

LAMIUM HYBRIDUM VILL.

By the late J. E. LITTLE (written in 1928).

Lamium hybridum Villars, 1786, *Hist. Pl. Dauph.*, **1**, 251; De Candolle, 1805, *Fl. Fr.*, **3**, 541.

L. purpureum var. c: (*hybridum*), 1787, *ibid.*, **2**, 385.

L. dissectum Withering, 1796, *Arr.*, Ed. 3, **3**, 527.

L. incisum Willd., 1800, *Sp. Pl.*, **3**, 89.

The history of this plant begins with Ray's account here transcribed:—

Lamium rubrum minus foliis profunde incis. Small cut-leaved red Archangel. Ray, 1686, *Hist. Plant*, **1**, 560.

“Hæc species primo nobis ostensa a Tho. Willisell in campis S. Jacobi dictis prope Londinium, postea variis in locis solo arenoso aut glareoso observata, *Lamio rubro minore vulgari* plerumque minor est, quamvis in lætiori solo in magnitudinem illius aemulam interdum proficiat. Radix ei simplex tenuis, unde et plantam annuum esse suspicamur. Caulibus et foliorum et florum situ cum *Lamio rubro vulgari* convenit. Differt ab eo foliorum incisuris. Cum enim in illo folia leviter tantum circa margines crenata sint, in hoc altius incisa et propemodum laciniata sunt, laciniolis seu mavis dentibus in acutos apices terminatis. Differt etiam florum parvitate et eorundem tubis brevioribus, adeo ut flores antequam explicentur vix e vasculis appareant.

Locus. In hortis oleraceis inque arvis requietis non raro invenitur, ut v.g. prope Brantriam in Essexia in calceto Bockingam ducente.”

Fortunately there is in Ray's *Hortus Siccus* (in *Hb. Mus. Brit.*, fasc. VIII, O. 10; middle left, three pieces “*Lamium purpureum parvum foliis magis incis.* N.D.”. Thus we have both description and authentic specimens. When Ray's *Historia* was published, he was living at The Dewlands, Black Notley, “to which he moved in June 1680, and in which he lived for the remainder of his life” (*Dict. Nat. Biogr.*). It is not unlikely that Ray's specimens were gathered at one of the two localities where he first observed it, either in St. James' Fields, Middlesex, or on the road from Braintree to Bocking. The latter (the -ham having been dropped since Ray's time) lies about two miles N. of Braintree, while Black Notley is about the same distance to the south. In any case they are first records for those counties, though G. S. Gibson (1862, *Flora of Essex*) makes no mention under *L. incisum* Willd. of Ray's locality.

The earliest figure is that of Plukenet (1691, *Phytographia*, t. 41, fig. 3), where Ray's name is cited. The figure of *L. incisum* in Reichb., 1858, *Ic. Fl. Germ.*, plate 1204, does not show clearly the character of the upper leaves. There is a good drawing by M. Denise in Coste, 1906, *Fl. Fr.*

In the Sloane Herbarium (Hb. Mus. Brit.) are several gatherings which carry on the history of the plant.

H.S.83.233. Top right corner, with ref. to Ray. Plukenet, European plants.

H.S.96.ii.127. Bottom right corner, with ref. to t. 41, fig. 3, as above. Plukenet.

H.S.121.19. The two bottom left-hand pieces (of which the lower is more doubtful). Buddle, British plants.

H.S.151.205. The bottom left-hand piece, with ref. to Ray's *Hist.*, I, 560. Petiver.

H.S.230.9. No. 4. This is a plant from Chelsea Garden by Philip Miller, circa 1727.

Although Villars names the plant *L. hybridum*, he does not say that he considers it a hybrid. He does however say (*op. cit.*, 2, 385):—"La variété (c.) qui mériteroit peut-être de faire une espece, a le port de celle-ci, et les feuilles petites comme la précédente [*L. amplexicaule*] ses feuilles pointues comme cella-là, et profondément découpées comme celle-ci, tiennent par conséquent de l'une et de l'autre; elle est beaucoup plus rare que les autres." In Vol. 1 he makes it a species; but in Vol. 2 a variety of *L. purpureum*. Accordingly, Thuillier (1799, *Fl. des Env. de Paris*, 290) quotes in the former sense, while Koch (1843, *Syn. Fl. Germ.*, 269) quotes *L. purpureum* β *hybridum* Vill.

The question whether our plant and *L. intermedium* Fr.* are hybrids has been discussed by various writers. Sonder (1851, *Fl. Hamburgensis*, 326) remarks of *L. intermedium*:—"In Meyer's *Fl. Hannov. excurs.* this species is placed as a hybrid under *L. amplexicaule* as *L. purpureo-amplexicaule*. As against this, it may be remarked, that it produces every year mature seeds capable of germination, and that no specimens either from Sweden or from England, from Oldenburg or from this district, show any evident transition to *L. purpureum* or *L. amplexicaule*."

Ascherson and Graebner (1899, *Fl. N.O.-deutschen Flachl.*, 600) place both (A) *L. intermedium* Fr. and (B) *L. dissectum* With. under *L. amplexicaule* \times *purpureum*. They remark:—"This plant, which usually sets seed freely, gives us the impression of a hybrid which has become a species. Ritschl and Marsson, despite the contrary opinion of Frier, Sonder and others, make at least (A) [*L. intermedium* Fr.] a hybrid. E. H. L. Krause makes (B) [*L. dissectum* With.] a gynæcious race (?), 'weibliche Rasse', of *L. purpureum*."

More recently, Dr. B. H. Danser (1926, *Ned. Kruidk. Arch.*, 1925, 407) has a paper "Are *Lamium hybridum* Vill. and *L. intermedium* Fr. hybrids?"

Finding three specimens of *L. intermedium* in a potato field at Franeker (Friesland) on Aug. 15, 1922, he was led to enquire whether they must be regarded as hybrids.

*Mr. Little used the name *L. intermedium* throughout and this has been retained, although *L. motucellifolium* Fr. is the correct name.

If these two are really so, what should we have to expect on sowing them?—(1) That they would prove less fertile than the reputed parents. If this were so in fact, then that would of itself be a strong argument.

(2) If they were fairly fertile [in the first generation], we should have to expect variability in the second and later generations.

But their complete fertility, combined with entire constancy, opens up the following possibilities:—

- (1) The hybrid is purely apogamous.
- (2) The so-called hybrid is a good species.
- (3) The so-called hybrid is a variety of one or other of the reputed parents.

The second or third points can be answered by crossing with the species of which it may be a variety. The first point is less easy to establish. Dr. Danser then mentions what he observed before he began to test by sowing, and what expectations his observations aroused.

Lamium hybridum is common on the 'terpenklei'* of Groningen and Friesland, but much rarer elsewhere. Localities: Franeker; on the Zuiderzee-dijk at Amsterdam; Halfweg; Dordrecht. It is abundant at Franeker, where *L. amplexicaule* is pretty uncommon, and in most stations of the former wholly wanting. *L. hybridum* produces as numerous and as well-formed fruits as the reputed parents.

Lamium intermedium is much rarer. He found once only three specimens in a field where *L. purpureum* and *L. hybridum* were common, and *L. amplexicaule* very scarce.

A close examination of the characters of the two *Lamia* under suspicion suggested the same conclusion. *L. hybridum* is much nearer *L. purpureum*, and therefore it is not surprising that it has been regarded as a variety of that species. The corolla-tube is longer [but see below], and the hair-ring more obscure. Dr. Danser found no form which on the whole had no hair-ring. This is evident or not according to the angle from which one views it, and according to the manner in which one opens the tube, and is not equally evident in all the flowers on the same plant. The calyx does not resemble that of *L. amplexicaule*, but agrees with that of *L. purpureum*.

L. intermedium is nearer in corolla- and in leaf-form to *L. amplexicaule*, and therefore a conclusion is not so easy. But the result of sowing seeds from the plants of 1922 was that in the second generation he obtained normal seed-bearing plants, and from this he argues that *L. intermedium* is no hybrid.

Similarly he sowed seeds of *L. hybridum* from Franeker and Dordrecht. The seedlings from each locality were alike, and were like those from the other station.

* 'Terpen' are artificial hills on which houses are raised above the level of the surrounding lands. 'Terpenklei' is a clay from these hills enriched by kitchen-midden refuse and distributed over the land as a fertiliser. (Dr. W. J. Yongmans, Heerlen in Limburg, *in litt.* to W. N. Edwards.)

Lastly, as he has never found intermediates between the four *Lamia* mentioned, he concludes that the two in question are not varieties of *L. purpureum* or of *L. amplexicaule*.

The bold hypothesis that *L. purpureum* and *L. amplexicaule* may hybridise, and thus not be apogamous, while the hybrids resulting may be wholly apogamous, might certainly be entertained if the so-called hybrids were intermediate in their characters between the supposed parents; but this, as has already been said, is not the case.

Dr. Danser adds a postscript. A. Muentzing, 1925, *Eine Art-Bastard in der Gattung Lamium, Hereditas*, 7, 215, is of the same opinion about the four *Lamia* herein treated, and has moreover raised a hybrid between *L. amplexicaule* and *L. hybridum* which is wholly barren.

THE RING OF HAIRS IN THE TUBE OF THE COROLLA.

L. purpureum has this ring. The first botanist to raise the question in respect of *L. incisum* was J. de C. Sowerby, who on the original drawing, No. 1933, for *Engl. Bot.*, ed. 1, 27 (publ. Sept. 1, 1808) and reproduced in the 3rd Edition as 1533, sketched the tube of *L. purpureum* with the note, 'observe the hairs in the tube of the corolla', to which J. E. Smith added 'I think this should be engraved on the plate and marked *L. purpureum*'. Accordingly it was engraved on the plate of *L. incisum*; but the note was never incorporated. (See also F. A. N. Garry, 1904, 'Notes on the Drawings for Sowerby's English Botany', *J. Bot.*, 42, 143.)

Bentham (1848, in DC. *Prodromus*, 12, 509) gives for *L. incisum* 'corollæ tubo recto basi intus piloso-annulato'.

Koch (1843, *Syn. Fl. Germ.*, 649) has, for *L. incisum*, 'tubo corollæ recto aequaliter cylindrico intus exannulato'. He adds:—"Anglica planta sec. b. Smith et cl. Babington tubum intus exannulatum habet. An igitur planta cl. Benthamii, quæ tubo intus piloso-annulato describitur, ad varietatem *decipientem L. purpurei* pertinet?" Accordingly we find that he adds under *L. purpureum* the var. β *decipiens*, "folia inæqualiter inciso-crenata, fere ut in antecedente, sed longiora ratione latitudinis, et tubus corollæ intus piloso-annulatus ut in illa: *L. purpureum* β *decipiens* Sonder in litt."

But when we turn to Sonder himself (*op. cit.*, 327) we find that under *L. incisum* he gives:—"tubo corollæ recto intus nudo vel annulo piloso prædito", and he merges *L. purpureum* β *decipiens* Sonder in Koch (*l.c.*) as synonymous with his *L. incisum*, and remarks:—"Corolla somewhat smaller than that of the following [*L. purpureum*], purple; the tube straight, having within above the base a delicate hair-ring, which in our local plants is never absent, but in specimens, otherwise agreeing in all respects, from Schleswig, Denmark and Westphalia is not present. Achene not distinguishable from that of the following. The frequent occurrence, and the constancy in development from seed, make extremely improbable the view of Prof. Meyer, according to which this plant is a hybrid: *L. amplexicaule-purpureum*."

Neither Ray, nor Villars, nor Withering, nor Willdenow made the absence of a ring of hairs a critical character. This first appears in *Engl. Bot. (l.c.)*, and is followed by Koch, but has against it the judgment of Sonder, Bentham, Hooker (1884, *Student's Flora*), Babington (1856, *Manual*, ed. 4) and Danser.

DISTRIBUTION.

In H. C. Watson's *Top. Bot.*, ed. 2, by J. G. Baker and W. W. Newbould (1883), *Lamium intermedium* is not shown to occur in any part of Great Britain S. of W. Lancs. (60); a note is added—10 (Wight), 40 (Salop), 49 (Caernarvon) insufficiently vouched.

L. incisum is shown for many vice-counties from Cornwall to Norfolk, and from Kent to Lancashire

Lancashire is thus the meeting-point of a form which with us is mainly northern (and unknown in France) with one which is mainly southern (and widely distributed in France).

Some personal and local observations of a plant which I believe to be identical with Ray's may now be given.

In north Hertfordshire the area round Hitchin constantly produces *L. hybridum*. During the last fifteen years I have noted some twenty distinct stations, and the plant can always be found, though not always in the same station since it is continually being destroyed by cultivation. Gardens, allotments, open fields, and more rarely hedgebanks all provide it with a congenial home, mostly on lighter land. The order of relative frequency is *L. purpureum*, *L. amplexicaule*, *L. hybridum*, and the three often grow intermixed. *L. hybridum* can be readily distinguished from normal *L. purpureum* in the field by its distinctive leaf-characters; as Bentham justly remarks (*l.c.*) 'Folia ut in *L. bifido incisum*'. This, which applies to the upper more distinctly than to the lower leaves, combined at times in spring with a suffused dark brownish-purple colour and less ascending habit, enables one to pick it out on an arable field at a distance of ten yards. There is one character which does not appear to have been specially noted, and this is, that throughout the winter it continues to produce abundant flowers which are usually cleistogamic and fertile, whereas *L. purpureum* either does not flower in winter or has flowers of the same character as its summer ones, i.e. brightly coloured and entomophilous. This seems to be a valuable and important mark of distinction.

During the last month (I write on Feb. 17) I have seen it in this state in four stations. This cleistogamic state begins in late autumn towards the end of October, and continues (with an exception mentioned below) until April of the following year, when the same plants put forth brightly-coloured entomophilous flowers, continue to ripen seed, and then die off when the hot weather begins. Their place is then taken by plants which have germinated in the spring and begin to flower in July. The length of the tube of the corolla in the cleistogamic state is 2.3 mm., and in *this state* the tube is in my experience wholly devoid of hairs. One may suggest as a possible reason that the economy of the plant does

not at this stage require the hair-ring. The tube of the entomophilous flowers is 8-10 mm. long, and may, as Dr. Danser says, have a ring of hairs, not however so definite as in *L. purpureum*. Between these two states there is a transition stage about March, in which the pallid short-tubed flowers expand as if open for insect visits; rarely, it is anticipated by an odd flower (Feb. 14, 1928). I have never seen a tube longer than 10 mm., but Bentham (*l.c.*) remarks:—'Variat uti *L. purpureum* corollis nunc breviter, nunc longe exsertis'. Mr. C. E. Salmon told me (16 Nov., 1927) that he had seen a form of *L. hybridum* with the tube of the corolla longer than in normal *L. purpureum*. This may account for some discrepancy in descriptions, and for Dr. Danser's remark that the corolla-tube is longer in *L. hybridum*. The colour of the corolla in the winter state is a washed-out bluish-purple; but sometimes the hood is greenish and only the middle of the tube is coloured. The middle of the tube is narrower than the base. In summer the corolla is not distinguishable by its colour from *L. purpureum*.

I have only recorded two stations for S.E. Bedfordshire (Southill 1912, 1914 and 1928, and Clophill 1914), but there also it will probably be found well distributed.

In Cambridgeshire I saw it in Sept. 1927 in a field of sugar-beet at White Hall Farm, Littleport. The field had been hoed several times in early summer, so that plants must have been summer-germinating seedlings. In this case also an obscure ring of hairs was present in the corolla-tube. Associated plants were *Veronica agrestis* L. (*sensu stricto*), *Galeopsis speciosa* Mill. and *Chenopodium polyspermum* (var. *acutifolium* Gaud. and var. *obtusifolium* Gaud.).

SUMMARY.

The balance of evidence is against the theory of a hybrid origin for *L. hybridum*. Its constancy and a sufficient number of correlated differences make reasonable its separation from *L. purpureum* as a species well enough marked in normal specimens to be distinguished at sight in the field. If the observations here recorded are correct, the hair-ring is not invariably absent. The leaf-cutting is much nearer to *L. bifidum* Cyr. than to *L. purpureum*.

I am much indebted to [the late] Mr. J. Ardagh, of the Department of Botany at the British Museum (Natural History), for assistance in referring to many of the works cited.

The above has been printed as Mr Little left it (with minor editorial changes). It may however be of interest to add a summary of more recent Scandinavian work on the subject. The first two papers, by Müntzing (1926, Ein Art-Bastard in der Gattung Lamium, *Hereditas*, 7, 215-228) and by Jörgensen (1927, Cytological and Experimental Studies in the Genus Lamium, *Hereditas*, 9, 126-136) were in fact published before Mr. Little's paper was written but were presumably not seen by him, although he quotes Danser as having seen the former.

Müntzing attempted crosses between the four species *L. amplexicaule*, *L. hybridum*, *L. molucellifolium* and *L. purpureum* in all six possible combinations and in both directions (the number of crosses made varying from 10 to 35) and found that only *L. amplexicaule* × *hybridum* succeeded (in both directions). He gives a full description and points out that the hybrid is completely sterile. He concludes that *L. molucellifolium* is not a hybrid between *L. amplexicaule* and *L. hybridum* as had been suggested by Lindman.

Jørgensen counted the chromosomes of various species of *Lamium* and found that *L. amplexicaule* and *L. purpureum* were diploids ($2n=18$) and that *L. hybridum* and *L. molucellifolium* were tetraploids ($2n=36$). This suggested to him that the two tetraploids might have originated from hybridisation between the two diploids. He, therefore, attempted the same hybrids as Müntzing but using far greater numbers of flowers (from 73 for *L. amplexicaule* × *hybridum* to 547 for *L. amplexicaule* × *purpureum*, including the reciprocal cross in each case). His results were the same as Müntzing's (viz. that only *L. amplexicaule* × *hybridum* gave offspring and that these were sterile triploids). He, therefore, suggests that the two tetraploids are unlikely to have arisen from hybridisation and that "the four plants being derived from a common ancestral type in which a spontaneous tetraploidy started the development of *L. dissectum* and *L. intermedium* while *L. purpureum* and *L. amplexicaule* kept the original chromosome number during their differentiation."

Bernström (1941, Polyploidy induced by Colchicine in *Lamium*, *Bot. Notiser*, 1941, 407-408; 1944, Two new hybrids in *Lamium*, *Hereditas*, 30, 257-260) attempted further experiments to see whether the species were phylogenetically related. He obtained tetraploids of both *L. amplexicaule* and *L. purpureum* by using colchicine. He then attempted hybridisations using his induced tetraploids, both with *L. hybridum* and *L. molucellifolium* and with the diploid of the other species, using 2 or more lines of each. He succeeded in obtaining hybrid progeny from *L. amplexicaule* ($4n$) × *molucellifolium* and *L. hybridum* × *purpureum* ($4n$). The other possible combinations all failed including *L. amplexicaule* ($4n$) × *hybridum* which succeeds when the former is diploid and all those between *L. amplexicaule* and *L. purpureum* whether diploid or tetraploid. Of the new hybrids, the former is sterile, and vegetatively poorly developed, the latter more vigorous and partially fertile; a short description of each is given. He draws no conclusions about the origin of the two tetraploid species.

In a later note, Bernström (1949, Cytogenetic studies in the genus *Lamium*, *Proc. 8th International Congress of Genetics*, 39-41) states that he has also produced the hybrids *L. amplexicaule* ($2n$) × *purpureum* ($4n$) and *L. molucellifolium* × *purpureum* ($4n$) and that these are also highly or completely sterile. He further states: "By studies on the chromosome pairing at meiosis of all these hybrids, in connection with genetical studies on the offspring of some of them, it has been possible

to prove that *L. intermedium* is an amphidiploid between *L. purpureum* and *L. amplexicaule*, whereas *L. hybridum* is an amphidiploid between *L. purpureum* and some other species." He believes the last to be *L. bifidum* Cyr. from S.E. Europe. There seems no reason to doubt these conclusions though I cannot find that the evidence on which they are based has yet been published.

From a taxonomic point of view, there can be no doubt that the four plants were treated as independent species.

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