

INHERITANCE OF THE THREE FORMS
IN TRIMORPHIC SPECIES.

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IN 1913 (*Journ. Gen.* Vol. III, No. 1) I published the first results of experiments on the inheritance of the three forms in the heterostyled species *Oxalis valdiviana* and *Lythrum salicaria*. I hoped to be able to carry the enquiry to a definite conclusion, for the inheritance of the three distinct forms which go to make a single heterostyled trimorphic species, seemed particularly amenable to a simple Mendelian solution. Moreover within one such species occur unique phenomena of partial and complete self-sterility and inter-sterility, the appearance of a high proportion of bad pollen grains and bad seed in certain cases:—I had hoped to make clear the connection of these phenomena with the main problem of the inheritance of the three forms. Since 1913, however, the work has been carried on intermittently. The present paper records such numbers as have been obtained, with a discussion of a schematic explanation of the results.

Dimorphic plants are recorded in several Natural Orders: Boraginaceae, Cordiaceae, Erythroxylideae, Gentianeae, Hypericineae, Linaceae, Oleaceae, Polemoniaceae, Polygonaceae, Primulaceae, Rubiaceae, Thymeliae, Verbenaceae.

Trimorphic species are only found in Geraniaceae, Lythraceae and Pontederiaceae [4], as far as I know. It may be as well to state briefly the physiological peculiarities of these plants, and to recapitulate the established facts with regard to their genetic behaviour.

In dimorphic species, there is one pollen tier to each form, agreeing approximately with the length of the style in the opposite form. But the degree of variability in length of the male and female sexual organs is far greater than was originally supposed, as Tischler has shown [8], thus weakening the case of those to whom the theory of adaptation was sufficient.

Not only are the stamens of the two forms distinguished by their length or place of insertion in the corolla tube, but also by the actual size of the contained pollen grains, those belonging to the long stamens

and Short-styled plant being in practically all cases larger than those from the short stamens of Long-styled plants [4, p. 249].

In trimorphic species, each of the three forms has two distinct pollen types, borne on stamens of different heights. The pollen differs in size according to the stamen length, and as in dimorphic plants, the long pollen is the largest.

Mr Rowbotham kindly made some measurements for me of the relative sizes of the pollen grains in *L. salicaria*. His results were in agreement with those of H. Müller, quoted in *Forms of Flowers*, p. 143. The long pollen of both forms is larger than the Mid, and the Mid is larger than the short pollen. He found the greatest divergence between the long pollen of the Short-styled, and the short pollen of the Long-styled plants, the ratio being 100:56·6.

He also made a few observations on the presence of bad pollen grains. In one large family of illegitimate offspring ($M \text{♀} \times \text{own pollen}$), some individuals had normal good pollen, whilst others had a large percentage of bad grains, and grains irregular in size. In another Mid of this family ($1^6/18$) he found the long pollen irregular, whilst the short pollen was normal in size and regular. Clearly segregation of some sort has taken place connected with the sterility problem. Unfortunately these promising indications have not so far been followed up. A further example of segregation is given by Darwin [5]. From an illegitimate union of Mid $\text{♀} \times$ Short ♂ of Long-style, 17 *L* and 8 *M* were raised. Five of these were observed for fertility, and two proved "moderately sterile, and three fully fertile." Not one of this family was dwarfed.

There is a further visible difference in *L. salicaria* in the colour of two of the pollen types from the four others. Long pollen is of a varying intensity of green, whilst Mid and Short pollen is pure yellow. Exceptions have been observed to this colour differentiation.

One other point may be mentioned here, as I have never seen any reference to it. The different tiers of stamens are borne by separate whorls; the inner whorl is always the longer. It therefore follows, that though long stamens are always carried by the inner whorl, and short stamens by the outer whorl, mid-length stamens are on whorls of different origin in the two forms; the Mid stamens of a Short-styled plant are on the outer whorl, and the Mid stamens of the Long-styled plant are on the inner whorl.

So much for outward differences. For factorial differences, neither the evidence of others nor my own, has ever shown that there has been any segregation of the characters for Long, Short or Mid-style in the

two pollen types of one plant, as might easily have been anticipated. But there has been segregation of another sort; the two ♂'s of one plant differ in their compatibility with the same ♀. Thus the mid-pollen of a Long-style sets a full complement of seed on Mid-style ovules, whereas the short pollen of the same Long-style plant, will set few, or more probably none. At some period in cell-division the two tiers of pollen have become differentiated; though of the nature of this differentiation we have no clear conception as yet. In this connection Stevens's work on the growth of pollen tubes in heterostyled plants is of interest [9]. After legitimate pollination in *Lythrum salicaria*, she found in 18 hours regularly a three-celled embryo, with at least three nuclear divisions in the endosperm. The result was the same in each form, in spite of the difference in the distance travelled by the pollen tubes. After illegitimate pollination very little growth of the pollen tube had been made in 24 hours. After three days in a very few cases, the tube had extended almost to the egg. In a few flowers, investigated 96 hours after pollination, an 8- or 16-celled embryo was found.

The pollen tube presumably draws its nourishment from the tissues of the style, and it is conceivable that development is only possible in pollen and styles of the same height owing to the formation of compatible chemical substances, as suggested by Jost. If the question of self-sterility could be attributed solely to chemical incompatibility between the tissues of the style and the pollen tube, we might expect that in the rare cases where ♂ and ♀ unite, zygote development would proceed normally. But the higher mortality in the seed-box (compared with that seen in the germination of legitimate seed) and the stunted form of illegitimate plants, even after years of growth, show that the lethal factor, or inhibitor, has not ceased its operation at the union of the germ-cells.

The question of self-sterility is further complicated by the different degrees obtaining in the various crosses. Darwin found that legitimate fertility also varied according to the form of the mother used. In plants setting seed spontaneously he found the following relationship existed :

Form	Average seed per capsule	
	Count I	Count II
Long	93	80
Mid	130	97
Short	83	61

From artificially fertilized capsules he found the same greater fertility of the Mid-styled plant.

The following table contains the legitimate and illegitimate crosses.

TABLE I.

Explanation of lettering used. The capital letter denotes the form of parent, the small type the height of pollen. Thus

$L \times lS$ = Long-styled ♀ × Long ♂ of Short-style plant.

Cross	Number of flowers fertilized	Percentage of flowers setting seed	Average seed per capsule	Cross	Number of flowers fertilized	Percentage of flowers setting seed	Average seed per capsule
$L \times LM$	13	38	51.2	$M \times lS$	15	93	69.5
$L \times lS$	13	84	107.3	$M \times sL$	13	54	47.4
$L \times mL$	15	20	12	$M \times sM$	12	0	0
$L \times mS$	12	only 1 set	20	$S \times sL$	12	83	31.3
$L \times sL$	15	20	5	$S \times sM$	13	61	64.6
$L \times sM$	14	only 1 set	3	$S \times mL$	10	only 2 set	18
$M \times mL$	12	92	127.3	$S \times mS$	10	" "	15
$M \times mS$	12	100	108	$S \times lM$	10	0	0
$M \times lM$	12	33	75	$S \times lS$	10	0	0

Thus the Mid not only sets a much larger number of seed when legitimately fertilized than do Longs and Shorts, but also Mids illegitimately crossed with the two long pollens, and also with the short pollen of Longs, set a fair number of seed.

To summarize our incomplete knowledge of the inter-fertility and inter-sterility factors, we find:

1. The seed maximum per capsule differs in the three forms, Mids giving most, and Shorts least. This is true both in legitimate and illegitimate fertilizations.

2. In the 12 more or less sterile illegitimate combinations out of the 18 possible unions within the species, we get a series of possibilities—complete absence of zygote development; a much reduced seed formation, increasing to a fair percentage of the normal. Of the seeds so formed, germination is bad, mortality of the seedlings is great, and the plant usually does not attain normal height in growth.

3. The gamete development of the plants so raised is not normal, the pollen having a large percentage of bad grains.

4. However from one illegitimate fertilization ($M \times lM$) there was a good percentage of seed per capsule, good germination, and quite a third of the offspring were normal in size. But many showed their illegitimate origin by bad pollen—though in some the inhibitor was apparently left out.

5. Both in *Lythrum* and *Oxalis*, illegitimate offspring showed a much greater tendency to vary in the length of stamen than legitimately raised plants. I have had in *O. valdiviana* a Mid-styled plant with one l stamen practically at the level of the styles: another with a S stamen

above the level of the styles; and another with four aberrant short stamens above the mid-length styles. I did not test these stamens for their factorial significance as I had done previously [1, footnote p. 55] when I found the aberrant stamen carried the factors for its new position, and not of its companions in the same whorl.

These side issues all require further investigation. They must have an important bearing on the main theme of this paper—the inheritance of the three forms; and there for the present we must leave them. Mechanically they affect greatly the obvious tests for gametic constitution, owing to the usual impossibility of selfing, and of crosses between like forms.

Established Facts.

In 1905 Bateson and Gregory [2] showed that the two forms of *Primula* were inherited in a straight forward Mendelian manner; Long-styled forms were homozygous and recessive and the heterozygous Short was indistinguishable in appearance from the homozygous Short.

Dahlgren [3] has recently published his numbers obtained in *Fagopyrum esculentum*, bearing out completely the above interpretation. He isolated the heterozygous from the homozygous Short, the one giving Shorts only when selfed, the other giving Shorts and Longs.

In trimorphic species, Darwin's Long-styled plants gave only Long-styled offspring; I have self-fertilized Long-styled plants of both *Oxalis valdiviana* and *Lythrum salicaria* and have always obtained Long-styled offspring only. The Long-styled form is therefore presumably hypostatic and homozygous.

I have already shown [1] that both in *Oxalis* and in *Lythrum* the cross Long \times Short and the reciprocal, and also the cross Long \times Mid and the reciprocal, give approximate equality of parental forms. In *Oxalis* a small number of the non-parental form did occur (from .8 to 1.7 per cent.), but this may be explained by insufficiently critical methods at the outset¹.

The crosses which promised the ultimate solution of the problem were those between Mids and Shorts.

In 1921 G. v. Ubisch [10] discussed my numbers of 1913, and applies to them the following bi-factorial scheme:

$$\begin{array}{l} \text{Long} = aabb \text{ ; gametes} = ab \cdot ab, \\ \text{Mid} = aaBb \quad \text{,,} \quad = aB \cdot ab, \\ \text{Short} = Aabb \quad \text{,,} \quad = Ab \cdot ab. \end{array}$$

¹ I cannot explain Hildebrand's results [6]. He grew seed from the six legitimate unions of *O. valdiviana* and obtained all three forms from each union.

It follows that $L \times M$ will give $1L:1M$; also that $L \times S$ will give $1L:1S$. $M \times S$ will give $ab.ab, ab.Ab, aB.ab, aB.Ab$ or $1L:1M:2S$, a well-established result in *Lythrum* and *Ovalis*. One Short will be of the original constitution $Aabb$, but the second will be $AaBb$, A being "grösser" than B . V. Ubisch further considers the cross $\text{Mid} \times \text{Short}$, where the new type of Short is used. $\text{Mid}(aB.ab) \times \text{Short}(AB.Ab.aB.ab)$ will give

$$1L(ab.ab):3M(1aB.aB, 2aB.ab):4S(1AB.aB, 2AB.ab, 1Ab.ab),$$

which ratio has been obtained, both in my previous numbers, and in the Tables to follow. I had arrived at a similar explanation of the results, but some obvious difficulties stood in the way, and I hoped to remove these by experiment before publishing the following results. But as the few experiments on *Ovalis* which I was able to do this year may still not remove the objections to be discussed, it seemed best to publish the present paper without further delay.

The chief obstacles to v. Ubisch's hypothesis are as follows:

1. The derived Short, of constitution $AaBb$ which will have gametes $AB.Ab.aB.ab$, when crossed with a Long ($ab.ab$), should give the ratio of $1L:1M:2S$. As already stated, $L \times S$ and $S \times L$ have always only given Longs and Shorts. It is true that the Short which on the above hypothesis should give all three forms when crossed with a Long, will be much more rarely met with than the normal type, but I cannot believe this a sufficient explanation.

A further assumption that in the derived Short $AaBb$, A and B are completely linked in gametogenesis, will remove the difficulty. No Mids should appear in the cross $AB.ab \times ab.ab$. But where now is our 1:3:4 ratio? A $\text{Mid} \times$ with the derived Short will now be represented by

$$\begin{aligned} M(aB.ab) \times S(AB.ab) \\ = 1L(ab.ab):1M(aB.ab):1S(AB.ab) + 1S(AB.aB). \end{aligned}$$

Again $1L:1M:2S$.

But we cannot have it both ways; we cannot explain the 1:3:4 ratio of $Ab.aB \times aB.ab$, which assumes the formation of gametes

$$AB.Ab.aB.ab,$$

and at the same time eliminate the difficulty that such a Short must give Mids when crossed with a Long.

2. The second difficulty applying to the simplest bi-factorial hypothesis is that an occasional $\text{Mid } aB.aB$ should be met with, giving Longs only when crossed with a Long, another result never obtained.

3. The *Oxalis* numbers of my previous paper are still unexplained.

4. The conflicting evidence of single cases given below.

Thus clearly the hypothesis requires further emendation, and until we get more experimental fact, the scheme must stand on an admittedly weak foundation.

Numbers obtained in Lythrum salicaria.

All the following families are derived from two original plants, Parent I (Short-style) and Parent II (Mid-style)

Cross I. *S* (Parent I) ♀ × *M* (Parent II) ♂ gave 32*L* : 27*M* : 73*S*,

„ II. *M* (Parent II) ♀ × *S* (Parent I) ♂ gave 25*L* : 29*M* : 66*S*.

Added together we get 57 : 56 : 139, or a near approximation to 1 : 1 : 2 (calc. = 63 : 63 : 126).

Mids from cross I were crossed back with Short Parent I.

TABLE II.

Mid ♀ × Short ♂	Gave	Long	Mids	Short
1/2 × I	„	19	23	41
1/4 × I	„	2	4	11
1/8 × I	„	26	38	62
1/9 × I	„	7	14	24
1/12 × I	„	1	5	3
1/19 × I	„	6	5	4
1/23 × I	„	5	4	10
1/24 × I	„	13	18	43
1/25 × I	„	34	27	39
<hr/>				
Short ♀ × Mid ♂				
I × 1/25	„	23*	17	41
„	„	14*	20	34
„	„	14*	14	31
„	„	2*	1	0
„	„	3*	5	10
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	Totals	56	57	116

* All crosses marked with an asterisk were made in 1918, and every precaution was taken to avoid error. Families without an asterisk cannot be considered as critical. The females of these asterisked families were emasculated, and the unused tier of pollen was removed from the bud of the male parent. This had not been considered necessary in *Oxalis valdiviana* owing to the much greater self-sterility of this plant. The germination of all 1918 seed showed great improvement over that of previous years. The method was adopted of sowing very lightly in the autumn and submitting to frost.

The grand total of Short I × offspring Mids is 169 Longs, 195 Mids, 356 Shorts (calc. 180 : 180 : 360). In other words Short I is *Aabb*, and all the Mids are *aaBb*.

The Shorts derived from cross I were crossed back with Mid-Parent II.

TABLE III.

Short ♀ × Mid ♂	Gave	Longs	Mids	Shorts
1/3 × II	„	2	32	29
1/5 × II	„	1	1	4
1/14 × II	„	0	1	3
1/18 × II	„	2	4	9
<hr/>				
Mid ♀ × Short ♂				
II × 1/1	„	15*	17	42
„	„	16*	23	45
	Totals	31	40	87
<hr/>				
II × 1/3	„	12*	29	22
„	„	8*	28	41
	Totals	20	57	63
<hr/>				
II × 1/5	„	5*	25	33
„	„	7*	35	36
	Totals	12	60	69
<hr/>				
II × 1/13	„	7*	25	37
„	„	10	20	18
„	„	7*	24	26
	Totals	24	69	81
<hr/>				
II × 1/14	„	5*	17	26
„	„	10*	24	63
„	„	11*	48	35
	Totals	26	89	124

* See footnote p. 139.

The total of Mid II crossed with derived Shorts is 118 Longs: 353 Mids: 469 Shorts. Probably however these should not all be classed together. If we take 1/1 as being a Short of constitution *Aa.bb*, and all the others as being *AaBb*, then we get:

$$\text{Mid } (aaBb) \times \text{Short } (Aabb) \text{ give } 31L:40M:87S \\ (\text{calc. } 39.5L:39.5M:79S),$$

and
give $\text{Mid } (aaBb) \times \text{Short } (AaBb) + \text{reciprocals}$
 $87L:313M:382S$ (calc. $98L:294M:392S$).

Thus of the six Shorts chosen at random from the original cross, only one was *Aabb*, and five were *AaBb*. We should expect the latter to be in the minority so that the occurrence of five in six is contrary to expectation, and rather a large deviation to be accounted for by chance.

A further point to note in Table III is in the cross $II \times 1/3$. In 1914 $1/3 \times II$ gave $2L:32M:29S$. In 1918 the reciprocal cross was made critically (see footnote) and the families raised from two separate capsules were counted separately. One gave $12L:29M:22S$, and the other gave $8L:28M:41S$. A similar discrepancy may be seen in the capsules of the cross $II \times 1/13$. Such results are discouraging, as they are unexplained by the given scheme. But as it is impossible to account for them by error, they must take a prominent position amongst the other established facts. It seems necessary to infer that some sort of patchwork distribution is going on in the plant, causing fairly wide deviation from flower to flower, and that only from the accumulation of large numbers will the proportion work out correct according to expectation.

A piece of disquieting evidence must now be considered.

Some few of the F_1 , M 's and S 's were intercrossed and the following numbers show that the simple scheme put forward by v. Uebisch will not work.

$S 1/1 \times M II$ gives (Table III) $31L:40M:87S$,
 $S 1/1 \times M 1/2$ gives $4L:11M:15S$.

If M 's are all similar then this should be $1:1:2$. But this last family is too small to cause serious anxiety. But more disquieting are the following:

$S 1/3 \times M II$ gives (Table III) $20L:57M:63S$,
 and $S 1/3 \times M 1/2$ gives $28L:30M:64S$.

Here we get the same S giving with one M the possible $1:3:4$ ratio, and with another the $1:1:2$ ratio. In fact the inference seems necessary that the M 's are different, and not in the only way to be accounted for in the scheme in its simplest form; that is as $aB ab$ and $aB aB$.

A further generation (F_2) was raised from the cross $II \times 1/3$.

		$S I \times M II$								
		32L			27M			73S		
F_1		L	M	S				L	M	S
}	19	23	44	$I \times -$	1/2	1/1	$- \times II$	31	40	87
	2	4	11	$I \times -$	1/4	1/3	$-- \times II$	22	89	92 = cross 14
	26	38	62	$I \times -$	1/8			(20	57	63 critically)
}	7	14	24	$I \times -$	1/9	1/5	$- \times II$	12	60	69
	1	5	3	$I \times -$	1/12	1/13	$- \times II$	24	69	81
	6	5	4	$I \times -$	1/19	1/14	$- \times II$	26	89	124
	5	4	10	$I \times -$	1/23	1/18	$- \times II$	2	4	9
	13	18	43	$I \times -$	1/24					
	73	61	119	$I \times -$	1/25					

The following table gives an analysis of the families derived from cross 14, or F_3 .

TABLE IV.

Parents Short ♀ × Mid ♂	Offspring			Parents Mid ♀ × Short ♂	Offspring			Reciprocals added together		
	Longs	Mids	Shorts		Longs	Mids	Shorts	Longs	Mids	Shorts
14/4 × 14/1	18	17	52	14/1 × 14/4	6*	2	5	38	33	85
—	—	—	—	—	5*	5	10			
—	—	—	—	—	9*	9	18			
14/4 × 14/2	12	12	18	14/2 × 14/4	4	3	4	16	15	22
14/4 × 14/3	5	4	15	14/3 × 14/4	25*	16	27	92	81	152
—	20*	21	23	—	27*	21	45			
—	—	—	—	—	15*	19	42			
14/5 × 14/1	5*	26	30	14/1 × 14/5	0	4	4	5	30	34
14/5 × 14/2	—	—	—	14/2 × 14/5	14	43	60	14	43	60
14/5 × 14/3	5	20	29	14/3 × 14/5	3	3	7	18	48	84
—	—	—	—	—	10*	25	48			
—	—	—	—	—	—	—	—			
14/6 × 14/1	8	7	14	14/1 × 14/6	—	—	—	26	21	42
—	12*	11	22	—	—	—	—			
—	6*	3	6	—	—	—	—			
14/6 × 14/2	—	—	—	14/2 × 14/6	5	4	11	5	4	11
14/6 × 14/3	14*	17	31	14/3 × 14/6	0	0	5	53	67	84
—	—	—	—	—	19*	20	25			
—	—	—	—	—	12*	13	15			
—	—	—	—	—	8	17	8			

* See footnote p. 139.

Clearly the Short 14/5 is differently constituted from 14/4 and 14/6. There is no evidence of any difference in the make-up of the Mids.

Factorially represented, we therefore begin by getting a very complete representation.

Short 14/4 ($Aabb$) × Mids ($aaBb$) gives

$$146L : 129M : 259S \text{ (calc. } 133.2L : 133.2M : 266.5S).$$

Short 14/4 was moreover tested with a Long-style, and gave the two parental forms only.

Short 14/4 ($Aabb$) × Long ($aabb$) gives

$$19L : 0M : 18S \text{ (calc. } 18.5L : 0M : 18.5S).$$

Turning to 14/6, some doubt begins to creep in,

$$\text{Short } 14/6 (Aabb) \times \text{Mids } (aaBb)$$

gives $84L : 97M : 137S$ (calc. $79L : 79M : 158S$).

Here is a serious lack of Shorts unaccounted for, yet we are confirmed in 14/6's constitution by the cross with a Long-style.

$$\text{Short } 14/6 (Aabb) \times \text{Long } (aabb) \text{ gave } 29L : 0M : 22S.$$

But now we must face the contradictory evidence about 14/5. Assuming that here we have a Short of constitution $AaBb$, we get:

$$\text{Short } 14/5 (AaBb) \times \text{Mids } (aaBb)$$

gives $37L : 121M : 178S$ (calc. $42L : 126M : 168S$).

This is an excellent example of 1 : 3 : 4 ratio, and it only remained to prove that a Short so constituted gave Mids when crossed with a Long, to put the factorial scheme upon an experimental basis beyond any doubts. But this same Short crossed with a Long gave $29L : 0M : 27S$. Of course if in the Short 14/5 ($AaBb$) A and B were linked, then no Longs would be expected, as explained on p. 138. But then the theoretical explanation of the 1 : 3 : 4 ratio must also fall to the ground.

This conflict of evidence is a very serious implication against the theory in its simplest form as put forward by v. Ubisch, and I see no means of reconciliation at present.

As before, it must be noted in Table IV that where several capsules resulting from the same cross were sown, considerable divergence appears in the resulting families. In the cross $14/3 \times 14/4$ the three capsules gave together

$$67L : 56M : 114S \text{ (calc. } 59.2L : 59.2M : 118.5S)$$

which we cannot doubt is the 1 : 1 : 2 ratio. But taken individually the capsules are

$$25L : 16M : 27S, \quad 27L : 21M : 45S \text{ and } 15L : 19M : 42S,$$

the first and last of which are anomalies when considered separately.

Self-fertilizations.

The evidence from self-fertilizations, and illegitimate fertilizations, is no more completely satisfying than that already given. Yet in some respects the numbers afford strong support to the theory.

TABLE V.

Parents				Year	Longs	Mids	Shorts	
$L \times m+sL$	—	8	0	0	} <i>CD</i>
$L \times \text{own } m+s$	—	48	0	0	
$M \times \text{own } l+s$	—	1	3	0	
$M \times lS$	—	14	8	18	
$M \times sL$	—	17	8	0	
$S \times \text{own } l+m$	—	1	0	8	
$S \times mL$	—	4	0	8	
<hr/>								
$M \times \text{own } l+s$	—	0	3	0	} <i>NB</i>
$S \times \text{own } l+m$	—	1	1	8	
$S \times \text{own } l+m (1/1)$	1912	1	1	2	
$S \times lS$	—	2	0	1	
$M \times \text{own } l+s (26/31)$	—	3	9	0	
$M \times \text{own } s$ (long emasculated) (26/15)	1916	1	2	3	
$M \times \text{own } l$ (26/15)	1917	28	89	0	
$M \times \text{own } l$ (s not emasculated) (26/15)	1918	16	74	1	

The preceding table gives my earlier *Lythrum* numbers, and those recorded by Darwin, together with my subsequent families.

All the numbers given by Darwin are in accordance with the scheme, assuming

$$\begin{aligned} L &= abab, \\ M &= aBab, \\ S &= Abab. \end{aligned}$$

The illegitimate unions $M \times S$, $M \times L$, $S \times L$ all give offspring according to expectation for the same legitimate unions.

L selfed gives Longs only,

M selfed gives $1L : 3M$ (expectation $1L : 3M$),

S selfed gives $1L : 8S$ (expectation $1L : 3S$).

My own numbers are not so easily explained, $S \times lS$ giving $2 : 0 : 1$ could fall into the $S(Aabb)$ giving $1 : 0 : 3$; and the $S \times l + mS$ giving $1 : 1 : 8$ could be explained if $S = AaBb$. But the $S1/1$ which gave $1 : 1 : 2$ crossed with a Mid is a serious stumbling-block. For if it can give an M when selfed, we must assume it to be $AaBb$. Yet in Table II we have evidence that it is $Aabb$ when crossed back with Mid Parent II. How this conflicting evidence can be explained I do not see.

The Mid 26/31 gave $3L : 9M$ exactly according to expectation.

The Mid 26/15 gave with short pollen $1L : 2M : 3S$; with long pollen $28L : 89M$, and with long and possibly some short, $16L : 74M : 1S$. What the presence of these Shorts means, I cannot say. Apart from them, the numbers $45L : 165M$ agree fairly well with the expectation of $1 : 3$ for $aaBb$ selfed.

Oxalis valdiviana.

I cannot bring my *Oxalis* numbers published in 1913 [i. p. 59] completely into the above scheme. $L \times M$ and $L \times S$ and reciprocals gave the two parental forms, with a few of the third form, possibly errors.

Dividing the $F_3 M \times S$ and $S \times M$ up into groups, we get

$$118 L : 121 M : 270 S,$$

possibly $1 : 1 : 2$.

Also $23L : 23M : 49S$ clearly $1 : 1 : 2$.

Also $6L : 102M : 101S$, where there were no L 's in the grand-parentage. This curious result recurred in F_4 . Table VI gives a summary of the results. Reciprocals are added together. All grand-parents were M and S only.

The first result, $M \times S = 0 : 232 : 202$ can be explained in the following manner:

$$M (aB aB) \times S (Ab ab) = aB Ab, aB ab, aB Ab, aB ab \text{ or } 2M : 2S.$$

The second group of results shows a similar ratio to the third F_3 group. If the S is $AaBb$, and the gametes are $LAB:nAb:naB:lab$, we could explain such ratios. But there is nothing else to warrant the assumption of such unequal gametic segregation.

TABLE VI. *O. valdiviana* F_4 .

	Longs	Mids	Shorts
$M \times S$	0	124	113
$S \times M$	0	108	89
Totals	0	232	202
$M \times S$	2	50	87
$S \times M$	3	53	44
Totals	5	103	131
$M \times S$	51	38	80
$S \times M$	84	76	133
Totals	135	114	213
$M \times S$	27	28	58
$S \times M$	8	4	10
Totals	35	32	68

In 1913 from the third group, giving $51L:38M:80S$, a further generation (F_5) was raised giving $M19/4 \times S19/1 = 0L:21M:33S$, and the reciprocal $S19/1 \times M19/4 = 0L:47M:53S$, again good evidence of an $M \times S$ ratio giving no L 's. Note the excess of Shorts.

From the first of these crosses three Mids were selfed. The first gave a total of $10L:44M$, or giving the capsules separately:

	Longs	Mids	
	1	9	
	0	2	
	4	9	
(26/1)	1	2	
	4	15	setting seed spontaneously under cover
	0	7	" " "
	10	44	

Many of these Mids had abnormal short and long pollen, individual stamens growing at heights not in accordance to rule. The seed raised from F_5 was all lost, as it was kept until 1919 when it was found that it had lost its power of germination.

A second Mid 26/2 gave $2L:7M:4S$.

And a third Mid 26/3 gave $1L:7M:1S$.

Two of these Mids were also tested when crossed with two different Shorts.

	Longs	Mids	Shorts
$S(5/1) \times M(26/1)$ gave	0	13	12
$S(5/1) \times M(26/2)$,,	2	14	25
$S(5/2) \times M(26/1)$,,	7	12	17
$S(5/2) \times M(26/2)$,,	10	3	15

Here we get fair accordance with the belief that

$$\begin{aligned} S5/1 &= AbaB \text{ and } M26/1 = aBab, \\ S5/2 &= Abab \text{ and } M26/2 = aBab. \end{aligned}$$

But there is another piece of conflicting evidence. For *M*26/2 selfed gave 4 Shorts, where none were anticipated, and this recurrence of Shorts in the selfed Mid families is too frequent to be accounted for by error.

I also got irrefutable evidence that *M*'s can differ in constitution in a manner unexplained by the scheme. Four different Mids with the same Short gave (reciprocals added together): 0:58:59, 0:34:28, 8:8:8, and 10:17:29. These same four Mids, all crossed with another Short, gave in the same order 0:57:44, 0:83:71, 127:106:205 and 25:15:39. The two first Mids must of necessity differ from the two last.

The final conclusion of this paper must be the unsatisfactory one that the only scheme so far suggested by no means fits all the facts. That Long = *aabb*, Mid = *aaBb*, and Short = *Aabb*—so promisingly simple at the outset—cannot possibly be the whole of the story, as observed phenomena have testified again and again. Nor will a substituted scheme, taking *L*, *M* and *S* as Multiple Allelomorphs, take us any further, that we can see.

The above work was carried out at the John Innes Institution, and I should like to take this opportunity of expressing my thanks for all the facilities that have been afforded me. I should like to thank Miss Irma Andersson for her help in 1919; also the members of the Staff who have recorded families and collected seed for me when I could not be present.

Whilst this was going through the Press, a further paper has appeared by v. Ubisch (*Zts. f. Bot.* xv.), which I cannot discuss here. Our main difficulties are unaltered.

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