

On some Variations in the Number of Stamens and Carpels. By
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[Read 17th January, 1895.]

THE capability of varying is admittedly a general property of all living organisms; but of how variation is affected by forces other than natural selection we know but little. In beginning this series of observations, commenced at the suggestion of Mr. J. C. Willis, I have had in view principally the object of ascertaining why stamens and carpels are often reduced in number. The literature bearing on this subject is much scattered, and principally turns upon the question of unfavourable conditions causing the total—not partial—disappearance of the andrœcium or gynœcium. To what degree do we understand how conditions affect the sexual organs in the individual, not the race? The elaborate experiments of H. Hoffmann¹, F. Heyer², C. Fisch³, and Düsing⁴ on the sex of the Hemp, and of Heyer⁵ on *Mercurialis annua*, have shown that here, for any variety, the proportion of male to female plants is the same under all conditions. Clos⁶, too, says that dwarfing does not affect the sex of the plant; in other words, the sex is, as Heyer says, present in the seed. But, on the other hand, Forsberg⁷ finds that the sex of the Juniper is influenced by the nature of the place in which it grows—the more inclement the spot, the greater the percentage of male plants. A similar result Hoffmann⁸ gets with *Spinacia*, *Lychnis*

¹ "Rückblick auf meine Variations-Versuche von 1855–1880." Bot. Zeitung, xxxix. p. 381 (1881).

² "Das Zahlenverhältniss d. Geschlechter." Deutsche landwirt. Presse, xiii. 1886, p. 163; *vide* Just's Jahresbericht, 1886, p. 814.

³ "Ueber die Zahlenverhältnisse d. Geschlechter beim Hanf." Berichte d. deutschen bot. Gesellschaft, v. p. 136 (1887).

⁴ "Die experimentale Prüfung d. Theorie v. d. Regulierung d. Geschlechtsverhältnisses." Jenaische Zeitschrift, xix. p. 108 (1885).

⁵ "Untersuchungen ü. d. Verhältniss d. Geschlechtes bei einhäusigen u. zweihäusigen Pflanzen." Inaug. Diss. Halle, 1883. Reviewed, Bot. Centralblatt, xv. p. 5.

⁶ "Du nanisme dans le règne végétal." Mém. Acad. Toulouse, 9^{me} série, i. p. 391 (1889).

⁷ "Ueber d. Geschlechtsvertheilung bei *Juniperus communis*." Bot. Centralblatt, xxxiii. p. 91 (1888).

⁸ "Ueber Sexualität." Bot. Zeitung, 1885, xliii. p. 145.

vespertina, Sibth., *Rumex Acetosella*, Linn., &c. Meehan⁹ observes that severe competition causes in *Ambrosia artemisifolia*, Linn., the proportion of male plants to be increased. Such observations, paralleled by those of Prantl, Borodin and Magnus on starved prothalli, and of Klein on *Volvox*, show that in many cases the sex in dioecious plants is influenced by external conditions.

Again, when, as abnormalities, female or hermaphrodite flowers appear on male or female plants, these generally occupy definite positions, showing that some influence is at work. Thus in *Salices* they are usually confined to the upper or the lower extremity of the catkin; and in the Hazel (*Corylus Avellana*, Linn.), when hermaphrodite flowers appear on the female catkin, or female flowers on the male catkin, they are at the base¹⁰. Many similar cases might be given, showing that in abnormal cases of monœcism in dioecious plants, as a rule, the abnormal flowers occupy a definite position, and are not scattered irregularly anywhere on the plants. In fact, the appearance of such a plant as *Typha* or *Arum*, where the male flowers are always fixed in position with regard to the female, is repeated in the abnormal cases quoted, showing that probably the position is due to definite causes, and not to spasmodic variation, such as Meehan terms "variety for mere variety's sake"¹¹.

Now passing from this to gynodioecism and gynomonœcism, we have evidence that active influences exist which, if not causing, determine in some degree the extent of them. Willis¹² has suggested that nutrition is a determining factor in the gynodioecism of *Origanum vulgare*, Linn. Warming¹³ accounts for the gynodioecism of the Caryophyllaceæ as due to the same cause. Ludwig explains it in *Erodium*¹⁴ as caused by unfavourable conditions, and as due to deficient nourishment, which in *Cerastium*

⁹ "Changes of Flowers normally of one Sex to the other." Proc. Acad. Nat. Sci. Philadelphia, 1880, p. 353.

¹⁰ For the literature relating to this, cf. Penzig, 'Pflanzen-teratologie,' Genoa, 1892-94.

¹¹ "Contributions to the Life-Histories of Plants. No. II." Proc. Acad. Nat. Sci. Philadelphia, 1888, p. 282.

¹² "On Gynodioecism in the Labiatae" (2nd paper). Proc. Camb. Phil. Soc. viii. p. 17 (1892).

¹³ "Om Caryophyllaceernes Blomster." Festskrift Bot. Foren. p. 194 (1890); *vide* Just's Jahresbericht, 1890, p. 530.

¹⁴ "Die Gynodioecie v. *Digitalis ambigua*, Murr., u. *D. purpurea*, L." Kosmos, 1885, xvi. p. 107.

perfoliatum is dependent on the time of the flowering period of the plant, and in *Hyoscyamus niger*, Linn., b. *agrestis*, Veit.¹⁵, is dependent on the position of the flower. Raunkjaer¹⁶ observes that female flowers on *Scabiosa succisa*, L., are more common in Denmark than in Württemberg.

Androdicæism and andromonæism are attributable to similar causes. Hermann Müller¹⁷ observed the abortion of the carpels in the Alps, and attributes it to insufficient nutrition.

But now coming to cases where the sexual organs of both sexes are present, but vary in number, we find very little information. Changes in the proportion of stamens to carpels have been noted in *Stratiotes* to have some relation to climate. Goethardt¹⁸ has observed in *Pavonia* that plants of warmer localities have more stamens in their flowers than those of colder places; but this characteristic exhibited a tendency to inheritance. For in seed grown at Göttingen, obtained from Breslau, Leipzig, Buda-Pest, and Palermo, the following average numbers of stamens were obtained:—25·25, 29, 30·4, and 32·1 respectively. Beyond this there are but few facts recorded; and the observations contained in this paper were commenced with a view to fill in part this gap in our knowledge. It is obvious that they have considerable bearing upon questions connected with gyno- and andro-dicæism and -monæism, and on the origin of dicæism and diclinism.

From the observations of many observers, cleistogamy is caused by the following influences:—according to Warming¹⁹, by cold (Caryophyllacææ); to J. Scott²⁰ (Acanthacææ), Michalet²¹ (*Viola*), Torrey and Gray²² (*Helianthemum*), and Hoffmann²³ (*Papaver*), by poor soil; to Eggers²⁴, by unfavourable atmospheric

¹⁵ "Weitere biologische Mittheilungen." Bot. Centralblatt, viii. p. 89 (1881).

¹⁶ "Nogle Jagttagelser over Planter med forskjelligformede Blomster." Bot. Tidsskrift, xvii. p. 238; *vide* Just's Jahresbericht, 1889, p. 554.

¹⁷ "Die Variabilität d. Alpenblumen." Kosmos, vii. p. 441 (1880).

¹⁸ "Beiträge zur Kenntniss d. Malvaceen-Androeicum." Bot. Zeitung, xlviii. p. 390 (1890).

¹⁹ *Loc. cit.*

²⁰ "Dimorphism in *Eranthemum*." Journ. of Bot. x. 1872, p. 161.

²¹ "Sur la Floraison des *Viola* de la Section *Nomimum*, de l'*Oxalis acetosella* et du *Linaria spuria*." Bull. Soc. Bot. de France, vii. 1860, p. 465.

²² A Flora of North America, vol. i. p. 151. New York, 1838-40.

²³ "Culturversuche ü. Variation." Bot. Zeitung; xlii. p. 226 (1884).

²⁴ "Kleistogamie einiger West-indischer Pflanzen." Bot. Centralblatt, viii. p. 57 (1881).

conditions; to Bennett²⁵ (*Stellaria*), Ludwig²⁶ and Vöchting²⁷, by want of light; to Graebner²⁸, by unsuitable relationships of light to temperature; and, according to Ludwig²⁹, in *Collomia grandiflora* it is the apical flowers which are cleistogamic. Further, there are many well-known cases in which cleistogamic flowers regularly precede or follow chasmogamic flowers on the same plant. Do such influences affect the number of sexual organs in a flower? It is very probable; for is not cleistogamy often associated with reduction in the sexual organs, and reduction in the corolla associated both with cleistogamy and with abortion of one sex in gyno- or andro-dioecism? Further experiments, it is hoped, will throw more light on this question.

STELLARIA MEDIA, Cyr.

The number of stamens in this plant is known to be very variable. A glance at Table I. will show that every possible number of perfect stamens, from 0 to 10, was found among the 5684 flowers recorded in it. Chasmogamic and cleistogamic flowers are not distinguished from each other in it.

Plants growing under different conditions were examined. The following explanations will suffice:—

(A) From a hayfield by the river Cam near Barnwell, close to Cambridge. These plants were examined weekly, through February and half of March, and afterwards as occasion permitted. They competed with the growing grass; and while this remained short, received sufficient sunlight. The locality is damp.

(B) From a garden almost adjoining the hayfield (A). There was no competition, but the locality is rather shaded. The plants were examined as in the last.

²⁵ "On the Fertilization of Winter-flowering Plants." *Nature*, i. p. 11 (1870).

²⁶ Review of Hoffmann's 'Culturversuche ü. Variation.' *Bot. Centralblatt*, xx. p. 266, footnote.

²⁷ "Ueber d. Einfluss d. Lichtes auf d. Gestalt u. Einlage d. Blüten." Pringsheim's *Jahrbuch*, 1893, xxv. p. 149.

²⁸ "Ueber gelegentliche Kleistogamie." *Verhandl. d. Bot. Vereins d. Provinz Brandenburg*, 1893, xxxv. p. 148.

²⁹ "Zur Kleistogamie u. Samenverbreitung d. Collomien." *Bot. Zeitung*, xxxvi. p. 739 (1878).

TABLE I.

Number and Percentage of Stellaria media of varying degree of completeness in Andræacium.

[illegible]

(C) From a warm sunny cinder-bed in the Cambridge Botanic Gardens (shaded after June 20th). The plants were examined almost every week throughout the whole time in which they flowered.

(D) From the Pinetum in the Cambridge Botanic Gardens. The plants grew in the dense shade of trees of *Cedrus*, *Thuja*, and *Taxus*, and received no direct sunlight. They were examined weekly almost to the end of their flowering period.

(E) and (F) From two pots grown from seed in the 'Intermediate (*i. e.* subtropical) pit' in the Cambridge Botanic Gardens. In E the soil was rich; in F it was mixed with an equal quantity of sand. The plants were examined three or four times a week during the time in which they flowered. Being under glass, they obtained slightly less sunlight than those on the cinder-bed, but received more heat. The pit is kept at an average temperature of 60°-65° during the day, and 55° at night.

(G) From gravelly ground, slightly shaded. Only two examinations were made, both in March.

(H) From damp but sunny ground on Coe Fen, Cambridge. One examination only, which was made in March.

(I) From the cinder-bed above mentioned. One examination, made in August, of the first flowers of a young growth.

(J) and (K) From two pots grown in the open. The same soil used as in E and F; K contained 50 per cent. sand, as in F. All the seed sown in these four pots (E, F, J, and K) was gathered at the same time and from the same place. The roots of these plants were able to spread more freely than those of E and F. Unfortunately an accident caused the death of the plants of both J and K, and prevented the examination of the later flowers.

(L) From the highest point of Seamer Moor, Scarborough (600 feet). The locality is sunny. A single examination made in April.

Extent of Variation.—Hermann Müller* has noted the variation in the number of stamens, remarking that the most weakly plants have the fewest stamens: he points out the frequency with which the stamens are reduced to three. A glance at Table I. shows at once the predominance of this number, no less than 41·70 per cent. of the flowers having three stamens; while

* "Weitere Beobachtungen ü. Befruchtung der Blumen durch Insekten." Verhandl. d. naturhist. Vereins d. preuss. Rheinland u. Westfalens, xxxvi. p. 228 (1879).

22·75 have four, and 20·53 per cent. have five stamens. There is no other number which is represented by so high a percentage as five. *Stellaria*, then, has a very strong tendency to be triandrous, and but very rarely (here ·12 per cent.) exhibits the ten stamens characteristic of the Caryophyllaceæ. In Table I., out of the possible total of 56,840 stamens, 21,154 (37·22 per cent.) are present, and 817 (1·44 per cent.) are represented as staminodes; therefore 61·34 per cent. of the possible number of stamens are aborted*.

Effect of Age of the Plant.—The younger the plant is, the more stamens do the flowers carry; thus in experiments E and F, which were not subject to changes of temperature, the following results were obtained:—

TABLE II.

Effect of Age of Plant on Number of Stamens aborted in the Flowers of Stellaria media.

Period.	E.		F.	
	No. of flowers.	Percentage of stamens aborted.	No. of flowers.	Percentage of stamens aborted.
April 13th to May 1st ...	80	54·5	40	51·75
May 2nd to 17th	63	62·22	27	60·0
May 18th to June 1st ...	70	63·43	19	69·47
June 2nd to 23rd	38	64·74	15	67·33

Nor is this result alone; J and K gave similar results; and A, B, C, and D all show a reduction in number of stamens towards the end of the life of the plant, but with certain irregularities.

Table IV., which gives the changes in A, B, C, and D from week to week, shows that towards the end of the life of the plant the average number of stamens draws nearer to three to a

* I cannot agree with Müller when he says that the honey-glands remain, while the stamens to which they belong abort; for from my observations I find the nectaries disappearing with the stamens. Cf. 'Fertilization of Flowers (London, 1883), p. 136.

flower, or 30 per cent. On the last occasion of my examining the plants on the cinder-beds (Aug. 7th), when those of C were showing that they certainly could not exist any longer, I took advantage of a young growth (I), 4 inches high, side by side with the old plants, to make a comparison, which gave the following result:—

TABLE III.

Effect of Age on Number of Stamens developed in the Flowers of Stellaria media.

	No. of flowers.	No. of stamens.	No. of staminodes.	Percentage of stamens present.
Very old plants.....	49	159	3	32·45
Very young plants ...	49	184	3	37·55

And so, as the ♀ organs do not change with age, the plant appears to become less ♂ (less ♀ by reduction of ♂) as it grows older.

Effect of Temperature.—Warmth, as Müller* thought possible, appears to have an effect in increasing the number of stamens; this is shown in Table I.: E and F were grown in the warmest place; and in them the flowers with three stamens (26·70 per cent.) were less numerous than those with four or five stamens (28·41 and 30·40 per cent. respectively): of the other columns, C was from a warmer place than the rest; and here the percentage of four- and five-stamened flowers is larger than in any other case, except that of E and F just quoted. In Table IV. the variation from week to week is given. From data kindly supplied to me by Mr. H. F. Newall I have endeavoured to find causes for the marked irregularity seen in it, but with no great success. The one marked Cold period (Feb. 18 to 24) *may* have had some effect, but otherwise, wet or dry, hot or cold weather seems to have passed without any definite influence.

* 'Fertilization of Flowers,' p. 135.

TABLE IV.—*Variation in the Percentage of Stamens and Staminodes developed, as observed from week to week.*

In week from	A.			B.			C.			D.		
	No. of flowers.	% of stamens.	% of staminodes.	No. of flowers.	% of stamens.	% of staminodes.	No. of flowers.	% of stamens.	% of staminodes.	No. of flowers.	% of stamens.	% of staminodes.
Feb. 4-10	44	31.13	.46	...	...	...	106	37.45	1.04	...	...	...
" 11-17	16	39.38	0	66	31.67	2.12	121	39.09	1.24	80	29.51	4.62
" 18-24	46	35.93	1.96	68	34.27	.29	124	42.26	.64	100	25.20	7.0
" 25-March 3 ..	64	39.06	.94	111	40.0	1.08	120	46.67	.33	120	31.59	1.83
March 4-10	91	35.93	.99	101	32.78	.89	113	40.97	1.68	91	30.11	2.64
" 11-17	120	37.83	2.0	82	34.27	1.10	79	41.65	1.01	83	32.17	1.69
" 18-24	...	...	...	...	...	...	137	40.44	.51	129	35.97	.23
" 25-31	...	...	...	...	...	...	108	43.24	.46	114	35.62	.26
April 1-7	...	...	...	...	...	...	109	40.09	.73	86	33.72	.35
" 8-14	...	...	...	...	...	...	74	41.35	.95	...	...	...
" 15-21	102	33.14	.20	54	40.37	.93	106	39.81	.57	...	...	...
" 22-28	...	...	...	...	...	...	...	...	...	...	...	...
" 29-May 5	...	...	...	...	...	...	60	40.50	.17	67	34.62	.75
May 6-12	...	...	...	...	...	...	...	...	...	...	...	...
" 13-19	...	...	...	...	...	...	102	39.40	.20	73	32.87	1.92
" 20-26	27	32.96	.37	78	29.61	.26	115	37.99	.18	63	34.76	.48
" 27-June 2	...	...	...	...	...	...	100	38.60	.80	...	...	...
June 3-9	...	...	...	...	...	...	...	...	...	...	...	...
" 10-16	...	...	...	...	...	...	131	37.62	.61	97	22.78	9.59
" 17-23	...	...	...	...	...	...	114	42.27	.35	119	20.16	12.02
" 24-30	...	...	...	...	...	...	97	36.46	1.03	52	29.62	.19
July 1-7	...	...	...	...	...	...	...	...	...	...	...	...
" 8-14	...	...	...	...	...	...	...	...	...	...	...	...
" 15-21	...	...	...	...	...	...	53	31.70	.321	...	...	...
" 22-28	...	...	...	...	...	...	82	40.48	.37	...	...	...
" 29-Aug. 4	...	...	...	...	...	...	...	...	...	...	...	...
Aug. 5-11	...	...	...	...	...	...	49	32.45	.61	...	...	...

flowers first produced, six had 3 stamens, and seven 4 stamens, the majority of the four-stamened flowers being on the plants in poor soil.

Staminodes.—The first question in connexion with these organs which one naturally asks is, Do the same conditions bring about contabescence (reduction of stamens to staminodes) which bring about the complete abortion of the stamens? In Table IV. is given the change from time to time observed in the percentage of stamens developed. Table VI., using the same facts, is an

TABLE VI.

Relation of Percentage of Staminodes developed in Stellaria media to Percentage of Stamens aborted.

Percentage of stamens completely aborted.	A.		B.		C.		D.		Total.	
	No. of flowers examined.	Percentage of staminodes.	No. of flowers examined.	Percentage of staminodes.	No. of flowers examined.	Percentage of staminodes.	No. of flowers examined.	Percentage of staminodes.	No. of flowers examined.	Percentage of staminodes.
52.5-55 %.....					120	.33			120	.33
55.0-57.5					538	.81			538	.81
57.5-60			165	1.03	798	.69			963	.75
60.0-62.5	200	1.50			554	.56			754	.81
62.5-65	137	1.31	82	1.10	97	1.03	373	.38	689	.74
65.0-67.5 ... }	173	.29	235	1.06	102	1.96	533	2.14	999	1.62
67.5-70							316	9.30	360	8.22
70.0-72.5			78	.26			52	.19	130	.23

attempt to express the relationship of the percentages of staminodes observed with regard to the percentages of completely aborted stamens found at the same times. Certainly, with reservation, we can say that a period of greater abortion of stamens appears to be connected with a greater production of staminodes, suggesting that the same conditions produce both the total and partial abortion of the stamens. But at both extremes the staminodes, as we might expect, regarding them as an intermediate

stage in the disappearance, are fewer in number. However, the facts to hand are insufficient to admit of any certainty.

A reduction in the number of stamens present in any individual flower does not predispose to contabescence in those remaining; for taking the figures in Table I., we find that in the 5243 flowers which contain no staminodes, the percentage of aborted stamens is 61·29 (38·71 per cent. stamens developed), while in the 443 flowers which contain staminodes this same percentage is 61·74 (19·92 stamens and 18·44 staminodes developed), *i. e.* they scarcely differ.

Further, Table I. shows us that just as the 3-stamened flowers are the most numerous, so amongst those with staminodes, flowers, where these and the stamens together make up three, are the most numerous, *i. e.* flowers with two stamens and one staminode, with one stamen and two staminodes, or with no stamens and three staminodes. Next to these in number come those where the stamens and staminodes together number four. This suggests that the staminodes are stamens of which adverse circumstances have caused the abortion (*i. e.* it is a reduction of the andrœcium beyond the average degree), and are not due to favourable circumstances calling forth an imperfect stamen in a place where otherwise nothing would have been developed: in other words, as far as *Stellaria* is concerned, contabescence and complete abortion are only forms of the same reaction differing in degree; the one is not consequential in any way of the other. Only we must remember that the more stamens are aborted, the fewer are present to be contabescent, and therefore the number of aborted and contabescent stamens cannot increase proportionally.

Position of the Stamens which most frequently abort.—In a large number of Chickweed flowers the position of the stamens was noted, and from the results we can trace two degrees in the reduction of the 10-androus flower to its present usual 3-androus condition:—

(i) Abortion of the outer ring of stamens of the obdiplostemonous flowers, *i. e.* those superposed to the petals.

(ii) Abortion of the two stamens of the inner ring which are superposed to the two outermost sepals of the quincuncially arranged calyx.

That these two degrees in the reduction of the stamens are

TABLE VII.—*Distribution in Position of Stamens developed in Flowers of Stellaria media.*

	No. of flowers.	No. of stamens.	Outer whorl.		Inner whorl.				Percentages of stamens deduced theoretically by the rules given.		
			No. of stamens of outer whorl.	X. per cent.	No. of stamens superposed to outer sepals.	Y. per cent.	No. of stamens superposed to inner sepals.	Z. per cent.	x.	y.	z.
1-androus.....	3	3					3	100·0			100·0
2 ".....	53	106			1	·94	105	99·06			100·0
3 ".....	1414	4242	1	·02	57	1·34	4184	98·64			100·0
4 ".....	688	2752	37	1·34	661	24·02	2054	74·64		25·0	75·0
5 ".....	592	2960	55	1·86	1128	33·11	1777*	60·03		40·0	60·0
6 ".....	97	582	117	20·10	173	29·73	292†	50·17	16·67	33·33	50·0
7 ".....	36	252	76‡	31·59	67	26·59	109†	41·82	28·57	28·57	42·85
8 ".....	17	136	57	41·91	28	20·59	51	37·50	37·50	25·0	37·50
9 ".....	6	54	26	48·15	10	18·52	18	33·33	44·44	22·22	33·33
10 ".....	6	60	30	50·0	12	20·0	18	30·0	50·0	20·0	30·0

* Two cases of doubling of one of the stamens (inner whorl).

† One case

‡ One

" " " (outer whorl).

correctly stated is proved by Table VII., in which the facts are summed up. In the last three columns, lettered x , y , and z , the percentages of the various stamens which should be present according to these two rules are given; while in the other columns the numbers and percentages actually found are stated. Columns X, Y, and Z correspond with the columns x , y , and z ; and it will be noticed that the discrepancy between the real percentages and those found by these two rules is in no case as great as 5 per cent. The constancy of the three stamens of the inner whorl superposed to the inner sepals is most marked, 1.03 being the greatest difference between the figures in columns Z and z . With regard to other stamens, it will be noticed that frequently the percentage of the stamens of the outer whorl is upwards of 5 per cent. greater than the theoretical figure of column x , while that of the stamens superposed to the outer sepals is the same amount too small. Then to this slight extent the stamens of the outer whorl have usurped the place which theoretically should belong to the two outer-sepaline stamens; in other words, the outer whorl does not exhibit so strong a tendency to abortion that it entirely disappears before abortion begins in the inner whorl.

It may be mentioned here that of the five cases in which a doubling of a stamen was observed, in four of these cases it occurred in the inner-sepaline stamens, once in the petaline stamens, and never in the outer-sepaline stamens.

With regard to the petaline stamens, that marked α in the accompanying woodcut is the one most frequently developed. Of the other four (β), none can be said to be much more frequent than the others.



Diagram showing position of stamens with regard to the sepals and ovary.

Petals not inserted. The stamens of the petaline whorl are indicated by the letters α and β , those of the sepaline whorl usually absent are shaded.

Changes in the Carpels.—The number of carpels entering into the ovary may be regarded as constant. Out of the 5697 flowers

examined (5684 of Table I. and 13 from second sowing in pots E and F), eight were found with 4 stigmas, and eight with 2. Besides these, two flowers were found with the ovary partly aborted and functionless. Thus we get andromonœcism as well as gynomonœcism; but perhaps we should say only as an abnormality. I have not yet found the gynodiœcism which Warming records*.

Correlations in Number of Parts.—In the eight flowers with only two stigmas, 26 stamens and a staminode were present, while in the eight flowers with four stigmas 35 stamens were present.

Other abnormalities were observed in the petals and sepals as follows †:—

TABLE VIII.

Abnormal Flowers of Stellaria media.

No. of flowers.	No. of sepals.	No. of petals.	No. of stamens.
1	6	6	4
4	6	5	4, 4, 4, and 5
1	4	4	4
2	4	5	3 and 4
1	5	6	5
1	5	2	4

Such numbers are too small to allow us to trace any correlation; but they show that abnormalities in the petals and sepals amount here to but little more than one in a thousand flowers.

It must not be thought that all the flowers, open at one time on a single branch, contain the same number of stamens; this is far from being the case; 3-, 4-, 5-, &c. stamened flowers stand side by side very frequently. The following Table (IX.), in which staminodes are counted in with the stamens, gives the number of cases in which flowers with the same and different numbers of stamens were associated together. No flowers are included which were not of the same age, or were removed from each other by several internodes.

* *Loc. cit.*

† 4-merous flowers (apetalous) are recorded as typical in Alpine Sikkim specimens. Hooker, 'Flora of British India,' i. p. 230 (London, 1875).

TABLE IX.

Number of Stamens in neighbouring Flowers of Stellaria media.

No. of stamens in one flower which was associated with :—	1	2	3	4	5	6	7	8	9	10
a 2nd flower containing 1 stamen in	0	cases.								
" " " 2 stamens	0	4								
" " " 3 "	2	20	240							
" " " 4 "	0	4	128	39						
" " " 5 "	0	1	69	81	39					
" " " 6 "	0	0	4	8	10	2				
" " " 7 "	0	0	0	2	4	1	0			
" " " 8 "	0	0	0	0	0	0	3	2		
" " " 9 "	0	0	0	1	1	0	2	1	0	
" " " 10 "	0	0	0	0	0	0	0	1	1	0

But though the Table shows that neighbouring flowers are not uniformly alike, it shows that where there is a difference, this difference is not great. Thus, two flowers with three stamens appeared side by side in 240 cases, but flowers with three and four stamens stood side by side in 128 cases; but in no instance were flowers with three stamens associated with flowers with more than six stamens. The greatest discrepancy observed was that a 4- and a 9-stamened flower in one case stood side by side. Summing up Table IX., we see that in

326 cases the neighbouring flowers were alike.

245 cases there was a difference of 1 stamen.

90 " " " 2 stamens.

7 " " " 3 "

1 case " " 4 ,

1 " " " 5 "

And so, though more often than not the neighbouring flowers were unlike, still there is a considerable tendency towards uniformity.

CALTHA PALUSTRIS, Linn.

Hoffmann * has pointed out that with the advancing season the flowers of *Papaver Rhœas*, L., on any given plant become smaller, the latest flowers being the smallest of all. Such is noticeably the case in *Caltha palustris* also: the terminal flower of a branch is always the largest; and, further than this, Table X. (p. 234) shows that it contains more stamens and carpels than the other flowers of the same stem. This Table is derived from the study of 102 flowers from the clay cliffs of Cayton Bay, near Scarborough. In it the first two figures of each line express the sums of the stamens and carpels (or their average) for the whole of the flowers of that rank. The terminal flower of a branch carrying five flowers is richer in stamens and carpels than the terminal flower where fewer flowers are present. And therefore the average obtained for the terminal flowers will depend largely upon how many weak and how many strong branches have been examined. To avoid error from this source, in Table X. the statistics of the total of stamens and carpels for the flowers of any rank are arranged according to the number of flowers borne by the inflorescence. Thus out of the 36 branches examined, three carried only a single terminal flower; and for these three flowers the number of stamens averaged 80·67, or considerably below the average of the terminal flowers where the inflorescence bore four or five flowers. And for this reason Table X. is so arranged that by glancing up the column one can see how the average number of stamens increases in flowers produced earlier on the same stems. It shows, then, that the oldest flowers carry the most stamens and carpels, and that the strongest branches, *i. e.* those which produce most flowers, have in these flowers more stamens and carpels than the flowers in corresponding positions on weaker stems.

RANUNCULUS ARVENSIS, Linn.

A number of plants gathered at Sawbridgeworth (Essex), and examined on May 31st, gave results showing that, as in *Caltha*, the first flower carries more stamens than the later flowers; the number of carpels varied irregularly. Owing to the very

* 'Rückblick auf meine Variations-Versuche,' *loc. cit.* p. 366.

TABLE X.—*Number of Stamens and Carpels in Flowers of Caltha palustris according to Strength of Branch.*

Branch	1-flowered.		2-flowered.		3-flowered.		4-flowered.		5-flowered.		7-flowered.		8-flowered.		9-flowered.		Ratio of stamens to 1 carpel.	
	Stamens.	Carpels.	Stamens.	Carpels.	Stamens.	Carpels.	Stamens.	Carpels.	Stamens.	Carpels.	Stamens.	Carpels.	Stamens.	Carpels.	Stamens.	Carpels.		
Terminal flower	242	14	825	76	486	42	1415	122	201	17	98	6	105	8	103	9	12.04	
Average	80.67	4.67	81.67	8.44	81.5	7.0	109.1	9.4	100.5	8.5	98.0	6.0	105.0	8.0	103.0	9.0		
1st lateral flower			784	58	541	46	1293	98	169	9	88	6	103	10	95	6	13.78	
Average			86.0	6.44	90.17	7.69	99.46	7.54	84.5	4.5	88.0	6.0	103.0	10.0	95.0	6.0		
2nd lateral flower					425	32	1123	94	167	14	85	7	108	9	100	10	12.10	
Average					85.0	6.4	93.6	7.53	83.5	7.0	85.0	6.0	108.0	9.0	100.0	10.0		
3rd lateral flower							129	6	155	11	85	6	111	8	93	8	14.77	
Average							64.5	3.0	77.5	5.5	85.0	6.0	111.0	8.0	93.0	8.0		
4th lateral flower									76	3					76	5	19.0	
Average									76.0	3.0					76.0	5.0		
1st branch of 1st lateral					68	6	980	77	64	4	85	4	106	8	88	7	13.10	
Average					68.0	6.0	81.67	6.42	64.0	4.0	85.0	4.0	106.0	8.0	86.0	7.0		
2nd branch of 1st lateral											74	4	106	7	84	7	14.67	
Average											74.0	4.0	106.0	7.0	84.0	7.0		
1st branch of 2nd lateral											69	4	96	7	80	8	12.89	
Average											69.0	4.0	96.0	7.0	80.0	8.0		
1st branch of 4th rank															71	6	11.82	
1 extra 1st lateral bud																	11.20	
Total.....																11,453 stamens..... 891 carpels.		12.85

fugaceous nature of the stamens, these were not counted in thirteen flowers in which the carpels were examined.

TABLE XI.

Number of Stamens and Carpels in Flowers of Ranunculus arvensis according to Position on Branch.

	No. of flowers.	Average no. of stamens.	No. of flowers.	Average no. of carpels.
Terminal flowers	12	15.6	23	6.04
1st lateral flowers.....	22	13.18	23	6.04
2nd „ „	20	14.0	21	6.29
3rd „ „	5	12.2	5	5.6
1st branch of 1st lateral ...	14	12.93	14	6.21
2nd „ „ „ ...	7	13.14	7	7.0
1st „ 2nd „ „ ...	9	13.33	9	6.44
2nd „ „ „ ...	2	12.5	2	6.0
Total	91		104	
Average		13.78		6.19

RANUNCULUS BULBOSUS, L.

Here, as in the last, the terminal flowers have more stamens than the lateral ones : Table XII. shows this. The plants examined were obtained from Chesterton, near Cambridge, on April 13th.

The long summer of 1893 caused this plant to begin a second flowering late in October of that year ; and, as a consequence of this, I obtained from the locality above mentioned, between January 29th and February 26th, 1894, twenty-four flowers. These flowers, developed in a very much colder period than the spring flowers, had much fewer stamens and carpels.

TABLE XII.

Number of Stamens and Carpels in Flowers of Ranunculus bulbosus.

	Average number		Ratio of stamens to 1 carpel.
	of stamens.	of carpels.	
Spring flowers. Terminal	64.0	35.89	1.78
„ „ Lateral	54.9	32.0	1.72
Winter flowers	42.17	21.08	2.0

From very poor soil at Watton, in Norfolk, I gathered in May a number of terminal flowers to see if the smallest flowers borne by dwarf plants had fewest stamens and carpels. Such in part seemed to be the case. Amongst the smallest flowers I obtained one in which all the stamens, fifty-two in number, were reduced to staminodes*.

RANUNCULUS FICARIA, Linn.

Effect of Time of Flowering on the Number of Stamens and Carpels.—As in the former case of *Stellaria media*, so here the later flowers borne by the plant have fewer stamens and carpels than the earlier flowers.

TABLE XIII.

Reduction in Number of Stamens and Carpels in later Flowers of Ranunculus Ficaria.

Locality.	Date.	No. of flowers.	Average				Ratio of stamens to 1 carpel.
			No. of sepals.	No. of petals.	No. of stamens.	No. of carpels.	
Cambridge, under trees.....	March 3rd	32	3.08	7.56	22.87	13.41	1.70
	April 16th	75	3.25	8.0	19.49	11.95	1.63
Cayton Bay, top of cliffs, open field.	March 31st	100	3.03	8.52	38.24	32.32	1.18
	May 4th	43	3.05	8.35	30.67	25.72	1.19
Cayton Bay, thin wood on cliffs ...	March 31st	56	3.05	8.68	37.96	35.41	1.07
	May 4th	12	3.0	8.42	30.0	25.92	1.16

Müller † states that in this plant and *Ranunculus Auricomus* the number of petals increases with the season.

Effect of Conditions.—A large number of flowers were examined besides those given in Table XIII., in order to see if different conditions affected the number of parts in the flowers. The results are contained in Table XIV.

* Whitelegge, "Gynodioecious Plants," Nature, xviii. p. 588 (1878), records female flowers of *Ranunculus bulbosus* as having the petals reduced in size.

† 'Fertilization of Flowers,' p. 73.

TABLE XIV.

*Number of Stamens and Carpels in Flowers of
Ranunculus Ficaria.*

Locality.	Date.	No. of flowers.	Average				Ratio of stamens to 1 carpel.
			No. of sepals.	No. of petals.	No. of stamens.	No. of carpels.	
<i>Under trees, poor soil.</i>							
Beresford Dale, } Staffordshire. }	March 26th	75	3.75	7.36	22.52	19.14	1.18
Forge Valley, } Scarborough. }	April 9th	67	3.01	8.45	27.24	18.15	1.50
<i>Sunny banks facing south.</i>							
Ashbourne	Mar. 21 & 22	84	3.13	8.42	30.42	17.59	1.73
Ravine, Filey ...	April 5th	28	3.03	8.25	34.36	20.25	1.69
<i>Slopes facing east.</i>							
Cliffs, Scarborough.	Mar. 29 & 30	64	3.13	8.52	38.03	32.89	1.16
Cliffs, Cayton Bay } (base)	March 31st	45	3.07	8.82	41.44	34.20	1.21
<i>Open field.</i>							
Top of Castle Hill, } Scarborough. }	April 4th	20	3.0	8.70	34.30	28.65	1.19
Coe Fen, Cambridge.	April 16th	86	3.02	8.07	30.67	20.55	1.49

That conditions do affect the number of parts seems certain ; but it is difficult to say what the conditions are. The flowers gathered from the somewhat inhospitable mountain limestone of Beresford Dale, near Hartington, are those in which the number of stamens is lowest. The flowers gathered in various spots from the boulder-clay near Scarborough, *i. e.* Cayton Bay (3), Castle Hill and cliffs, all show a large number both of stamens and carpels, and the ratio of stamens to carpels varies but little. On the contrary, the proportion of stamens to carpels is much higher in plants from Forge Valley, Ashbourne, and Cambridge. The Filey plants were from boulder-clay, but do not agree with the other boulder-clay plants,—perhaps because of the steepness of the bank on which they grew. The plants from Coe Fen, grown under similar conditions to those from the top of the cliffs at Cayton and on the Castle Hill at Scarborough, *i. e.* amongst grass, instead of resembling these, resemble those

from under trees in Cambridge. Such being the case, it appears as if the soil might influence the proportion of stamens to carpels, if not also the number of these.

Correlations.—The foregoing Tables show that there is a proportion between stamens and carpels, probably constant under the same conditions, and at any rate unaffected by the decrease in number of parts which occurs as the flowering period passes over (*cf.* Table XIII.). But beyond this the number of stamens and carpels possesses a definite relation to the number of petals, most decidedly shown throughout the flowers which I examined*. The following will serve as instances :—

TABLE XV.

*Correlation in increase in number of Petals, Stamens, and
Carpels in Flowers of Ranunculus Ficaria.*

Flowers with 3 sepals.	Cambridge No. 1.			Ashbourne.			Cayton Cliffs, Top, No.1.		
	No. of flowers.	Average of stamens.	Average of carpels.	No. of flowers.	Average of stamens.	Average of carpels.	No. of flowers.	Average of stamens.	Average of carpels.
7 petals...	11	22.54	12.91	1	23.0	16.0	4	37.0	39.0
8 „ ...	18	23.55	13.88	53	30.45	16.77	60	36.73	31.33
9 „ ...	0			19	31.05	18.21	19	40.26	36.68
10 „ ...	0			4	34.0	22.0	13	42.54	42.23

But with regard to the sepals there is no such correlation. In the flowers obtained from Beresford Dale there was a considerable number with more sepals than three, the petals usually being reduced in number corresponding with the increase in number of the sepals. Table XVI. shows this.

* H. Müller has given for *Myosurus minimus*, 'Nature,' xxvi. p. 81, 1882 (and x. p. 129, 1874), the results of the examination of approximately 400 flowers. His figures show, but not very distinctly, some correlation between the numbers of petals and stamens; and he remarks that the greater number of organs was accompanied by greater size of the flower.

TABLE XVI.

*Want of Correlation in increase between Sepals and Stamens and
Petals and Carpels in Ranunculus Ficaria.*

No. of flowers.	No. of sepals.	No. of petals.	Average no. of stamens.	Average no. of carpels.
20	3	8	22.75	17.6
14	4	7	20.36	18.43
8	5	6	17.0	19.12

Then while the number of stamens proved to decrease with the number of petals, the number of carpels increased. Such a result is curious, and a natural supposition would be that some very abnormal flowers had interfered with the correct results. But this is not the case; and, further, the results of the examination of flowers from other places all show that the more sepals are present, the more nearly equal are the numbers of the stamens and carpels.

THALICTRUM FLAVUM, Linn.

Effect of Position of Flower on Number of Carpels.—In this plant the stamens are too fugaceous to yield reliable results. Nearly all the flowers of the inflorescence mature at the same time; but their position determines, to a great extent, the number of carpels. In the axil of each bract usually arise two branches, the lower of which generally bears a single flower, while the upper may branch and carry three or more flowers (as at

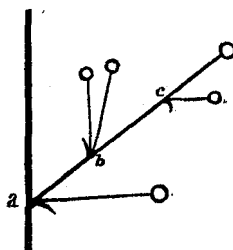


Diagram showing common arrangement of flowers in *Thalicttrum*.

a in the diagram). This upper branch is usually the strongest. Often only one branch is present (as at *c* in the diagram). When

two branches are present each with only one flower (*b* in the diagram), the lower shows itself stronger in producing more carpels: when the inflorescence is more vigorous, the upper branch and not the lower takes the lead, producing 2 to many flowers; but these, as a rule, carry fewer carpels than the terminal flower of the lower branch.

TABLE XVII.

Number of Carpels in Flowers of Thalicttrum flavum according to Position on Branch.

	No. of cases.	Average no. of carpels in terminal flower of lower branch.	Average no. of carpels in terminal flower of upper branch.	Average no. of carpels in lateral flowers of upper branch.
One branch only developed (<i>c</i>)	30	8.8		
Upper branch unbranched (<i>b</i>).....	44	9.86	8.02	
„ „ 2-flowered	4	10.75	9.0	8.25
„ „ 3 „	6	10.33	6.5	8.67
„ „ 4 „ (<i>a</i>)	1	11.0	8.0	7.67
„ „ 5 „	4	10.0	8.0	9.75
„ „ 6 „	1	9.0	Aborted.	8.0
„ „ 9 „	2	11.5	7.5	10.0

This Table shows that the more vigorous (in number of flowers) the upper branch, the more carpels does the lower branch bear; and so the number of carpels is affected by the strength of the axil from which arise the flowers containing them. The lower branch does not itself branch so readily as the upper. When this upper branch carries many flowers, the terminal flower carries fewer carpels than the lateral flowers.

In plants which have usually three branches in the axil instead of two, as is sometimes the case, the results are similar. The plants examined were gathered in Waterbeach Fen, near Cambridge, in July.

BOCCONIA CORDATA, Willd.

The number of stamens in a flower depends on the strength of the branch which bears it; and consequently there is a definite relation between the number of flowers and the number of stamens; thus the flowers of branches of secondary rank, bearing five flowers, carry more stamens than those on branches bearing three.

TABLE XVIII.

Number of Stamens in Flowers of Bocconia cordata according to Vigour of Branch.

	Average number of stamens in flowers of	
	Branches bearing 5 flowers.	Branches bearing 3 flowers.
Terminal	33	30
Lowest lateral	26·2	26·83
2nd „	27·4	24·29
3rd „	25·4	
4th „	25·2	

If we arrange the flowers according to rank, we see that the branches of higher order carry fewer stamens, thus:—

TABLE XIX.

Number of Stamens in Flowers of Bocconia cordata according to Position on Branch.

				Average no. of stamens.
2 flowers terminating branches of primary rank				33·0
20 „ „ „ secondary „				30·1
35 „ „ „ tertiary „				26·0

In order to avoid error by stamens falling off, the flowers were examined when the buds had not yet opened.

PRUNUS PADUS, *Linn.*

In this plant the number of stamens varied from 26 to 34. The lower flowers of the inflorescence are the first to mature, and usually carry the supernumerary stamens. Thus in 199 flowers on eight inflorescences, the lowermost 103 flowers had the average of 30·62 stamens to a flower, while the upper 96 flowers had the average of 30·46—*i. e.* 16 more stamens per 100 flowers in the lower than in the upper part of the inflorescence.

PRUNUS LAURO-CERASUS, *Linn.*

In this case the flowers of the inflorescence mature from above downwards, being just the reverse of *Prunus Padus*; and so the upper, older flowers possess the most stamens.

54 lower flowers carried 991 stamens—average 18·35.

54 upper „ „ 1064 „ „ 19·70.

CRATEGUS OXYACANTHA, *Linn.*

In this plant we have a cyme, and here the terminal flower usually carried the most stamens, the others following in ascending order. Two examinations of Hawthorn-flowers were made, one having large (A), the other small flowers (B); both were from the neighbourhood of Cambridge.

TABLE XX.

Number of Stamens in the Flower of Cratægus Oxyacantha according to Position on Axis.

	A. No. of stamens.	Average.	B. No. of stamens.	Average.
Terminal flowers	336	18·5	208	14·9
1st lateral „	239	18·4	111	13·9
2nd „ „	334	18·4	111	13·9
3rd „ „	365	18·2	185	14·3
4th „ „	270	18·0	166	13·8
5th „ „	124	17·7	95	13·6
Branches of higher order...	92	18·5	70	17·5

ROSA CANINA, *Linn.*

This follows the rule that the terminal flowers carry more stamens and carpels than the lateral flowers.

TABLE XXI.

Number of Stamens and Carpels in Flowers of Rosa canina according to Position on Axis.

8 inflorescences.	Average no. of stamens.	Average no. of carpels.	Ratio of stamens to 1 carpel.
Terminal	82.0	26.87	3.05
1st lateral	69.62	20.25	3.44
2nd „	67.86	20.0	3.39

The terminal flowers *uniformly* carried more stamens and carpels than the lateral flowers.

QUERCUS ILEX, *Linn.*

In the male catkins the basal flowers carry more stamens than the upper flowers: thus, in eight catkins—

141 basal flowers carried 849 stamens—average 6.02.

141 apical „ „ 682 „ „ 4.84.

By basal flowers those uppermost in the pendulous catkins are implied.

SAGITTARIA MONTEVIDENSIS, *Cham.*

In the male flowers the lowest carry more stamens than the uppermost, as shown in Table XXII. (p. 244).

ALISMA RANUNCULOIDES, *Linn.*

In plants from Dernford Fen, near Cambridge, in all the inflorescences examined, the oldest carried more carpels than the youngest.

TABLE XXII.

*Number of Stamens in Flowers of Sagittaria montevidensis
according to Position on Axis.*

	No. of flowers.	No. of stamens.	Average no. of stamens in a flower.
Lowest whorl	5	192	38·4
2nd " 	6	193	32·17
3rd " 	7	209	29·86
4th " 	9	277	30·78
5th " 	6	186	31·0
6th " 	5	151	30·17
7th " 	5	143	28·6
8th " 	5	137	27·4
9th " 	5	135	27·0
10th " 	4	114	28·5
11th " 	4	108	27·0

SUMMARY.

In this paper are given the results of the examination of nearly 5700 flowers of *Stellaria media*, Cyr., of upwards of 800 flowers of *Ranunculus Ficaria*, Linn., and of smaller numbers of several other plants, i. e.:—*Caltha palustris*, Linn. (102), *Ranunculus arvensis*, Linn. (104), *R. bulbosus*, Linn. (66), *Thalictrum flavum*, Linn. (242), *Bocconia cordata*, Willd. (57), *Prunus Padus*, Linn. (199), *P. Lauro-Cerasus*, Linn. (108), *Cratægus Oxyacantha*, Linn. (227), *Rosa canina*, Linn. (24), *Quercus Ilex*, Linn. (282), and *Sagittaria montevidensis*, Cham. (60)—numbers in themselves absolutely insufficient to establish any fact other than that the plants do vary; but yet worthy of consideration, inasmuch as they support the main contention of this paper, that *the position of the flower on the axis affects the sexual organs, if they vary*. We have seen how the earlier-formed flowers on the plant carry more stamens or more carpels, or perhaps more

of both organs, than those formed later in the season; and, again, we see that the flowers formed earliest, or holding any position of advantage on an inflorescence, *i. e.* terminal on a cyme or at the base of a raceme, even if not maturing earliest, *e. g.* *Thalictrum*, carry more stamens or carpels, or more of both, than the other flowers of the same inflorescence. *Stellaria media* and *Ranunculus Ficaria*, where the early and late flowers are separated from each other by a considerable interval of time, show the reduction in later flowers, not necessarily on the same axes as the earlier ones.

The other plants examined show how in the same inflorescence we can appreciate a reduction—now in the stamens, now in the carpels—in the later-formed flowers. What other influences act is a question too involved to answer other than conjecturally. I have suggested temperature in the case of *Stellaria* and *Ranunculus bulbosus*, but am not able to hazard any other cause with any degree of safety. What experiments follow will, I hope, throw further light upon this tangled question.

Apart from these considerations, I have been able to show that the order of abortion in the stamens of *Stellaria media* is fixed and definite; and that in several plants there exists a correlation between the numbers of petals and stamens and of stamens and carpels—a higher average number of one organ being present, there will be a corresponding increase in the other organs.

In conclusion, I desire to express my thanks to Mr. Francis Darwin for much kindly advice, and to Mr. H. F. Newall for the data of temperature and rainfall with which he supplied me. To Mr. R. I. Lynch I am indebted for many services; and, above all, my thanks are due to Mr. J. C. Willis, to whom I owe the original suggestion in regard to these investigations, and who has moreover, rendered me considerable assistance.
