MIMULUS HYBRIDS IN BRITAIN

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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-carmine, 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* × *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* × *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 × breadth in mm) in hybrid *Mimulus* after pollination with pollen from different sources

Pollen source:		
M. luteus	M. guttatus	*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* ♀ × *M. luteus* ♂ occurs readily and gives a reasonably good seed-set, from a proportion of which highly variable F_1 plants result; the majority are large and vigorous. These F_1s 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* ♀ × *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.

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