THE HYBRIDS OF *MIMULUS CUPREUS*

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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* × *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* × *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* × *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* × *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-carmine, 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* × (*luteus* × *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* × *luteus*.

Localities from which the hybrid M. guttatus × 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 Ebudes: 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**).

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References

Bailey, L. H. (1927). *The Standard Cyclopedia of Horticulture*. New York.
Grant, A. L. (1924). A monograph of the genus *Mimulus*. *Ann. Missouri Bot. Gard.*, **11**, 99–388.
McClintock, D. & Fitter, R. S. R. (1956). *The Pocket Guide to Wild Flowers*. London. Supplement by D. McClintock (1957).
Pennell, F. W. (1951). In Abrams, L.R., *Illustrated Flora of the Pacific States*, **3**, 688–731, Stanford, California.
Roberts, R. H. (1964). *Mimulus* hybrids in Britain. *Watsonia*, **6**, (1), 70–75.
Stebbins, G. L. (1950). *Variation and Evolution in Plants*. New York.
Vickery, R. K. (1959). Barriers to gene exchange within *Mimulus guttatus* (Scrophulariaceae). *Evolution*, **13**, 300–310.