech crowns.

These are the first two volumes of a new Flora of Slovakia, which is being prepared under the general editorship of Doz. J. Futák, of the Slovak Academy of Sciences. The authors of Volume 1 are J. Dostál, J. Futák & F. A. Novák, and of Volume 2, J. Futák, M. Jasičová & E. Schidláay.

Volume 1 has an introduction in Slovak, Russian and German which sets out the history of the project, the methods used in preparing the flora, and the system on which it is arranged. The whole of the remainder of the volume is devoted to a survey of plant morphology, item by item; every term is defined (its Latin equivalent being given) and most of them are illustrated by large, clear diagrams. There is an excellent index to the Latin terms, with 1200 entries.

Volume 2 is the first volume of the Flora proper, and it covers the Pteridophyta and Coniferophytina. The treatment of both groups is up to date. Families, genera and species are keyed and concisely described. Place of publication is given for the species and basionym and synonyms are cited. There are notes on ecology and chorology, and chromosome number (usually from the literature) is given; localities are often given in detail, herbarium specimens frequently being cited. There are good habit drawings (3 or 4 to a page) of every species; and dot distribution maps, on a reasonably large scale, of about half the species. There are also, at intervals in the text, short lists of literature references; this is an excellent feature.

We can heartily recommend this new arrival to the list of European Floras; Dr. Futák and his colleagues are to be congratulated on a well produced and well organized piece of work. The Flora will be complete in 7 volumes.

D. H. VALENTINE

ERRATA

p. 86, lines 5–6 from bottom should read:

- | | |
|--|----|
| 1. Leaves up to four times as long as broad | 2 |
| Leaves more than four times as long as broad | 17 |

p. 87, lines 23–24 should read.

- | | |
|--|--------------------|
| 15. Leaves dentate | 7. <i>dovrense</i> |
| Leaves finely denticulate or subentire | 16 |

p. 87, lines 29–30 should read:

- | | |
|------------------------------|----------------------------|
| 18. Leaves over 20 mm. broad | 10. <i>attenuatifolium</i> |
| Leaves under 20 mm. broad | 19 |

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