JOURNAL

OF THE

ASIATIC SOCIETY.

PART II.—PHYSICAL SCIENCE.

No. III.—1867.

On the Reproductive Functional Relations of several Species and Varieties of Verbasca.

By John Scott, Esq.,
Curator of the Royal Botanical Gardens, Calcutta.

In this paper, I purpose giving an account of a numerous and carefully performed series of experiments on the hybrid and cross-unions of several species and varieties of Verbasca, with the view of illustrating those functional relations, or differences existing between the results of unions of distinct species on the one hand, with those of different varieties of the same species on the other. I believe, the generally accepted view of naturalists on this point is, that a certain degree of sterility always results from the union of distinct species in their first hybrid produce, and that their progeny are absolutely infertile one with another; while in the cross-unions of varieties of a species, the fertility is in no respect affected in the first cross, and the progeny are, in every case, perfectly fertile, one with another. These relative differences, then, in the products of hybridism and mongrelism are strongly maintained to be decisively demarcative of the factors, included under the terms "species" and "varieties," affording, so to speak, an unequivocal analysis, whereby nature's original and immutable units—species—may at once be discriminated from those diverged forms—varieties—to which they have given rise, and with which, from the important structural differences they frequently assume, they might be hopelessly confounded. Such, at least, is the opinion of those naturalists who regard species as the result of distinct creative acts. On the other hand, those naturalists who believe in derivative hypotheses, and look upon all existing organisms as the genealogical connections of other and earlier kinds, entertain the directly opposite view, and maintain that no such essential differences as those above stated exist between the results of hybridism and mongrelism; though they readily admit a difference in degree. This point has been ably and philosophically discussed by Mr. Darwin, who, after a careful and impartial examination of all the evidence he could collate, considers himself justified in concluding, that "first crosses between forms known to be varieties, or sufficiently alike to be considered as varieties, and their mongrel offspring, are very generally, but not, as is so often falsely stated, universally fertile.........consequently that neither fertility nor sterility afford any clear distinction between species and varieties; but that the evidence from this source graduates away, and is doubtful in the same degree, as is the evidence derived from other constitutional and structural differences."*

Though Mr. Darwin thus clearly anticipates an essential accordance between the result of hybridism and mongrelism, it is to be observed that the extreme paucity of experimental observations on the latter phenomena prevents his illustrating the subject so fully and satisfactorily as its importance demands. The want of such observations, and the importance of their bearing on that theory of the "origin of species" proposed by Mr. Darwin, has been frequently and strongly insisted on by Professor Huxley. Thus in his "Essay on Man's Place in Nature," p. 106, we find the following remarks: "Our acceptance of the Darwinian hypothesis must be provisional so long as one link in the chain of evidence is wanting, and so long as all the animals and plants certainly produced by selective breeding from a common stock are fertile, and their progeny are fertile one with another, that link will be wanting." Again in his Lectures on our knowledge of the cause of the phenomena of organic nature, Lecture VI. p. 147, after

* Darwin's "Origin of Species," 3rd Edition, pp. 271 and 300.

discussing the obligations of a hypothesis, he remarks, that "Mr. Darwin, in order to place his views beyond the reach of all possible doubt, ought to be able to demonstrate the possibility of developing from a particular stock, by selective breeding, two forms which should either be unable to cross one with another, or whose cross-bred offspring should be infertile with one another," ...." Now it is admitted on all hands that at present so far as experiments have gone, it has not been found possible to produce their complete physiological divergence by selective breeding..........If it should be proved, not only that this has not been done, but that it could not be done, I hold that Mr. Darwin's hypothesis would be utterly shattered." Professor Huxley, however, though thus strongly insisting upon the absence of facts showing that any degree of sterility has resulted from the crossing of varieties known to have originated from a common stock, states that he does not know a single fact which would justify the assertion that such sterility could not be produced by proper experiment, expressing his belief that it may and will be produced.

Considering then the as yet positively equivocal nature of the relations between the phenomena of hybridism and mongrelism, together with its important bearings on the converse theories which now divide the scientific world, I trust the reader will bear with me, while giving a somewhat detailed statement of my own experiments on the above phenomena. I venture to premise that they show pretty clearly the relative claims of the two views now held by naturalists on our acceptance, and illustrate also one or two other points of high interest in theoretical natural science. First, for the union of *V. phœniceum* vars. *roseum* and *album* and *V. nigrum.*

TABLE 1.—Results of Pure and Mixed Unions of *Verbascum phœniceum*, var. *roseum* and *album*; and *V. nigrum.*	No. of flowers fertilished.	Capsules produced.	Seeds produced.	Average of seeds per capsule.	By calculation.	
					Capsules.	Seeds.
No.						
1. *Verbascum phœniceum* by pollen of *V. phœniceum roseum*, ...	10	8	193	24	20	483
2. *V. phœniceum, roseum* by pollen of *V. phœniceum*, ...	12	9	306	34	20	680

TABLE 1, *(Contd.)*—Results of Pure and Mixed Unions of *Verbascum phœniceum*, var. *roseum* and *album*; and *V. nigrum*.

No.		No. of flowers fertilised.	Capsules produced.	Seeds produced.	Average of seeds per capsule.	By calculation. Capsules.	By calculation. Seeds.
3.	*V. phœniceum*, by pollen of *V. phœniceum, album*, ...	10	6	120	20	20	400
4.	*V. phœniceum, album* by pollen of *V. phœniceum*, ...	16	11	287	26	20	522
5.	*V. phœniceum, album* by pollen of *V. phœniceum, roseum*, ...	8	4	116	29	20	580
6.	*V. phœniceum, roseum* by pollen of *V. phœniceum, album*, ...	8	0	..	...	...	...
7.	*V. phœniceum*, by pollen of *V. nigrum*, ...	10	3	57	19	20	380
8.	*V. phœniceum, album* by pollen of *V. nigrum*, ...	10	6	110	18	20	367
9.	*V. phœniceum, roseum* by pollen of *V. nigrum*, ...	10	7	107	15	20	306
10.	*V. phœniceum*, by own pollen, ...	18	0	...	...	...	...
11.	*V. phœniceum, roseum* by own pollen, ...	18	0	...	...	...	...
12.	*V. phœniceum, album* by own pollen, ...	18	0	...	...	...	...

The following descriptive notice of the plants in Tab. 1, will show their close morphological relations. First, *V. phœniceum ; stem* somewhat downy, simple, producing upwards a racemose panicle. *Leaves* crenate, oblong-ovate, nearly glabrous above, deep green. *Radical* subcordate, ovately-acuminate, petiolate. *Upper cauline* crenulated, semi-amplexicaul. *Bracteas* lanceolate. *Raceme* elongated. *Flowers* lax, solitary ; pedicels longer than the bracteas. *Corolla* purplish-violet, beset with violet hairs at its base. *Stamens ;* filaments of the three shorter stamens covered with long glandular purplish hairs, these of the two longer naked, except on the upper side, where there are a few similarly characterised hairs. *Anthers* of the three longer stamens nearly circular, and covered with purple and white glandulose hairs, these of the shorter stamens, reniform and nearly naked. *Pollen* copper-coloured. Second, *V. phœniceum, roseum* differs from the above only in the less elongated raceme and the rose-coloured flowers. Third, *V. phœniceum, album* is of a more robust habit than the other two.

Radical leaves ovate-lanceolate, light green. *Flowers* white and rather larger than the others, wfth a few whitish glandulose hairs near the base of petals. *Filaments* and form of *anthers* similar to these of *V. phœniceum*, but beset with white instead of purple, glandular hairs. *Pollen* similarly copper-coloured in each.

Thus, judging from the characters of these three forms alone, there can be no doubt as to their being other than conspecific. In addition to this I may add, on the authority of Mr. Stirling of Edinburgh, that they have been raised from pure seed of the *V. phœniceum*, the rose-coloured variety frequently appearing amongst the seedlings of *V. phœniceum*, the white presenting itself more rarely.

In the first part of Tab. 1, the number of flowers fertilised, and the simple results are shown, and in the right hand, for the sake of comparison, the calculated produce of the number of seeds from 20 capsules of each is given.* If we compare the results, we see that reciprocal unions may be effected becween the *V. phœniceum* and varieties, with one exception, viz., *V. phœniceum, roseum*, by pollen of *V. phœniceum, album*, in which case I have found that though the pollen tubes are abundantly developed and freely penetrate the stigmatic tissues, the capsules nevertheless drop prematurely. The goodness, however, of both the male and female elements of the above varieties is nevertheless shown by their reciprocal unions with *V. phœniceum*. The individual potency of the respective sexual elements of these varieties, in their reciprocal relations, is clearly shown; whereas by those experiments given in the three last lines of the table, in which the stigmas of each variety were covered by their own good pollen, no unions were effected, each proving utterly self-sterile!

This absolute, or conditional, sterility of the three varieties of *V. phœniceum*, when treated by their own good pollen, led me to examine

* From Mr. Darwin's suggestion in "The Origin of species" that the decreased fertility of mixed unions, as compared with that of the pure unions, might possibly be increased by the fact, that for perfectly satisfactory results, castration is necessary in the cross-unions; whereas in the latter, in pure unions, this not being necessary, we may have indiscriminate comparisons, of the two results though clearly castration may have a direct sterilising influence. In view of this prudent suggestion, I took the precaution to castrate every flower both of the pure and mixed unions, from which I intended to draw results. The sole exception to this is that given in the first line of Table 2 of *V. phœniceum* as I was unable to get any of the plants under me to produce seed by their own pollen. Whatever be the effects of castration then on the fertility of the plants so treated, in the present cases, all having undergone it, the results will be mutual.

into the apparent cause, as in certain cases we find it arising from the non-emission or non-penetration of the pollen tubes; the pollen through some mysterious cause being thus utterly impotent on its own stigma. The results of my present examination will, I trust, be found of sufficient interest to permit of my stating them here. They are as follows: first, I applied the pollen of each of the three varieties, reciprocally, to their stigmas; on dissecting these, I found them abundantly permeated by pollen tubes, many of which I distinctly traced into the ovary. Secondly, I fertilised several flowers in each variety, with its own pollen; on examining the stigmas of a few of these flowers, I found that many of the pollen grains had emitted tubes, but comparatively few had penetrated the stigmatic tissue, and of these still fewer permeated the conducting tissues of the styles. Several of the latter, however, I traced into the vascular bundles of the placenta, the pistillary cords, and in one or two instances, I believe that I detected them in the nucleus of the ovule. Nevertheless we have seen that, though these pollen tubes are developed, they most ineffectively perform their deputed function, inasmuch as not one of these matured even a single ovary! I have here to observe, however, that these pollen tubes do not seem utterly void of the fecundative influence, as many of the ovaries did undergo a certain degree of development; and on examination of these, as they dropped off, I found that the ovules also had undergone a partial and variable degree of development. In general, the fleshy albuminous envelope of the embryo was largely developed, whereas the embryo had undergone a very slight development, judging from a comparison of other good seeds of a similar stage, not at all proportionate to the size attained by the albuminous parts. In nearly all the embryos which came under my observation, the development had ceased ere they exhibited any distinct separation of parts; a few only had reached that stage in which the axial and lateral projections were visible.

We thus see, that whatever be the real cause of the inveterate self-sterility of the three varieties of the *V. phœniceum*, it does not arise, as has been shown in other cases, from the non-emission of the pollen tubes. In these, as I have elsewhere noticed it, in certain individual plants of different species of Oncidia, Maxillaria, and Passifloræ, sterility apparently results from some slight differentiation of the male element with respect to its own female element. I have also to remark, that the ultimate conditional sterility of these plants is not, relatively considered, an absolute but a graduated quantum; this is shown by the different degrees of development the embryos had undergone, thus illustrating a most interesting, though as yet imperfectly known fact, namely, that the male element, even though reaching the female element, may nevertheless fail to communicate that amount of vital stimulus necessary to the complete development of the embryo. Furthermore, I may in passing briefly refer to the perfect parallelism between these phenomena, and those occasionally observed in hybridisation, at least in the zoological kingdom, for unfortunately we are as yet nearly void of information on this point in the vegetable kingdom, hybridists having, in most instances, satisfied themselves by attending to the ultimate results, without troubling themselves to examine into the nature or degree of embryonic sterilisation. From the published papers of the Hon'ble and Rev. W. Herbert, we find, as might indeed be expected, that this point did not escape observation: thus in one case he remarks, "It has, I believe, not been duly considered, that the fecundation of the ovules is not a simple, but a complicated process. There seems to me to be three or four several processes: viz., the quickening of the capsule of the fruit, of the outer coats of the seed itself, of the internal parts or kernel, and lastly, the quickening of the embryo."........."It is further to be observed," he continues, "that there is frequently an imperfect hybrid fertilisation, which can give life, but not sustain it well. I obtained much good seed from *Hibiscus palustris* by *H. speciosus*, and sowed a little each year till it was all gone, the plants always sprouted, but I saved only one to the third leaf, and it perished then."

To recur, however, to the above parallelism, of which we have here additional and important illustrations: it has been stated by Mr. Darwin* on the authority of Mr. Hewitt, that in the hybridisation of gallinaceous birds a frequent cause of sterility in *first crosses* is the early death of the embryo. Again Mr. Salter records similar results from his experiments on the fertility *inter se* of several *hybrid Galli*,† thus concluding, "the one striking point of these experiments (which I believe has never been noticed before) is that a large proportion of

* loc. cit. p. 286.

† Nat. Hist. Rev. 1863, p. 276.

these eggs from hybrid birds breeding *inter se* have failed to produce young, not from absolute sterility, but sterility in degree, from an amount of vitalization insufficient to carry out the whole result of reproduction, in which the young individual has been completed, leaving it with vital resistance insufficient to maintain life and cope with common and customary external influences." And thus in those curious cases of sterility of structurally hermaphrodite organisms, whose sexual elements have become differentiated with respect to their mutual fertile conjunctions, so in the phenomena of sterility from hybridism, we find, as Mr. Salter well remarks, with respect to the relations of hybridism and parthenogenesis, "that the sterility is not absolute but in degree, and that the stimulus, whatever it may be, which starts the embryonic changes is feeble and imperfect rather than wholly wanting."

I have now shown that a regular more or less early embryonic abortion results from the self-fertilisation of certain individual plants of *V. phœniceum* and *vars. roseum*, and *album ;* whereas by their reciprocal fertilisation, highly fertile unions may in general be effected. By again consulting Table 1, however, it will be seen that besides a reciprocal fertilisation, these three plants are also susceptible of fertilisation by pollen of other species. Thus in lines 7, 8, 9, of Table 1, the male element of *V. nigrum* is singularly enough effective in the fertilisation of each, while in a succeeding Table—4—the goodness of the male elements is also similarly shown by each effectively fertilising the female element of the *V. lychnitis, lutea.* Again, we have fuller illustrations of these curious sexual phenomena in Table 2, in which one of the above plants, *V. phœniceum*, yields a varying degree of fertility to four other distinct species; namely the *V. ferrugineum*, *Blattaria lutea* and *alba ; Lychnitis lutea* and *ovalifolia.* These are indeed remarkable physiological revelations. How strange that an individual plant could be fertilised by the pollen of five distinct species, and yet not by its own good pollen: how singular also, as shown above, to see three hermaphrodite individuals incapable of self-fertilisation, yet having each sexual element reciprocally meeting and fertilising the opposite elements of other species. Thus, for example, the male element of *V. phœniceum* and *vars. roseum* and *album* fertilise the female element of *V. lychnitis*, while the female elements of the three former are also susceptible of fertilisation by the male element of *V. nigrum*. The full explanation of these curious and complicated sexual relations, I leave for more sagacious and ingenious investigators, and simply confine myself to remarking on the apparent support that these and more especially those other cases which I have communicated to the Linnean Society,* on the fertilisation of certain species of Passifloræ, —in which I showed that individual plants perfectly self-sterile readily effected reciprocal unions with other similarly characterised individuals of the same species—give to that view which Mr. Darwin has propounded regarding the existence of a law in nature necessitating "an occasional cross with another individual, or, that no hermaphrodite fertilises itself for a perpetuity of generations," but "that some unknown great good is derived from the union of individuals which have been kept distinct for many generations."†

In the following table, the results of the pure unions of *V. phœniceum* given on the first line are taken from capsules on a specimen in the Edinburgh University Herbarium, as I have not yet been successful in getting good capsules from any of the plants which I have had an opportunity to experiment upon by their own pollen. The other plants of *V. phœniceum* and varieties mentioned in the table are the same as those from which I had the results given in Table 1. Indeed, in one or two instances, the same experiments are re-stated, with a view to show more clearly the relative degrees of sterility resulting from the crossing of undoubted varieties of a species on the one hand, with those from the hybridisation of distinct species on the other.

Table 2.—Pure and Mixed Unions of *Verbascum phœniceum* and var. as ♀	No. of flowers fertilised.	No. of capsules produced.	No. of seeds.	Average of seeds per capsule.	By calculation. No. of capsules.	By calculation. No. of seeds.	The comparative fertility of the different unions.
No. 1. *Verbascum phœniceum* L. (wild plant naturally fertilised), ...	..	4	142	36	20	710	1000

* "Journal Linn. Soc." Vol. 8. p. 197.

† Orchid Fertilisation, pp. 1—360.

TABLE 2. *Contd.*—Pure and Mixed Unions of *Verbascum phœniceum* and var. as ♀	No. of flowers fertilised.	No. of capsules produced.	No. of seeds.	Average of seeds per capsule.	By calculation.		The comparative fertility of the different unions.	
					No. of capsules.	No. of seeds.		
No.								
2. *V. phœniceum, rosea,* by pollen of *V. phœniceum* L.,	12	9	306	34	20	680	..	957.7
3. *V. phœniceum, alba,* by pollen of *V. phœniceum, rosea,*	7	5	154	31	20	616	..	867.6
4. *V. phœniceum, alba* by pollen of *V. phœniceum,* ...	16	11	287	26	20	522	..	735.2
5 *V. phœniceum,* by pollen of *V. phœniceum, rosea,* ..	10	8	193	24	20	483	..	680.3
6. *V. phœniceum* by pollen of *V. phœniceum, alba,* ...	10	6	120	20	20	400	..	563.4
7. *V. phœniceum* by pollen of *V. ferrugineum,* Andr., ...	12	7	148	21	20	423	..	595.8
8. *V. phœniceum* by pollen of *V. blattaria, lutea* L., ..	12	7	112	16	20	320	..	450.7
9. *V. phœniceum* by pollen of *V. blattaria, alba,* ..	12	4	54	13	20	270	..	380.2
10. *V. phœniceum* by pollen of *V. lychnitis lutea,* L., ...	12	8	102	13	20	255	..	359.1
11. *V. phœniceum* by pollen of *V. ovalifolium,*	12	5	43	8	20	172	..	242.2

In addition to the simple and calculated results given on Table 1, I have, in the above, given at the right hand, for the sake of comparison, the calculated product from an assumed 1,000 seeds of the pure unions relatively to those yielded by the cross and hybrid unions. By a further comparative study of these results, we find that the fertility of the pure unions of *V. phœniceum,* relatively to that of its cross-unions with the white and rose-coloured varieties, is, in the least differentiated or most highly fertile unions, viz., *V. phœniceum, rosea* by pollen of *V. phœniceum,* as 100 : 95; whereas in the least fertile unions, *V. phœniceum* by pollen of *V. phœniceum, alba,* the proportions are as 100 : 56. The average fertility of the *five* cross-unions given in the table, relatively to the pure unions given in the first line, is as 100 : 75; so that the pure unions thus exceed in fertility the cross-unions, in nearly the proportions of 4 : 3. Again by a similar comparative study of the relative fertility of the pure unions of *V. phœniceum* and the different hybrid unions given in the Table, we find that the highest degree of fertility results from the union of *V. ferrugineum* (which perhaps is correctly regarded by De Candolle and others as a mere variety of *V. phœniceum*) with *V. phœniceum*, the proportions of the pure to the hybrid unions being as 100 : 59, in favour of the former. The lowest degree of fertility results from the unions of *V. ovalifolium*, with *V. phœniceum*, the proportion of the pure to the hybrid-unions in this case being as 100 : 24.) Lastly the average fertility of the *five* hybrid unions given in the latter lines of the Table, relatively to the pure unions of *V. phœniceum*, is nearly as 100 : 40, or as 2.5 seeds of the pure unions to one of the hybrid unions. Thus, the relative differences in the degree of sterilisation resulting from the hybridisation of distinct species, and that from the cross-impregnation of varieties of a species, relatively in either case to the pure unions, is in the former as 2.5 : 1, and in the latter as 4 : 3.

Table 3.—Pure and Mixed Unions of *V. lychnitis*, L. var. *alba* as ♀.	No. of flowers fertilised.	No. of capsules produced.	No. of seeds.	Average of seeds per capsule.	By calculation.		The comparative fertility of the different unions.	
					No. of capsules.	No. of seeds.		
No. 1. *Verbascum lychnitis*, var. *alba* of gardens, by own pollen, ...	6	6	250	42	20	833	1000	
2. *V. lychnitis*, *alba*, by pollen of *V. lychnitis*, *lutea*, L.,	8	8	274	34	20	685	..	822.3
3. *V. lychnitis*, *alba*, by pollen of *V. thapsus*, L. var. *alba*, of gardens, ...	10	5	98	20	20	392	..	470.5
4. *V. lychnitis*, *alba*, by pollen of *V. phœniceum*, L. var. *alba* of gardens, ..	5	4	113	28	20	565	..	678.2

TABLE 4.—Pure and Mixed Unions of *V. lychnitis, lutea,* L. as ♀	No. of flowers fertilised.	No. of capsules produced.	No. of seeds.	Average of seeds per capsule.	By calculation.		The comparative fertility of the different unions.	
					No. of capsules.	No. of seeds.		
No.								
1. *V. lychnitis, lutea,* L. by own pollen, ..	6	6	226	38	20	753	1000	
2. *V. lychnitis lutea* by pollen of *V. lychnitis, alba,*	8	7	249	36	20	711	..	944.2
3. *V. lychnitis, lutea* by pollen of *V. phœniceum,* L., .	5	3	75	25	20	500	..	664.0
4. *V. lychnitis, lutea* by pollen of *V. phœniceum,* L. var. *alba* of gardens, ..	5	3	63	21	20	420	..	557.7
5. *V. lychnitis, lutea* by pollen of *V. phœniceum,* L. var. *alba* of gardens, ..	5	2	37	18	20	370	..	491.3
6. *V. lychnitis, lutea* by pollen of *V. blattaria,* L. var. *alba* of gardens, ...	8	4	85	21	20	425	..	564.4
7. *V. lychnitis, lutea* by pollen of *V. blattaria, lutea,* L., ..	8	5	97	19	20	388	..	515.2
8. *V. lychnitis, lutea* by pollen of *V. thapsus, lutea,* L., ..	10	7	123	18	20	351	..	466.1
9. *V. lychnitis, lutea* by pollen of *V. thapsus,* L. var. *alba* of gardens, ...	10	5	75	15	20	300	..	398.4
10. *V. lychnitis, lutea* by pollen of *V. nigrum,* L., ..	10	6	182	30	20	607	..	806.1
11. *V. lychnitis, lutea* by pollen of *V. virgatum,* With., ..	10	5	111	22	20	444	..	589.6
12. *V. lychnitis, lutea* by pollen of *V. thapsiforme,* Schrad, .	8	3	52	17	20	347	..	460.8

In Table 3 we have first the results of the pure unions of *V. lychnitis, alba,* and by comparing them with those resulting from fertilisation with the pollen of *V. lychnitis, lutea,* we find that the latter cross-unions undergo the proportionately decreased fertility of 100 : 82. By the hybrid-unions of *V. lychnitis, alba,* with the pollen of *V. phœniceum, alba,* a slightly higher degree of sterilisation results; the proportion in this case being as 82 : 67, relatively to 100 produced by the pure unions of *V. lychnitis, alba.* The highest degree of sterilisation in this Table results from the union of *V. lychnitis, alba,* by pollen of *V. thapsus, alba,* the proportion of the pure to the hybrid unions being here as 100 : 47.

The results of my experiments on the yellow variety of *V. lychnitis* are given in Table 4. By a comparative examination of this Table, we have the following general results: first, the fertility of the pure unions of *V. lychnitis, lutea* exceeds that resulting from the cross-unions of the latter with pollen of *V. lychnitis, alba,* in the proportion of 100 : 94. The degree of sterilisation induced by these unions, though less than that resulting from the converse unions given in Table 3, is nevertheless sufficient to show a sterilising influence in the conjunctions of varieties of a species, characterised only by those, systematically considered, trifling differences in colour—the one being white, the other yellow. Secondly we have the results of unions of similarly and dissimilarly coloured forms of distinct species, with *V. lychnitis, lutea.* Thus the pollen of *V. phœniceum,* with purplish coloured flowers, applied to the stigmas of *V. lychnitis, lutea,* gives an average fertility of 66; the pollen of the white variety *V. phœniceum, alba,* gives an average of 55; while that of the rose-coloured variety is productive of the highest degree of sterilisation, giving only 49—relatively to 100, the produce of *V. lychnitis, lutea* by its own pollen. Mr. Darwin, on the authority of Gartner, states in his "Origin of Species," that similarly coloured varieties of distinct species are more fertile when crossed than are the dissimilarly coloured varieties of the same species. The particular illustration of this point will be found in a subsequent part of this paper; I will here merely state that, in the above unions, the degrees of fertility are by no means regulated by the colour affinities. Thus, we have first yellow and violet, then yellow and white, and lastly yellow and rose yielding a successively decreased fertility; whereas, judging by the colour affinities, the arrangement ought to have been, beginning with the most fertile, yellow first with white, then with rose, and lastly with violet. Secondly, with pollen of the *V. blattaria, vars. alba* and *lutea,* we see, that the *V. lychnitis, lutea* yields the higher degree of fertility with the former: *V. lychnitis, lutea,* yielding with pollen of *V. blattaria, alba,* 56, and with that of *V. blattaria, lutea,* 51, relatively to 100, the product of fertilisation with its own pollen. Thirdly, in the unions of *V. lychnitis, lutea,* by pollen of the yellow and white varieties of *V. thapsus,* we find that unions of the similarly coloured flowers are the more fertile. *V. lychnitis, lutea,* yielding with pollen of *V. thapsus, lutea,* 46, and with the pollen of *V. thapsus, alba,* 39, relatively to 100, the results of fertilisation with its own pollen. Fourthly, in accordance with recognised systematic affinities, we find the following descending scale of sterilisation resulting from the unions of *V. nigrum*, *V. virgatum* and *V. thapsiforme* with the *V. lychnitis*. Thus with the pollen of *V. nigrum*, the average fertility of *V. lychnitis*, *lutea*, is 80, with that of *V. virgatum* 58, and with that of *V. thapsiforme* 46, relatively, in each instance, to 100, the product of fertilisation by its own pollen. A similar accordance is observable between the functional and systematical relations of *V. blattaria* and *V. thapsus* with the *V. lychnitis*. In the unions, however, of *V. phœniceum* and varieties with the *V. lychnitis*, no such accordance is observable. The different unions vary greatly in the degree of fertility *inter se*, and judging indeed by the relative functional potency of the pollen of the three varieties on the stigmas of *V. lychnitis*, the different results are comparable with those from distinct species, and would cause their interpolation into systematically considered false positions, showing us that the functional and systematic affinities of the species of a genus are by no means strictly co-ordinated.

Table 5.—Pure and Mixed Unions of *Verbascum blattaria*, L. var. *alba* of gardens.	No. of flowers fertilised.	No. of capsules produced.	No. of seeds.	Average of seeds per capsule.	By calculation.		The comparative fertility of the different unions.	
					No. of capsules.	No. of seeds.		
No. 1. *Verbascum blattaria*, L. var. *alba* of gardens by own pollen, ..	8	8	438	55	20	1095	1000	
2. *V. blattaria*, *alba* by pollen of *V. blattaria*, *lutea*, L., ..	6	5	217	43	20	868	...	792.6
3. *V. blattaria*, *alba* by pollen of *V. thapsus*, *lutea*, L.,	6	2	36	18	20	360	...	328.7
4. *V. blattaria*, *alba* by pollen of *V. thapsus*, L. var. *alba* of gardens, ..	6	4	95	24	20	475	...	433.7
5. *V. blattaria*, *alba* by pollen of *V. lychnitis*, *lutea* L., .	8	5	65	13	20	260	...	237.4
6. *V. blattaria*, *alba* by pollen of *V. lychnitis*, L. var. *alba* of gardens, ...	6	4	79	20	20	395	...	360.7

TABLE 6.—Pure and Mixed Unions of *V. blattaria, lutea*, L. as ♀	No. of flowers fertilised.	No. of capsules produced.	No. of seeds.	Average of seeds per capsule.	By calculation. No. of capsules.	By calculation. No. of seeds.	The comparative fertility of the different unions.	
No. 1. *Verbascum blattaria, lutea*, L. by own pollen, ..	8	7	354	50	20	1011	1000	
2. *V. blattaria, lutea* by pollen of *V. blattaria, alba* of gardens, ..	6	3	147	49	20	980	...	969.3
3. *V. blattaria, lutea* by pollen of *V. thapsus, lutea*, L.,	6	4	103	26	20	515	...	509.4
4. *V. blattaria, lutea* by pollen of *V. thapsus, alba* of gardens, ...	6	2	62	31	20	620	...	613.2
5. *V. blattaria, lutea* by pollen of *V. lychnitis, lutea*, L.,	8	4	81	20	20	405	...	410.4
6. *V blattaria, lutea* by pollen of *V. lychnitis, alba* of gardens, ...	8	1	23	23	20	460	...	454.8

The results of experiments on the *V. blattaria*, varieties *lutea* and *alba*. are given in the above Tables : they comprise 12 unions between the white and yellow varieties of three species. Let us briefly compare the results of their reciprocal unions. First, the fertility of *V. blattaria, alba*, when fertilised by its own pollen. undergoes the highly proportionate sterilisation of 98 : 78 when fertilised with the pollen of the yellow variety—*V. blattaria, lutea.* In the converse case, the sterilising influence of the cross relatively to the pure unions of these forms is much decreased, the pure union of *V. blattaria, lutea*, yielding more seed in the proportions of 90 : 88 than from its cross-union with the white variety—*V. blattaria, alba.* Secondly, as to the hybrid unions with the pollens of the yellow and white varieties of *V. thapsus.* In these the pollen of the white variety is the more potent. Thus *V. blattaria, alba*, fertilised by pollen of *V. thapsus, alba*, affords an average fertility of 43, whereas by that of *V. thapsus, lutea*, the produce is reduced to 32, relatively in both cases to 100, the average fertility of *V. blattaria, alba*, when fertilised by its own pollen. By the union of the yellow and white varieties of *V. thapsus* with the yellow variety of *V. blattaria*, we see that the relative differences in the potency of the two pollens on the stigmas of *V. blattaria, lutea,* are much less than those we have above noticed when *V. blattaria alba* is used as female ; and also that the potency of the two pollens is greater on the stigmas of the yellow than those of the white variety of *V. blattaria lutea ;* and again that the white variety of *V. thapsus* is more fertile than the yellow, in their respective unions with the *V. blattaria, alba.* Thus *V. blattaria, lutea,* by pollen of *V. thapsus, alba,* gives an average fertility of 61 ; by pollen of *V. thapsus, lutea,* 50, relatively to 90, the product of fertilisation by its own pollen. Lastly, we have the different unions of the two pollens of the white and yellow *V. lychnitis* on the stigmas of the yellow and white varieties of *V. blattaria.* In these unions we see first that with *V. blattaria, alba* as female, the pollen of the white variety exceeds that of the yellow in the proportion of 36 : 23; secondly, with the *V. blattaria, lutea,* as female, the pollen of the white variety is again singularly enough the more fertile, exceeding that of the yellow variety, in the proportion of 45 : 41. Thirdly, we find that here also the yellow variety of *V. blattaria* yields a higher degree of fertility,—taking the conjoint products of the two unions with the pollen respectively of *V. thapsus, lutea* and *alba,*—than the white variety of *V. blattaria* when similarly treated, the proportions being as 70 of the *V. blattaria* to 47 of the *V. blattaria, alba,* or nearly as 3 : 2.

This leads me to notice a curious fact prominently brought before us in the above Table, whatever may be its real signification, namely, that the yellow varieties of *V. lychnitis* and *blattaria,* though yielding a higher grade of fertility to the pollen of the white and yellow varieties of distinct species than do the respective white varieties of the above species when similarly fertilised, are nevertheless less productive of seed than the white, when both are fertilised with their own pollen. This will be seen by consulting the following tabular arrangement, in which I have given a reduced approximate of the relative fertility of the different unions, selecting from the hybrid unions in each instance only the most fertile.

1. *V. lychnitis, alba,* by own pollen is as 83 : 75 of *V. lychnitis, lutea,* by its own pollen.

2. *V. lychnitis, alba,* by pollen of *V. lychnitis, lutea,* is as 68 : 71 of *V. lychnitis, lutea,* by pollen of *V. lychnitis, alba.*

3. *V. lychnitis, alba,* by pollen *V. thapsus, alba,* is as 39 : 30 of *V. lychnitis, lutea,* by pollen of *V. thapsus, alba.*

4. *V. lychnitis, alba,* by pollen of *V. phœniceum, alba* as 56 : 42 of *V. lychnitis, lutea,* by pollen of *V. phœniceum, alba.*

5. *V. blattaria, alba,* by its own pollen, is as 98 : 90 of *V. blattaria, lutea* by its own pollen.

6. *V. blattaria, lutea,* by pollen of *V. blattaria, alba* is as 96 : 79 of *V. blattaria, alba,* by pollen of *V. blattaria, lutea.*

7. *V. blattaria, lutea,* by pollen of *V. thapsus, alba,* as 61 : 43 of *V. blattaria, alba,* by pollen of *V. thapsus, alba.*

8. *V. blattaria, lutea* by pollen of *V. lychnitis, alba,* as 45 : 36 of *V. blattaria, alba,* by pollen of *V. lychnitis, alba.*

We thus see, from the eight pure, cross, and hybrid unions of *V. blattaria alba* and *lutea* given in the above comparative table, that though the white variety exceeds in fertility the yellow variety, when both are fertilised by their own pollen, the yellow variety, in the mixed unions, is in every case more highly fertile than the white. In the different unions of *V. lychnitis, alba* and *lutea,* there is some little discordance, this, however, is confined to the hybrid unions which are as yet very insufficiently illustrated, as may be seen by consulting Tables 3 and 4. In the case of the pure and cross unions, we see, as in those of *V. blattaria,* that in the *pure unions* the *white* variety, and in the *cross unions* the *yellow* variety is the more fertile.

I know not whether this concordance is casual or otherwise, but I was so forcibly struck with it in the comparative study of my Tables, that I have thus ventured a special statement. I have been more especially induced to notice it also from its evidently bearing and illustrating, as I am inclined to think, that view of Mr. Darwin, (*loc. cit.*) respecting the good derived from cross fertilisation; inasmuch as we see that the yellow and original, or normally coloured, form of the species is less fertile than the white or derivative form in the pure unions, whereas in general, in the mixed unions, the yellow variety relatively exceeds the white in the degree of fertility. Any how, the mere fact of such variations occurring, whether or not they have any bearing on other points of theoretical natural science, seems to me worth noticing, as affording an additional link to that broken chain of evidence which is said to disjoin the serial continuity of the phenomena of mongrelism and hybridism.

Table 7.—Pure and Mixed Unions of *Verbascum thapsus, lutea,* L. as ♀.	No. of flowers fertilised.	No. of capsules produced.	No. of seeds.	Average of seeds per capsule.	By calculation. No. of capsules.	By calculation. No. of seeds.	The comparative fertility of the different unions.	
No. 1. *Verbascum thapsus, lutea,* L. by own pollen,	8	8	920	115	20	2300	1000	
2. *V. thapsus, lutea* by pollen of *V. thapsus* var. *alba* of gardens,	4	2	218	109	20	2180	...	947.8
3. *V. thapsus, lutea* by pollen of *V. lychnitis, lutea,* L.,	6	1	54	54	20	1080	...	465.2
4. *V. thapsus, lutea* by pollen of *V. lychnitis,* var. *alba* of gardens,	6	3	187	62	20	1246	...	541.7
5. *V. thapsus, lutea* by pollen of *V. nigrum,* L.,	10	4	275	69	20	1375	...	597.8
6. *V. thapsus, lutea* by pollen of *V. pyramidatum,* Beib.,	10	6	374	62	20	1246	...	541.7
7. *V. thapsus, lutea* by pollen of *V. thapsiforme,* Schrad,	10	8	408	51	20	1020	...	443.2
8. *V. thapsus, lutea* by pollen of *V. virgatum,* With.,	10	5	222	44	20	888	...	386.0
9. *V. thapsus, lutea* by pollen of *V. blattaria, lutea* L.,	8	3	98	33	20	653	...	283.9

In Table 7 we have several unions of the yellow variety of *V. thapsus.* If we compare these results, we see that the fertility of the *V. thapsus, lutea,* by its cross-unions with the *V. thapsus, alba,* is decreased in the proportions of 94 relatively to 100, the product of fertilisation by its own pollen. We also see a great difference in the degrees of potency of the two pollens of the white and yellow variety of *V. lychnitis* on the stigmas of the yellow variety of *V. thapsus;* the pollen of *V. lychnitis, alba,* exceeding in its fertilising influence that of *V. lychnitis, lutea,* in the proportion of 54 : 46. Judging from the results of the seven hybrid unions given in this Table, we also see how little the recognised systematic affinities of species guide us in pronouncing *a priori* as to the degree of fertility of their several unions. For example *V. thapsiforme, V. virgatum* and *V. blattaria,* though much more closely allied to the *V. thapsus* than the others given in Table, are nevertheless least effective in their conjunctive fertility with the latter species. Furthermore, we see by those unions of *V. thapsus, lutea*, as female, with the yellow and white varieties of *V. lychnitis*, and of *V. pyramidatum;* that though the pollen of *V. pyramidatum* is equally potent on the stigma of *V. thapsus lutea*, as is that of *V. lychnitis, alba*, there is nevertheless a considerable decrease in the proportionate fertility of the unions with *V. lychnitis, lutea.* Hence, as we have before shown it to be with the varieties of *V. phœniceum*, and judging by the physiological test, the *V. pyramidatum* would interpolate itself between these slightly different and undoubted varieties of a species.

In the foregoing Tables, then, I have given nearly all the results of my experiments in the unions of Verbasca. Before considering the nature of the evidence they afford us as to the relationship of mongrelism and hybridism, I will briefly attempt to show how far these results accord with those of Gartner, who has also largely experimented on these plants. I may premise, however, that as my experiments are much less numerous than Gartner's, comprising some 57 distinct unions, in which 527 flowers were artificially fertilised,—whereas, as will be seen beneath, Gartner subjected no less than 1085 flowers to experiment,—they would induce very different conclusions, in certain points, to those arrived at by that careful experimentalist. I readily acknowledge therefore the higher claim of the latter to a provisional acceptance, until further experiments show more conclusively their relative correctness. I have also to notice a cause of some little discordance in such a comparative examination as that which I am about to institute; namely, that I have given in every case the *average* number of seeds produced *both* by *pure* and *mixed unions*, whereas Gartner gives the *average number* of seeds in the *pure unions* only, taking in each case the *maximum* or highest number produced by a single capsule in the *mixed unions.* I was not aware of this peculiarity in Gartner's deductions when I counted the seeds in my own experiments, otherwise, I should have drawn them up for the sake of comparison on a similar basis; even though I consider it a less fair method than that which I have adopted, in all such cases as the present, in which the ovaries contain an *indefinite* number of ovules. And this the more especially if, as in my own experiments, *castration* and *artificial impregnation* be performed in both *pure* and *mixed* unions. In drawing comparisons between *uncastrated* pure unions, and *castrated* mixed unions, the *average* of the former, with the *maximum* of the latter would certainly be the fairer method, as affording a complement for the sterilising influence of castration.

For the following digest of Gartner's experiments I have to thank Mr. Darwin, who kindly sent it to me from his yet unpublished MS. illustrations of these phenomena: "To show the scale on which Gartner worked, I may state that, in the genus Verbascum, he crossed no less than 1085 flowers and counted their seed, and recorded the results. Now in two of his works he distinctly asserts that similarly coloured varieties of *V. lychnitis* and *V. blattaria* are more fertile together than when differently coloured varieties of the same species are crossed. But Gartner chiefly relied on the crosses which he made between the yellow and white varieties of these two species and nine other distinct species, and he asserts that the white-flowering species yielded more seed than did the yellow-flowered varieties when crossed with the same white varieties of these two-flowered species, and so conversely with the yellow flowering varieties with the yellow species. The general results may be seen in his Table. In one case he gives the following details; the white *Verbascum lychnitis* naturally fertilised with its own pollen had on an *average* in 12 capsules 96 good seeds: 20 flowers artificially fertilised with the pollen of its yellow variety gave as the *maximum* 89 good seeds. I should have thought that this slight difference might have been wholly due to the evil effects of castration; but Gartner shows that the white variety of *V. lychnitis*, fertilised by the pollen of the white and yellow varieties of *V. blattaria*, in both of which cases there must have been previous castration, bore seeds to the white variety in the proportion of 62, to 43 when pollen of the yellow variety was used."

First then, in regard to the greater fertility of the unions of similarly coloured varieties, relatively to that of the unions of dissimilarly coloured varieties of the *same* species. To these phenomena I will apply in the subsequent parts of this paper the following terms: "*Homochromatic*" to the unions of similarly coloured varieties, and "*hetero-*

chromatic" to those in which dissimilarly coloured varieties are united In the following table we will at once see the comparative fertility of these different unions given in the previous ones.

RELATIVE FERTILITY OF THE HOMOCHROMATIC AND HETEROCHROMATIC UNIONS.

1. *V. phœniceum* by its own pollen, . . .	1000	
2. *V. phœniceum, rosea*, by pollen of *V. phœniceum*, ...		958
3. *V. phœniceum, alba*, by pollen of *V. phœniceum, rosea*,		867
4. *V. phœniceum, alba*, by pollen of *V. phœniceum*, ...		735
5. *V. phœniceum*, by pollen of *V. phœniceum, rosea*, ...		680
6. *V. phœniceum*, by pollen of *V. phœniceum, alba*, ...		563
7. *V. lychnitis, alba*, by pollen of *V. lychnitis, lutea*, ...		822
8. *V. lychniits, lutea*, by pollen of *V. lychnitis, alba*, ...		944
9. *V. blattaria, alba*, by pollen of *V. blattaria, lutea*, ...		792
10. *V. blattaria, lutea*, by pollen of *V. blattaria, alba*, ...		969
11. *V. thapsus, lutea*, by pollen of *V. thapsus, alba*, ...		947

Here the comparative fertility is shown by calculation from the number of seeds produced by 20 assumed capsules of both unions. The various cross-unions of *V. phœniceum* and its varieties are in each case to be considered relatively to the assumed results of the pure unions of *V. phœniceum* given in Table 2, these plants experimented upon being individually self-sterile as shown in Table 1. The unions, on the other hand, of *V. lychnitis, blattaria*, and *thapsus*, with their respective varieties, are each to be considered relatively to the 1000 seeds produced by the pure union of that variety given as female. Now in all the above heterochromatic unions, as compared with the homochromatic, we have the clearest evidence of reduced fertility. Thus, taking the 10 heterochromatic unions given, and comparing them with a similiar number of homochromatic unions, we find that the average proportion in which the former exceeds the latter, is as ·05 to ·23. On again confining ourselves to those species alone which have the yellow and white varieties, and keeping the unions of white as ♀ with yellow ♂, distinct from those of yellow as ♀ with white as ♂, we find that the cross-unions with white as female are to the pure unions of the latter as ·04 to ·28; and in those cross-unions with yellow as female, the proportions are as ·23 to ·29, relatively to the pure unions of the latter. Thus, in whatever way we proceed, the general results are the same, testifying to the highly remarkable fact announced by Gärtner, that varieties of a species, characterised by no other differences than that of colour, are occasionally so differentiated functionally, that the cross-unions, as compared with the fertility of the pure unions, invariably indicate a certain degree of sterilisation!

In connection with this higher relative fertility of homochromatic to that of heterochromatic unions, as limited to the crossing of varieties of a single species, I will venture to add that this law not only holds, but, as I believe, extends to and regulates the functional relations in accordance with the relative colour affinities of the varieties crossed. Thus for the sake of illustration, we may take the three primary colours of the cyanic series, namely, blue, violet, and red. Now beginning with red, we know that greater physiological changes must take place in the minute anatomy of the petals of an originally red-coloured flower to give the impression of blue than that of violet. Hence we might suspect that a species presenting varieties characterised by such differences in colour, would likewise afford different degrees of fertility in their conjunctive functional relations, the blue and red yielding less fertile unions, than the violet and red; while the violet holding an intermediate colour position between these, might be equally as fertile in its unions with the blue as the red variety. In practical illustration of these relations, we may take the results of the various unions of *V. phœniceum* and varieties given in Table 1. Thus the *V. phœniceum* with purplish-violet flowers yields more seeds when fertilised by the pollen of the rose-coloured variety, than by that of the white variety, in the proportion of 5 to 4. Again the white variety of *V. phœniceum* fertilised by the pollen of the rose variety yields an average of 29 seeds per capsule, and by that of the purplish violet variety the average per capsule is 26, that is as 9 to 8, in favour of the unions of the rose and white varieties. We see here evident co-relations between the degrees of fertility and the colour affinities of these plants in their respective sexual unions, and I venture to look for more marked differences in these respects, had we as subjects of experiment, varieties of a species presenting three, or at least two, of the primary colours with intermediate shades irrespective of the white. The latter being rather unsatisfactory from its similar relations to the primary colours, though in such instances as the above of the purplish-violet, rose and white, in which we have secondary colours forming intermediate steps between the primary and white, by a gradual dilution of the colouring principle, we find that the white, agreeably to the above views, form less fertile conjunctions with the violet than the rose-coloured flowers. Before passing from this point of my subject, I will now only add that I have thought these indications of a tangible law, co-relating and regulating the sexual functions of varieties when crossed—dim though they as yet undoubtedly are— worth noticing, as we are as yet in utter ignorance of anything like definite or specific laws in these phenomena, the results being considered as most capricious and uncertain.

Gärtner's second proposition is, that in the hybridism of differently coloured varieties of distinct species of Verbasca, the conjunctions of the similarly coloured flowers are more fertile than these of dissimilarly coloured flowers. For example Gärtner shows* that on the calculation of *V. lychnitis*, *fl. alba*, yielding with its own pollen 1.000 seeds, it yields when fertilised with the pollen of *V. blattaria fl. alba*, 0.622 seeds, and with that of *V. blattaria*, *fl. lutea*, only 0.438, so that the similarly coloured unions of these species are more fertile than the dissimilarly coloured unions in the proportion of 3 to 2. Let us now see then in how far this law of the differences in the fertility of the homochromatic relatively to the heterochromatic unions, is borne out in the case of my own experiments as given in the preceding Tables. And here again, for the sake of clearness, and facility of reference, I will restate them in a tabular form, and show as clearly as possible the differences in the relative fertility of the homochromatic and the heterochromatic unions, in each case, by making calculations from an assumed 100 seeds produced by the more fertile of the two unions compared. The results may be conveniently arranged under three heads; thus, first, the heterochromatic unions, or those in which the unions of differently coloured flowers are the more fertile: second, the homochromatic unions, or those in which similarly colour-

* Versuche über die Bastarderzeugunj, 1849, section 216.

ed flowers are the more fertile: and lastly, the irregular unions in which no relations are observed between the degree of fertility and affinity of colours.

A. 1.—Heterochromatic union, *the* more *fertile.*

1.	*V. lychnitis, lutea,* by pollen of *V. blattaria, alba,* .	100	
2	*V. lychnitis, lutea,* by pollen of *V. blattaria, lutea,* .	,,	to 91
3.	*V. blattaria, lutea,* by pollen of *V. thapsus, alba,* .	100	
4.	*V. blattaria, lutea,* by pollen of *V. thapsus, lutea,* .	,,	to 83
5.	*V. blattaria, lutea,* by pollen of *V. lychnitis, alba,* .	100	
6.	*V. blattaria, lutea,* by pollen of *V. lychnitis, lutea,* .	,,	to 88
7.	*V. thapsus, lutea,* by pollen of *V. lychnitis, alba,* .	100	
8.	*V. thapsus, lutea,* by pollen of *V. lychnitis, lutea,* .	,,	to 87

B. 2.—Homochromatic unions, *the* more *fertile.*

1.	*V. lychnitis, lutea,* by pollen of *V. thapsus, lutea,* .	100	
2.	*V. lychnitis, lutea,* by pollen of *V. thapsus, alba,* .	,,	to 85
3.	*V. blattaria, alba,* by pollen of *V. thapsus, alba,* .	100	
4.	*V. blattaria, alba,* by pollen of *V. thapsus, lutea,* .	,,	to 76
5.	*V. blattaria, alba,* by pollen of *V. lychnitis, alba,* .	100	
6.	*V. blattaria, alba,* by pollen of *V. lychnitis, lutea,* .	,,	to 66

C. 3.—Degree of Fertility and affinity of Colour Irregular.

1.	*V. lychnitis, lutea,* by pollen of *V. phœniceum,* .	100	
2.	*V. lychnitis, lutea,* by pollen of *V. phœniceum,* .	,,	to 80
3.	*V. lychnitis, lutea,* by pollen of *V. phœniceum,* .	,,	to 74

In A. and B. of the above comparative tables, I have arranged those unions in which a certain regularity is observed between the colour relationship and the degree of fertility. Now, by comparing the 14 unions therein given, we find that the heterochromatic unions are, in the greater number of cases, more fertile, viz., as 8 to 6, than the homochromatic unions, and that this higher fertility, in every case, results from those unions in which the yellow variety of the species is treated as female. Again that the average proportion of the four heterochromatic to the four converse homochromatic unions in the first of the above tables is nearly as 7 to 6 in favour of the former. In B. 2 of the tabulated results, we see in one instance the homochromatic unions with yellow as female exceed in fertility the converse heterochromatic union; but in the other cases given in lines 3 and 5, this higher fertility of the homochromatic unions is yielded by the white variety; the relative proportions of these being much more marked than in the above cases of the heterochromatic union with the yellow variety as female, viz., as 4 to 3, whereas, as we have seen, in the heterochromatic, A. 1, the proportions are as 7 to 6. In further illustrations of this point we see in B. 2 that the yellow homochromatic union of *V. lychnitis, lutea*, by pollen of *V. thapsus, lutea*, relatively to the heterochromatic unions of the former with pollen of *V. thapsus, alba*, is nearly as 5 to 4, so that we here again see (as in the heterochromatic and homochromatic unions in A 1) a more intimate approximation between the products of these two unions, than occurs in the other cognate unions of B. 2, in which the white variety is the more fertile.

These curious relations, however, as I have already shown, are partly explained by the fact,—though we can only dimly see why it should be so,—that in the pure unions of the white and yellow varieties of the above mentioned species, the white, in every case, yields more seed than the yellow; whereas in the cross-unions the yellow variety in general is the more productive. But, it may be asked, how is the greater potency of the pollen of the white variety relatively to that of the yellow variety, as shown in the above tables to be accounted for? Does it really imply that the female element of the yellow variety yet retains its normal or original potency, the male element alone having become absolutely less potent, as compared with the male element of the white variety. This hypothesis, analogically considered, does not seem to me at all improbable. I think we have clearly seen by the comparative results of the pure and mixed unions of the yellow variety with those of the white, that the pure unions of the yellow do not yield a degree of fertility at all proportionate to that of the like unions of the white variety, as judged by the relative fertility of their cross-unions; and that accordingly this would seem to be due to an acquired weakness in the generative powers of the yellow variety. In noticing this point in a former part of my paper, I treated it as if both sexual elements had undergone a similar decrease in their generative powers;

but we here see that it is more particularly, if not altogether confined to the male element. Now, as the results of hybridisation show that the pollen is more susceptible to the concomitant sterilising action of hybridism than the female element, may we not suppose that the debilitating effect of continued self-impregnation will also manifest itself more quickly in the male than in the female element, and thus afford an explanation of the decreased sexual powers of the male, as compared with the female element, in the yellow varieties of the above species of Verbasca furthermore, showing us that as it has been a slowly acquired quality, so will it be in its elimination and regainment of its pristine vigour.

The relations of the several reciprocal unions in the above tables is another point which we must briefly consider, as having most important bearings on the subject of our present enquiry. A hasty examination suffices to show that these are much complicated. Thus *V. lychinitis, lutea,* in its two unions with the white and yellow varieties of *V. blattaria,* the heterochromatic unions are the more fertile; whereas in its two unions with the white and yellow varieties of *V. thapsus,* we find it yields the more fertile by a homochromatic union. Again *V. blattaria, lutea,* in its four distinct unions with the white and yellow varieties of *V. thapsus* and *V. lychnitis,* yields the higher degree of fertility in the heterochromatic unions, while the *V. blattaria* in its similar unions with the white and yellow varieties of *V. thapsus* and *lychnitis* is, singularly enough, more highly fertile in the homochromatic than the heterochromatic unions. Lastly the *V. thapsus, lutea,* yields more seed by its heterochromatic unions with *pollen* of the *V. lychnitis, alba,* than by its homochromatic unions with the *V. lychnitis, lutea;* whereas in the converse unions we have seen that the *V. lychnitis, lutea,* is more fertile in the homochromatic unions with *V. thapsus, lutea,* than in the heterochromatic unions with *V. thapsus, alba!*

The tabulated experiments given in C. 3, afford another source of complexity to the question under examination, inasmuch as they are quite irregular in the relative degree of fertility produced by the affinity of colour. Thus by the three unions of *V. lychnitis, lutea,* with pollen of the three varieties of *V. phœniceum,* the most highly fertile is that in which *V. lychnitis, lutea,* is treated with pollen of the purplish violet, or normal form, the average in this being 25 seeds per capsule; then follows the unions with pollen of the white variety, the average of seeds being in these 21 seeds per capsule; and lastly in the unions with the variety with rose-coloured flowers, the fertility of *V. lychnitis, lutea*, is reduced to the low average of 18 seeds per capsule. Thus judging by the degrees of fertility, we clearly see that the natural functional co-relations of these plants in place of being regulated by their respective colour affinities, arrange themselves in an entirely independent and opposite scale; the extremes in the scale of colour given, viz., the purplish-violet with yellow, manifesting the nearest functional co-relation. Again as a further complication we find that the white and yellow unions, —the most closely allied of the colours mentioned,—hold a medial position between the purplish violet and rose. How obviously futile then, we may well remark, would our *á priori* conclusions have been, as to the degrees of fertility of the above unions, on a presumed coordination between colour and function in the phenomena of hybridism!

It would thus appear from the results given in the foregoing tables that in the hybridisation of varieties of distinct species characterised by differences of colour alone, no definite relations whatever can be observed between the affinities of colour, and the degrees of fertility, but that in these cases as in the reciprocal hybridisation of pure species, the relative fecundity is a most variable and unpredicable quantum. This view seems to me to be further supported by the results of my experiments on the reciprocal hybridisation of the dimorphic species of Primulæ* in which I showed that the laws of dimorphism were limited in their action to the unions of the two forms of a species; the heteromorphic and homomorphic unions of distinct species proving irregularly the more fertile. From considering the important functional co-relations of the two forms of dimorphic species, and their trifling morphological characteristics, together with the specifically limited extent of their operations, we have less reason to be surprised, if a similarly limited relationship should ultimately prove to regulate the degree of fertility of those unions of differently coloured varieties of a species as in Verbascum and analogous cases. Indeed, judging

* Linn. Soc. Jour. Vol. 8, p. 78.

from my previous remarks on the co-relations between the degree of fertility and affinity of colour in the crossing of varieties of a species, together with the results of the hybridising differently coloured varieties of distinct species, this law seems clearly indicated, that the relative degree of fertility of the cross unions between the differently coloured varieties of *certain* species is inversely proportionate to the less or more mediate colour affinities of these unions. Further that this law does not extend to, or regulate the hybrid unions of differently coloured varieties of distinct species, but is strictly limited in its operations to those unions of varieties of a single species. Such at least is the conclusion which my own experiments would induce me to hold, but seeing that they are so directly opposed to the results of Gärtner's large experience, I would rather avoid at present anything like definite or positive conclusions, until subsequent experiment affords us a crucial array of data.

In conclusion, I will now by a cursory retrospect of the above details, re-state a few of the more important points, which elucidate the mooted relations between the phenomena of the hybridisation of a species and the mongrelism of the varieties of a species. First then in *hybridism* we see on the calculation of *V. lychnitis* yielding with its own pollen 100 seeds, it yields upon fertilisation with pollen of *V. nigrum* 80 seeds, by the pollen of *V. virgatum* 58 seeds, by that of *V. phœniceum* 66 seeds and by that of *V. thapsiforme* 46 seeds. In the unions of varieties of a species, with these of other species we find differences in the sexual powers, so that the pollen of the one variety of a species is less potent than that of the other on the stigmas of the same variety of another species. Thus *V. lychnitis* fertilised by the pollen of *V. blattaria, lutea,* yields 51 seeds, by that of *V. blattaria, alba,* 56 seeds, and again by pollen of *V. thapsus, lutea, V. lychnitis* yields 46 seeds, by that of *V. thapsus, alba,* 39 seeds, relatively in each case to the 100 seeds produced by its own pollen. Again we have evidence also of reciprocal differentiation in the relative sexual powers of varieties of a species, and those of other species. Thus in the case mentioned above of *V. blattaria*, the pollen of variety *alba* is more potent on the stigma of *V. lychnitis* than that of variety *lutea*, whereas in the converse unions of these forms, we find that the pollen of *V.*

lychnitis is more potent on the stigmas of *V. blattaria*, *lutea*, than that on those of the variety *alba*, in the proportion of 40 to 26.

Secondly, in mongrelism, we also find variabilities in the relative sexual powers of varieties of a species, by differences in the degrees of fertility resulting from their simple and reciprocal unions. Thus on the calculation of *V. phœniceum*, yielding 100 seeds by fertilisation by its own pollen, it yields with that of the variety *rosea* 68 seeds, and by that of the variety *alba*, 56 seeds, or nearly as 5 to 3. In the reciprocal unions of these varieties, we also find variabilities in their converse sexual powers. For example, in the reciprocal unions of *V. phœniceum* and varieties, the potency of the pollen of *rosea* relatively to that of *alba* on the stigmas of the normal form is nearly as 5 to 4; whereas the pollen of the latter on the stigmas of *rosea* and *alba* is as 4 to 3. This difference in the reciprocal sexual powers of varieties when crossed is so regulated however by colour affinities, that unlike the irregular and indefinite results of the reciprocal unions of varieties of distinct species, judging by my own experience, we see that the pollen of *rosea* is more potent on the stigmas of the normal form than these of *alba* and so conversely, the pollen of the normal form is more potent on the stigmas of *rosea* than on those of *alba*. In those cases, however, in which colour differences do not come into play the pollen of one variety, relatively to that of another variety of the same species is so differentiated with respect to their reciprocal stigmatic relations that the grade of fertility of the pure unions of these varieties does not at all correspond with that of the cross unions. For example, in the pure unions of varieties *lutea* and *alba* of *V. blattaria*, the fertility of the latter exceeds that of the former in about the proportions of 12 to 11; whereas in their converse unions, *lutea* exceeds *alba* in the higher proportions of 6 to 5! Thus in the inter-crossing of varieties of a species, as in the inter-crossing of varieties of distinct species, there are converse variabilities in the reciprocal sexual powers of their respective elements.

As the facts stand then, it appears to me that in the first crosses of the varieties of certain species, as in the first hybrid crosses of distinct species, a variable degree of sterilisation results, and again, that the relative sterilising influence is as highly intensified in the crossing of undoubted varieties of certain species, as it is in the hybridising of several undoubtedly distinct species. There is also a parallelism between the results of reciprocal hybridisation of varieties of distinct species, on the one hand with those of the reciprocal inter-crossing of varieties of a single species on the other. The sole difference in the two lines at least is merely as to the degree of extension; species relative to species occupying a higher point in the divergingly extended line, than do the varieties of a species relatively to each other, and accordingly yielding in general more intensified results, harmoniously testifying to the truth of Mr. Darwin's remark that sterility is simply a superinduced quality due to incidental differences in the reproductive system....As in the varieties of a species, however, we find that the relative amount of physiological divergence,—as judged by the fertility of their reciprocal conjunctions,—is by no means regularly or definitely co-ordinated with their morphological; so in the hybridisation of the different species of a genus, the most distinct morphologically are often found to be most nearly allied in their physiological characteristics, and thus there being no necessary co-ordination of these characteristics we can readily understand how the sterility of the first crosses of varieties of a species may, and occasionally does, exceed that of well-marked and undoubtedly distinct species.