

ON INHERITANCE OF A MUTATION IN THE COMMON
FOXGLOVE (*DIGITALIS PURPUREA*).

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[PLATE I AND TEXT-FIGS. 1-12.]

THE common Foxglove is well known for its frequent habit of sporting, and references to various monstrous forms abound in teratological literature. Most of these abnormalities come under the head of fasciation, proliferation, synanthly or peloria. In the present case the modification is of quite a different character and is confined to the corolla, the members of which are more or less completely disjoined (dialysis), some or all of the petals being furthermore converted into stamens (staminody). The result is a flower which is hardly recognisable as a foxglove at all. This curious form, though less commonly met with than the peloric variety, has been known for a considerable time. Penzig¹ speaks of it in conjunction with synanthly and peloria as a "classic" monstrosity; as early as 1826 it was figured and described by de Chamisso,² who names it *D. purpurea heptandra*. Later, in 1882, a specimen which had been gathered at Tilburstow Hill, Surrey, and sent to him, was described and figured by Henslow.³ Analogy with the case of peloria would lead us to suppose that the peculiar modifications characteristic of the *heptandra* form might also be found to be inherited. This expectation finds a certain confirmation in various scattered references recording the reappearance of this form from time to time. De Chamisso,⁴ it is true, states in a later note that none of the three plants which he obtained from the *heptandra* parent showed any trace of the peculiarity, but as the *heptandra* parent was not apparently isolated, this observation can hardly be used as evidence on this point. On the other hand a writer in "The Gardeners' Chronicle" states that a seedling foxglove exhibiting staminody of three of the petals was derived from a parent similarly deformed.⁵ In another instance seedlings from a specimen observed by Mr. Smith of Daisy Hill Nursery, Newry, are stated all

¹ Pflanzen-Teratologie 2, p. 210.² *De Digitali purpurea heptandra*. Linnæa I, p. 371, Tab. VI.³ Journ. Linnean Soc., XIX, Botany, pp. 216-218, 1882.⁴ Linnæa IV, p. 77.⁵ G. C., 1874. 2, p. 78.

to have reproduced the deformity.¹ The number of plants raised is not, however, stated. Again recently, while this account was already in progress, a specimen was exhibited at a meeting of the Linnean Society by Professor Dendy, on behalf of Dr. N. C. Macnamara.² The spike in question had, according to the account, been cut from a plant grown from seed of a sport that had appeared in 1907, and showed the extreme form in which the five divisions of the corolla are represented by five stamens. Here too it was observed that the peculiarity came true from seed. In none of these cases, however, have we full information regarding the statistical evidence on which the general statement as to inheritance is based, nor have I been able to find any account of observations continued beyond the first generation. The following experiments were therefore undertaken with a view to ascertaining to what extent this form breeds strictly true, and the nature of its relation to the type. From the results which follow it will be seen that offspring of heptandra parents all show dialysis and staminody of the corolla, but the extent to which these malformations are exhibited varies not only in different individuals, but in different flowers on the same individual; further, that the heptandra form is related to the type as recessive to dominant.

A specimen of *D. purpurea*, exhibiting the peculiarities above described was shown to me in 1906 by a friend, in whose garden in Cambridge it had appeared among a number of normal plants which had been grown from a single packet of seed.³ It was then already late in the season, and none of the flowers which were artificially fertilised set seed. A considerable number of good capsules were, however, gathered from the flowers which had been exposed and naturally fertilised. From seed thus obtained a first generation of plants were flowered in 1908, and a second in 1910. The following account contains the results of observations made during these two seasons.

I.—DESCRIPTION OF *D. purpurea heptandra*.

All individuals showing the general features previously mentioned, viz., dialysis and staminody of the corolla, are included under this title.

In *heptandra*, as in the type form, the axillary buds at the

¹ Ibid., 1904, 2, p. 208.

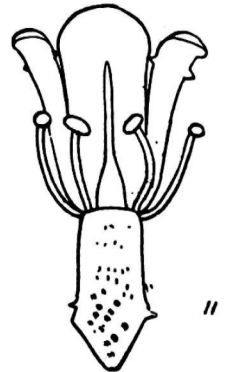
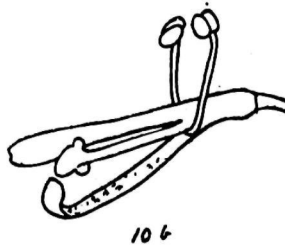
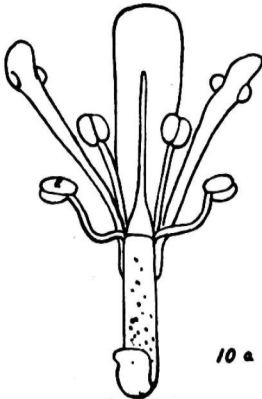
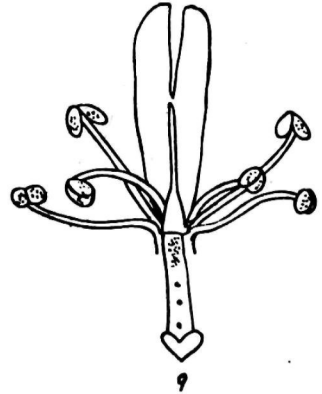
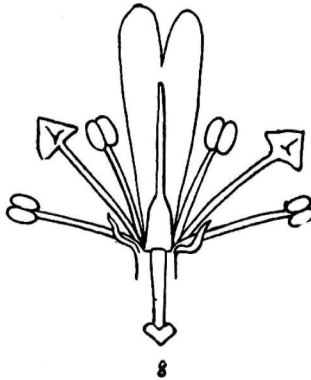
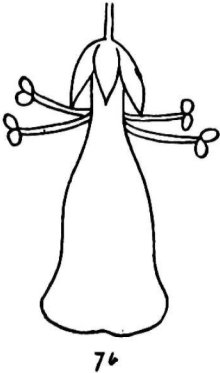
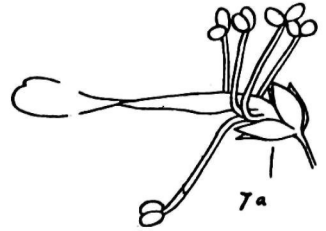
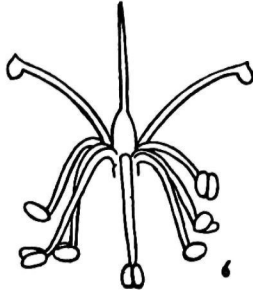
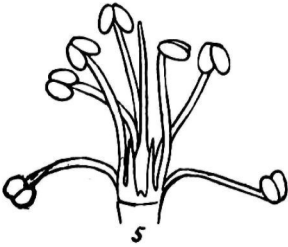
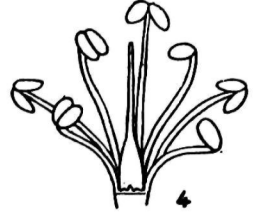
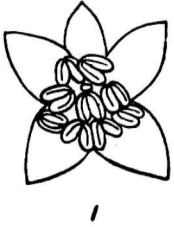
² See Proceedings of the Linnean Society for 1910, p. 106.

³ Most observers have, as in this case, recorded only a single sport in the first instance, though Henslow's case appears to have been an exception.

lower nodes develop in most cases into short shoots bearing a few leaves below the flowers. At the succeeding nodes, as a rule though not universally, the shoot is replaced by a single flower bud which does not reach full development. Some of these buds remain quite rudimentary, others develop further and may produce functional organs; but even in this latter case growth ceases while the parts are still enclosed in the calyx. Afterwards follow the fully developed flowers which continue to near the top of the spike, where they may again be replaced by buds which never unfold. It may happen, however, that no buds are arrested at the base of the spike, in which case the full-sized flowers follow immediately upon the leafy shoots.

Only a few of the *heptandra* individuals exhibit a complete absence of petal-like structures *throughout the whole of the inflorescence*; though now and again an individual will be found to show this condition from top to bottom of the spike. In these cases the *apparently* total absence of corolla gives the spike a very curious, albeit, quite uniform appearance. In the great majority of the plants, however, it is noticeable that in travelling up the spike the flowers present a graduated series; dialysis and staminody of the corolla gradually diminish, and reversion may even be carried so far that eventually normal flowers are produced near, or at the top of the inflorescence. This increasing tendency towards normality may extend to the summit of the spike, or it may reach high-water mark below, but so near the apex, that whatever stage in the progressive series is reached at this point is maintained upwards to the top. In other cases the wave may spend itself some distance below the summit, and the later flowers then form a downgrade series ending in partial, or occasionally, if arrested flowers occur in this region, in complete return to the extreme *heptandra* condition

The choice of the name *heptandra*, as it proves, is not altogether happy, for although it correctly describes the condition occurring in the great majority of the flowers (*i.e.*, those having the three petals of the lower lip replaced by three stamens more or less similar to those of the androecium proper, thus making seven stamens in all), it is not strictly applicable in those cases where a greater or lesser degree of deviation from the normal occurs. Thus, on the one hand, almost every stage may be found between the true heptandrous condition and the normal flower with four stamens; while at the other end of the scale we meet with the extreme case in which both lips of the corolla are replaced by stamens, so that nine (or rarely ten) stamens are present, and the flower appears to lack all five



Text-figs. 1-11.

petals.¹ Several intermediate forms occur, and the various modifications which form a progressive series will be most easily exhibited in the accompanying table.

Modifications of the Corolla.

(a). *Upper lip.*

1. The upper lip may be wholly wanting. The posterior part of the tube is then reduced to a mere rim with an even concave outline (see fig. 3).

The upper lip may be represented by:—

2. Two projections on the posterior rim of the tube (see fig. 4).

3. Two filaments presenting all stages between 2 and 4 (see fig. 5).

4. Two filaments equal in length to those of the ordinary stamens, and bearing a one-lobed anther which forms normal pollen and dehisces when ripe (see fig. 6).

5. Two stamens bearing bilobed anthers similar to those of the ordinary stamens. (Only observed in very few cases). (See fig. 1).

¹ This extreme stage does not appear to have been present in de Chamisso's plant.

Text-figs. 1—11, shewing various forms of *heptandra* flowers seen in different views. All the figures are taken from full-sized flowers, except figs. 1 and 2.

1. Arrested flower seen from above with calyx and nine stamens.
2. Arrested flower seen from the side showing an upper lip of two small petals and seven stamens. Calyx removed.
3. Flower seen from the back showing seven stamens. The lower lip of the corolla is represented by three stamens, distinguished from the andræcium proper by the divergent anther lobes; upper lip wholly suppressed, the posterior side of the flower tube being reduced to a mere rim with an unbroken concave outline. Calyx removed. The speckled anthers show that if the corolla had been normal, the spots would have been coloured red.
4. Flower showing three small projections on the posterior rim of the flower-tube which probably represent the rudiments of the upper lip, and the posterior stamen; otherwise as fig. 5.
5. Flower showing a rudimentary upper lip in the form of two filaments; otherwise as fig. 6.
6. Flower in which the upper lip is represented by two stamens, each bearing a half anther. Calyx removed. Seen from the front.
7. Flower with upper lip of two completely fused petals. (a). Seen from the side. (b). Seen from above.
8. Flower with upper lip of two partly fused petals. The three structures representing the lower lip still bear anthers, but they are gradually becoming petaloid. Two outgrowths—the *lacinulae corollinae* of de Chamisso—are seen on either side. Calyx removed. Seen from the front.
9. Flower showing an upper lip of two partly fused petals. The central one of the three structures representing the lower lip has become more distinctly petaloid. Calyx removed. Seen from the front.
10. Later stage in reversion. (a). Seen from the front. (b). Seen from the side. The speckling on the anthers has been omitted here and in fig. 11.
11. Later stage still. Seen from the front.

6. Two small flattened structures, more or less coherent, in shape like miniature petals, but green, and remaining enclosed within the calyx. (Chiefly found in the arrested flowers). (See fig. 2).

7. Two large petal-like structures, either only partly coherent and appearing like narrower or broader strips of a normal corolla, or completely fused (see figs. 7-10).

(b). *Lower lip.*

The lower lip may be present as :—

1. Three stamens with normal anthers resembling those of the andrœcium proper, or with the lobes slightly divergent (see figs. 1-6).

2. Three stamens with very divergent lobes to the anthers. The anthers thus become sagittate in form, whereas those of the andrœcium proper are oval (see figs. 8, 9).

3. Two lateral stamens with broad flattened filaments, and an anterior structure which becomes increasingly petaloid, with an anther lobe on either margin. As the petal-like form of all three structures becomes more pronounced the anther lobes gradually disappear (see figs. 10, 11).

4. A single petaloid structure of three coherent petals which shows progressive stages of fusion with the upper lip until a normal corolla results.

Modifications of the Andrœcium.

1. The posterior stamen may be present bearing a normal anther. Such cases occur rarely among the arrested flowers, and the ten stamens are then so arranged that the flower becomes almost actinomorphic.

2. A small, often coloured, projection may arise from the rim of the flower-tube in the position of the posterior stamen, which may represent a stage in the suppression of this structure (see fig. 6).

3. The filaments of two adjacent stamens may fuse so that the resulting single structure bears a double anther.

In addition to the anther-bearing structures representing the corolla, described above, linear outgrowths of the tube—the "*lacinułæ corollinæ*" of de Chamisso—are often to be found in those flowers exhibiting the more extreme degrees of staminody (see fig. 8).

In all the *heptandra* forms the members of the corolla and andrœcium unite at the base to form a short tube region, so that these parts still become detached as a whole just as in the type. In the more extreme cases the stamens, instead of being grouped



Fig. 12. A characteristic spike of the *heptandra* form proper. In the lower flowers the corolla appears to be wholly wanting. In those above staminody of the lower lip still persists, but the upper lip develops as a flattened petaloid structure. The stamens, unrestrained by a corolla-tube, are seen diverging in different directions,

together and curving forwards, diverge in a horizontal and backward direction, owing no doubt to the absence of the restraining force exerted, in the case of the type form, by the enclosing tube of the corolla. At the same time the ovary and style are directed upwards, this again is no doubt due to the absence of a corolla tube. As a result of this upward inclination of the style, the ring of stamens, although becoming detached when the flower is over, remains *in situ* long after it is withered, threaded as it were by the style; thus a spike which has finished flowering may still be covered through-out its length with these withered remains. In the more petaloid intermediate forms the weight of the detached portion of the flower is sufficient to bend down the style, and the whole structure slides off before withering as in the type form.

Bees are able to work all the various *heptandra* forms, and in fact seem to visit type and variety indiscriminately. But though a good quantity of seed is usually obtained from exposed *heptandra* plants, the yield from covered individuals is always scanty, and in a wet season may be almost *nil*, for both pollen and stigma are fully exposed to rain, and the rotting of the deciduous parts *in situ* favors the growth of mould,

II.—RESULTS OF BREEDING EXPERIMENTS:

From the results obtained it appears that *D. purpurea heptandra* breeds true in that from *heptandra* individuals only *heptandra* forms have been obtained. As stated above, however, the extent to which the characteristic features of dialysis and staminody are exhibited by any individual is not generally constant throughout the flowering period, but varies in the different flowers according to their position (level) on the spikes (fig. 12). As a rule the flowers in order on an axis form a graduated series, but the particular grade with which the series begins and ends, and the number of grades exhibited vary in different individuals. Further, the series may be either wholly up-grade, approximating more and more to the normal as we approach the top of the spike, or the culminating point in the reversionary series may be reached below the apex, and may be followed by a series of down-grade stages. We have as yet no very definite knowledge of the forces regulating this wave-like tendency, but it can hardly be doubted that it is not assignable to any single cause, but is due to the combined action of a number of factors, of which some exert a preponderating influence at one time, some at another, with the result that the balance is inclined at first towards, and later, perhaps, away from the condition of normality. We can thus understand how it is that the phase exhibited by the open flowers on a lateral branch may not correspond with that of those opening simultaneously on the main axis; or again that the condition of fasciation is often accompanied by a sudden break in the regularity of the series. It is not surprising that the state of vigour of a lateral branch beginning to flower should be different from that of the main axis which is already probably well advanced in its flowering period; hence on the lateral branch the first flowers may start from a point in the series behind that already reached by the open flowers on the main axis, but yet not so far back as to recapitulate the whole series. In the case of fasciation, flowers borne at the level where fasciation begins to occur may show a sudden jump as regards increased size of the petaloid structures, as compared with the flowers borne immediately below the fasciated region, or with those opening simultaneously on a normal stem of the same individual. The *heptandra* individuals are, however, easily sorted

from the type plants notwithstanding this grading, for in most cases the distinction between variety and type is absolute, all the flowers on the spike being deformed in some degree in the one case, and normal in the other. Even when this is not the case there is still a very wide gap between the heptandrous individual which eventually produces a small number of normal flowers and the type plant which shows a trace of the abnormality in some of the earliest flowers. No true intermediates were observed in any of the matings. If they occur, they are evidently rare. Within the *heptandra* class we may conveniently group the several grades as follows:—

1. Extreme *heptandra* form. Plants in which all, or almost all, the flowers are without petal-like structures.

2. *Heptandra* form proper (fig. 12). Plants in which only the flowers in the lower region of the spike and those at the extreme top appear to have no corolla. In the intervening region the upper lip appears as a conspicuous petaloid structure which is usually deeply bifid. By far the larger number of *heptandra* plants belong to this group.

3. Intermediate *heptandra* form. Plants in which all, or nearly all, the flowers are more or less petaloid. The lowest flowers, in which an upper lip is often already well-developed, are succeeded by others in which a lower lip also gradually makes its appearance, and finally tubular or even quite normal flowers may be found towards the top.

As previously stated the only seed obtained in 1906 was collected from exposed flowers on a single individual. It was therefore to be expected that much of this seed would have resulted from crossing with neighbouring type plants, but that some would be due to self-fertilisation. Some 240 plants raised from this seed were flowered in 1908 of which more than 100 showed the *heptandra* characters, while the remainder resembled the type. In this case the precise numbers have no value as the fertilisation of the seed-parent was not controlled, but from the appearance of so many *heptandra* offspring it was scarcely doubtful that, when self-fertilised, this form would be found to breed true; the results in 1910 have shown that such is the case. Six of the *heptandra* individuals flowering in 1908 were self-fertilised and all the 256 offspring were *heptandra*.¹ The numbers obtained in each case were as follows:—

¹ A single type plant was found in the rows, but that this was a rogue was evident from the fact that it possessed the smooth stem occurring in certain other families, but not otherwise found in the six families above mentioned, the 256 individuals composing them all showing the normal degree of hoariness (see p. 60).

Form of Union.	Reference Number of Family.	Number of Offspring obtained in the 2nd generation.	
		<i>Heptandra.</i>	Type.
<i>Heptandra</i> × Self	1	88	<i>Nil.</i>
	2	47	"
	3	50	"
	4	44	"
	5	7	"
	6	20	"
	Total	256	<i>Nil.</i>

Families 1, 4, 5, and 6 were derived from plants of the *heptandra* form proper, the total offspring of 159 included :—

8 extreme *heptandra* form (*i.e.*, with all, or nearly all, the flowers non-petaloid).

143 *heptandra* form proper (*i.e.*, with a large number of flowers having a petaloid upper lip).

1 intermediate *heptandra* form (*i.e.*, with some flowers having both the upper and the under lip petaloid).

7 particular form not recorded.

—
159

In the one intermediate *heptandra* plant recorded in this group of families normal flowers were not produced. The furthest point reached in the reversionary series was that in which the lower lip was deeply lobed, and only united for a short distance with the upper lip to form a tube.

Families 2 and 3 were derived from plants of the intermediate *heptandra* form ; the total offspring of 97 included :—

7 extreme *heptandra* form,

36 *heptandra* form proper,

49 intermediate *heptandra*,

5 particular form not recorded,

—
97
—

About two-thirds of the intermediate *heptandra* plants eventually produced some normal flowers.

From the facts given above it is evident that the *heptandra* character is inherited, and that from *heptandra* parents only *heptandra*

offspring are obtained. Further observation, however, is required to determine how far the degree of heptandry exhibited by the parent is reproduced in the offspring. So far as it goes, however, the evidence indicates that the offspring of a plant with a range from a moderate to a high degree of reversion will exhibit, on the whole, a greater degree of reversion than the offspring of a plant whose range in the reversionary scale is lower. At the same time certain facts observed in regard to the distribution of the various forms in the different beds suggest that, though the *heptandra* character is evidently transmitted to all the offspring, it is probable that the external conditions affect the precise degree in which this modification is exhibited. The facts were as follows:—

In the case of family 2 the mixed seed of several capsules had been divided into two lots, which were sown, pricked out, and planted separately, lot 1 in a narrow bed facing south, lot 2 in the middle of a bed facing east, and somewhat shaded to the south and west. The bed containing lot 1—a strip lying between a privet hedge and the path—was particularly dry and fully exposed to the sun. Out of a total of 27 classified plants in this bed only 4 eventually produced flowers with a normal or nearly normal corolla, while in as many as 16 of the remainder the late flowers were still of the *heptandra* form proper with 6 and 7 stamens. On the other hand among the 17 classified plants in the other bed, 8, *i.e.*, nearly half, eventually produced normal or almost normal flowers, and only 5 showed the *heptandra* form proper at the end of the season. Again in family 3, which had been similarly treated, the inequality in the distribution of the various grades in some of the beds was no less striking, though in this case the influence of the environment as a whole seems to result, in a lessening, rather than in an increase of the reversionary tendency in the more shaded lot of plants, as compared with those situated rather more in the open. Thus of 28 classified plants growing in a bed very much overshadowed by trees, only 1 eventually produced flowers at all approaching to normal, whereas in another lot planted a little more in the open all the 13 classified plants eventually produced flowers with a tubular corolla, and in 10 out of these 13 the late flowers were completely normal.

From the foregoing facts we may then conclude that the variety *heptandra* transmits its peculiar constitution to all its offspring, but the extent to which the abnormality is developed in an individual inheriting this disposition to heptandry may be in some degree influenced by external conditions, among which

variations in amount of light and moisture are probably to be reckoned. Whether other factors are also concerned, and how far they may be opposed in their action, further experiment must decide. These conclusions are in harmony with the view held by Peyritsch¹ and others that the condition of peloria is also to some extent affected, if in some cases not actually induced by the stimulus of changes in the environment. So far as I am aware, however, no critical experiments on this point have as yet been carried out.²

It is further evident that the *heptandra* form is related to the type as recessive to dominant. Plants derived from the original *heptandra* parent but resembling the type—hence evidently cross-breeds—invariably gave a mixed offspring, the numbers approximating to the ratio 3 Type : 1 *Heptandra*, or 1 Type : 1 *Heptandra*, according as they were fertilised with their own or sister pollen, or were crossed back with the *heptandra* form. Details of the breedings are as follows:—

(1). Nine of the putative crossbreeds derived from the original *heptandra* plant were self-fertilised, and one of these individuals was also intercrossed with a sister plant. In all ten families the offspring were mixed; the total numbers obtained were 183 Type (including one plant showing slight abnormality in the first four flowers) and 49 *heptandra* (including ten plants with some normal or nearly normal flowers), where, on the basis of a 3 : 1 ratio, we should expect 174 Type and 58 *heptandra*.

(2). Three of the crossbreeds, of which two were among those self-fertilised in the preceding experiment, were crossed back with various *heptandra* individuals. The four resulting families were all mixed, the totals obtained being 69 type (including seven individuals with a few abnormal flowers) and 59 *heptandra* (including six individuals with a few normal flowers) where we should have expected equality.

¹ Untersuch. über die Aetiologie pelorischer Blütenbildungen. Denkschr. d. k. Akad. Wien. Bd. XXXVIII.

² Gallardo's observation on the higher proportion of peloric individuals occurring among a batch of foxgloves grown under favourable conditions as regards space and illumination, as compared with another batch of similar origin, raised simultaneously, but less exposed to the sun and more crowded together, cannot be used as evidence in this connection, since the peloric parents were not apparently protected from crossing. Had intercrossing with type plants been prevented, all the plants in both batches would presumably have been peloric since peloria in the foxglove comes true from seed. (See Gallardo. Notes morphologiques et statistiques sur quelques Anomalies héréditaires de la Digitale. Rev. gén. de Botanique XIII., 1901, p. 163).

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Table showing the proportion of type and variety in each of the F_2 families derived from the putative crossbreds by self-fertilisation or by crossing *inter se*.

Reference number of family.	Form of Union.	Number of individuals in F_2 families.	
		Type.	Heptandra.
7	Crossbred \times self	33	7
8	"	21 ¹	8 ²
9	"	15	3 ³
10	"	24	5
11	"	13	8 ⁴
12	"	22	5
13	"	14	5 ⁵
14	"	9	4
15	"	11	1
16	Crossbred \times sister crossbred	21	3
Totals		183	49

A ratio of 3 : 1, calculated to the nearest whole number, would give 173 type and 58 *heptandra*.

- ¹ Including one individual with a few abnormal flowers.
- ² Including two individuals with a few normal flowers.
- ³ Including one individual with a few normal flowers.
- ⁴ Including three individuals with some normal or nearly normal flowers.
- ⁵ Including four individuals with some normal or nearly normal flowers.

In the eight F_2 plants in which a slight abnormality in the first few (1-8) flowers was observed, the abnormality was in the form either of a lateral notch in the corolla edge, or of a longitudinal cleft which extended for a longer or shorter distance down one side. In other respects these flowers were normal as was also the whole of the rest of the spike. It is of interest to note that among the F_2 individuals classed as *heptandra* the proportion which eventually produced a few normal or nearly normal flowers was no higher, in one case rather fewer, when the *heptandra* form had been introduced twice into the pedigree than when the plants resulting from a first cross were self-fertilised or fertilised *inter se*. Thus the two crossbreds which produced plants of this grade when the breeding was in the form DR \times R, yielded respectively four such plants in a total of twelve, and two in a total of nineteen, whereas on self-fertilisation the numbers obtained from these same crossbreds were respectively 1 in 3 and 2 in 8. (See families 8, 9, 17; and 18).

Table showing the proportion of type and variety in each of the F_2 families obtained from the crossbreds by crossing back with the *heptandra* form.

Reference number of family.	Form of Union.	Number of individuals in F_2 families.	
		Type.	<i>Heptandra</i> .
17	Crossbred \times <i>heptandra</i>	10	12 ⁴
18	„	26 ¹	19 ⁵
19	„	15 ²	8
20	„	18 ³	20
	Totals	69	59

A ratio of 1 : 1 would give 64 type and 64 *heptandra*.

- ¹ Including five individuals with a few abnormal flowers.
- ² Including one individual with a few abnormal flowers.
- ³ Including one individual with a few abnormal flowers.
- ⁴ Including four individuals with a few normal flowers.
- ⁵ Including two individuals with a few normal flowers.

In both experiments the results obtained point to segregation in accordance with Mendelian principles, the numbers recorded lying within the range of deviation which we might reasonably expect from the strict ratio 3 : 1 in the one case and 1 : 1 in the other.

Observations made in the course of the work on various characters unconnected with modifications of the corolla are briefly given below.

Fasciation and torsion of the stem were of frequent occurrence but of very varying degree.

Not a single case of peloria occurred among the whole number of plants raised.

It was noticed that certain families included a number of individuals of a bright green colour in marked contrast with the usual grey-green of typical plants. On investigation it was found that in these plants the stem during the greater part of its length was hardly hairy at all, and that the leaves were also much less hairy than usual. In two out of the six families in which these smooth plants occurred, the parents, both F_1 crossbreds, had been self-fertilised, and in both families the smooth plants were in excess of the hairy; the numbers recorded were six hairy and twenty-three smooth, and five hairy and thirteen smooth respectively, or almost exactly three smooth to one hairy. One or other of these two F_1 plants had also

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been used as a parent in the case of the other four families, but instead of being self-fertilised they were each crossed back with two different *heptandra* individuals. Each again gave a mixture of hairy and smooth, but the proportion of smooth was now greatly diminished, as shown below.

Comparison of the six mixed families derived from the two F_1 crossbreds (plants A and B) showed the following results:—

	Hairy.	Smooth.
Plant A × self gave	6	23
Plant B × self gave	5	13
	—	—
Totals	11	36
	—	—
	Hairy.	Smooth.
Plant A × <i>heptandra</i> plant 1 gave	29	16
× <i>heptandra</i> plant 2 gave	11	12
Plant B × <i>heptandra</i> plant 3 gave	13	9
× <i>heptandra</i> plant 4 gave	17	7
	—	—
Totals	70	44
	—	—

It is somewhat surprising, in view of the relation which experiments in other cases have shown commonly exists between the hairy and the smooth condition that the two sporting individuals in this case should have produced an *excess* of smooth plants on self-fertilisation. For an explanation of this result we must await the evidence from later generations.

The observations made in regard to the inheritance of flower colour are in entire accord, so far as they go, with the facts already published last year by Keeble, Pellew and Jones,¹ *viz* :

(1). That in all individuals whether white or coloured the lower lip is spotted, the spots being of various sizes.

It was noticed that in some families the spot area was occupied by large irregular blotches of colour, the appearance suggesting that a number of spots of ordinary size had become confluent. In one family this blotching was observed in ten out of the twenty-eight individuals recorded; in the remaining two families in which this peculiarity was seen the proportion was very much fewer. It is hoped to obtain evidence in regard to the inheritance of this character in the next generation.

(2). That among white flowered plants there are two kinds of individuals:—

(a) White-flowered plants with yellowish-green spots.

(b) White-flowered plants with red spots.

¹ The Inheritance of peloria and flower colour in Foxgloves (*Digitalis purpurea*). NEW PHYTOLOGIST, Vol. IX., 1910.

It was noticed that in many of the white plants with yellowish-green spots, the spots turned brown sooner or later, but the moment at which the colour change occurs, varied considerably. In some cases it occurred in the fully open but still unfaded flower, in others not until after the corolla had begun to fade, in others again while the corolla was still closed; in the latter case, however, the original yellowish-green could be seen in the younger buds.

(3). White-flowered plants with yellowish-green spots breed true, and even when faded show no sign of ground colour.

(4). White-flowered plants with red spots may either breed true or give a mixture of whites with red spots (dominants) and whites with greenish-yellow spots (recessives). The flowers frequently become tinged as they get older.

(5). In coloured plants the spots are always red.

Among plants of this class almost every shade could be found between deep purplish red and white with a faint flush.

SUMMARY.

1. The characteristic features of *D. purpurea heptandra*, viz., dialysis and staminody of the corolla appear to be transmitted by heptandrous plants to all their offspring.

2. The degree in which these peculiarities are exhibited varies not only among the individuals of a pure-bred family, but also among the flowers of one individual.

3. This variation in the case of the individual has the appearance of being due to a wave of reversion which advances steadily up to a point and then declines somewhat towards the close of the flowering period. Where the evenness of this wave-like advance is broken, as sometimes happens, it is probably due to an alteration in the condition of vigour at the level of the break. Such an alteration may well occur at the level of transition from a non-fasciated to a fasciated condition, or again, there may well be a difference in vigour between the upper region of a main axis and the simultaneously flowering base of a lateral branch.

4. The range of variation includes every grade from flowers with androecium and corolla normal, except for a lateral notch or cleft in the latter structure, to flowers *apparently* destitute of a corolla, and with nine or ten functional stamens united at the base, so that they form a single structure which falls as a whole.

5. Heptandrous individuals showing at first the extreme heptandrous condition (*i.e.*, no apparent corolla) may exhibit this

condition throughout or almost throughout the spike, or they may reach the *heptandra* condition proper which has a petaloid upper lip and seven stamens. Heptandrous individuals exhibiting this latter condition at the outset often produce eventually a few normal flowers.

6. The distinction between the variety *heptandra* and the type, in all individuals so far observed, is well defined. Where a heptandrous individual was found to produce a few normal flowers the heptandrous character was always evident throughout the rest of the long crowded spike, and conversely, a type plant with a notch or slit in a few of the lowest flowers would show a normal structure throughout the remaining length of the axis.

7. There is some indication that the degree of heptandry exhibited may be influenced by external conditions, among which variations in amount of light and moisture are probably to be reckoned.

8. The variety *heptandra* behaves to the type as recessive to dominant.

9. Two new forms appeared in the course of the experiments, *viz.*, one with stem and leaves nearly smooth, and one in which the spots on the lower lip of the corolla had fused to form large blotches. The inheritance of these two forms is being investigated.

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I wish here to express my thanks to Miss D. F. M. Pertz to whom I am indebted for the drawings, and to Miss M. Pallis who kindly took the photograph.

EXPLANATION OF PLATE I.

ILLUSTRATING MISS E. R. SAUNDERS' PAPER ON INHERITANCE OF A
MUTATION IN THE COMMON FOXGLOVE (*Digitalis purpurea*).

Photograph showing *D. purpurea* type and variety *heptandra*, growing side by side in the same bed. Both are in full flower. The heptandrous plants show the numerous irregularly diverging stamens which give the spikes their characteristic appearance. In some of the flowers of the left-hand group the upper lip is becoming petaloid.

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