

## F.—FORMS OF FLOWERS.

## CHAPTER XXIV.

(1.) *The forms of flowers in regard to sex.*

THE next book from the pen of Darwin which calls for investigation has for its full title "The different forms of flowers on plants of the same species." It has been previously shown that cross-fertilisation is more advantageous to plants than self-fertilisation. This volume is devoted to the account of still further experiments that lead to the same conclusion. Following its author we shall consider: (1.) The different forms of flowers as far as the arrangement of their sexual organs is concerned. (2.) The different cases of plants that have both sexes in the same individual blossom, each flower, therefore, possessing a gynœcium, that is female reproductive organ, and andrœcium, that is male reproductive organ. (3.) Plants in which the sexes are to a greater or less extent separated. (4.) What are known as Cleistogamic flowers, that is flowers completely closed, and therefore not admitting the possibility of insect entrance. The derivation of the word Cleistogamic is from κλεις, key, and γαμος, marriage. There will follow a few words on (5.) Personal characteristics of the writer.

(1.) *The different forms of flowers as far as the arrangement of their sexual organs is concerned.*

(a) Bisexual Plants. The majority of plants belonging to the great flowering sub-kingdom have their sexes united in the same individual flower. Such plants are known as bisexual or hermaphrodite. Five prominent types of these hermaphrodite plants present themselves.

(i.) Bisexual plants, in which the gynœcia and andrœcia are of different lengths so that the stigma of the former and the pollen-bearing stamens of the latter occupy different levels in any given flower. These plants are known by the general name of heterostyled (from ἕτερος, different). A

full account of these has already been given in the history of cross and self-fertilisation. Example: the Cowslip.

(ii.) Plants having in each individual plant two kinds of flowers, one of which ( $\alpha$ ) is quite perfect, contains male and female organs, and yet expands in the usual fashion, whilst the other ( $\beta$ ) is very minute, completely closed, and with the reproductive organs partially aborted. Yet these cleistogamic flowers are perfectly self-fertile, and evidently effect their fertilisation with the smallest possible quantity of pollen. Example: Violet.

(iii.) Plants bearing ( $\alpha$ ) conspicuous and entomophilous flowers at the same time as they also bear ( $\beta$ ) less conspicuous blossoms. The latter are not closed as in the case of the cleistogamic flowers, but are evidently a step in the direction of these. Self-fertilisation occurs with them as in the cleistogamic. Another slight difference is that in this particular case the conspicuous cross-fertilised flowers and the humbler self-fertilised occur on different plants of the same kind. I have named these heterochromous ( $\epsilon\tau\epsilon\rho\sigma$  = other,  $\chi\rho\omega\mu\omicron\varsigma$  = color). Example: Pansy.

(iv.) Plants that present at certain parts of their inflorescence or collection of flowers ( $\alpha$ ) blossoms much larger and more notable than ( $\beta$ ) the ordinary flowers. Generally speaking the attractive blossoms are upon the outside of the inflorescences. The radiating florets white in hue of the flower of the daisy are instances of the specialisation now mentioned. These I name hetero-megathic ( $\mu\epsilon\gamma\alpha\theta\omicron\varsigma$  = size).

(v.) Plants carrying ( $\alpha$ ) perfect flowers and also ( $\beta$ ) buds entirely closed and never expanding. These colored buds remind us of the cleistogamic flowers, but differ from them in two ways. They are not self-fertile and they are much larger and more noticeable. Example: Feather hyacinth. These I name hetero-gemmous ( $\gamma\epsilon\mu\omega$  = I bud).

(b) Plants presenting a greater or less separation of the sexes one from another.

(i.) Polygamous ( $\pi\omicron\lambda\upsilon\varsigma$  = many,  $\gamma\alpha\mu\omicron\varsigma$  = marriage). This term, not one of the best, is applied to plants bearing flowers some of which are perfect and some imperfect. Some flowers will have both sexes present in them, others only one sex. This term should be rigidly applied only where bisexual, male and female flowers all occur. This polygamous division falls into yet further groups.

( $\alpha$ ) Monoicous ( $\mu\omicron\nu\omicron\varsigma$  = one,  $\omicron\iota\kappa\omicron\varsigma$  = a house). If all forms are on the same plant these polygamous plants will be monoicous. The Maple is an example of a plant having bisexual, male and female, flowers all on the same plant.

( $\beta$ ) Dioicous ( $\delta\iota\varsigma$  = two). Where the three forms are found on two plants only. A satisfactory example of this at present it is difficult to name.

( $\gamma$ ) Trioicous ( $\tau\rho\iota\varsigma$  = three). If the bisexual flowers, male flowers and female flowers, are all found on different plants the name trioicous is given. The Ash is an instance of this.

(ii.) The next great division of plants when their sexual relations are under consideration is that including all those that present only two forms, that is bisexual and male or bisexual and female. These are generally called polygamous, but Charles Darwin very wisely points out that it is important to distinguish between plants bearing three kinds of flowers, as in the former case, and plants bearing only two kinds of flowers, as in the present case. Whilst he thus distinguishes the groups he does not give a name to that set of plants presenting only two distinct arrangements of the sexual organs. I venture to suggest for these the name of Diplogamic ( $\delta\iota\pi\lambda\omicron\varsigma$  = double). Two types of this two-fold sexual arrangement occur.

( $\alpha$ ) Monoicous. Where the bisexual flowers and the unisexual flowers are on the same plant. Of these two divisions will exist according as the unisexual flowers are female or male.

1. Where the unisexual flowers are female; the gynomonioicous ( $\gamma\upsilon\nu\eta$  = woman). Example: Atriplex.

2. Where the unisexual flowers are male; the andromonioicous ( $\alpha\nu\eta\rho$  = man). Example: Bedstraw.

( $\beta$ ) Dioicous. Where the bisexual flowers and the unisexual flowers are on different plants. Of these two divisions will exist according as the unisexual flowers are female or male.

1. Where the unisexual flowers are female; the gynodioicous. The Thyme is an example.

2. Where the unisexual flowers are male; the androdioicous. No cases of this have been satisfactorily determined.

(iii.) Unisexual. In this division the sexes are completely separated in all the flowers, that is each individual flower is

either wholly male or wholly female, and no bisexual flowers exist.

(a) Monoicous. The andrœcia and gynœcia are in these cases on separate flowers, but the two kinds of flowers are borne on the same plant. Example: the Birch.

(β) Dioicous. The andrœcia and gynœcia are in these cases on separate flowers. Example: the Oak. Thus any given Oak tree is wholly given up to the bearing of flowers that are either male or female. There will be observed upon it in spring-time only the long yellow tails, which children call "cat's tails" and the botanist male inflorescences, or the simpler green-colored gynœcia with their red-tipped stigmas.

This somewhat complex division of plants according to their sexual relationships will now be illustrated in a tabular form.

a. Bisexual.	{	i. Hetero-styled — styles of different lengths ... ..	}	α. Dimorphic—of two lengths ...	Cowslip.			
					β. Trimorphic—of three lengths ...	Loosestrife		
						ii. Cleistogamic—perfect and cleistogamic ... ..	Violet.	
							iii. Hetero-chromous—conspicuous and inconspicuous ... ..	Pansy.
								iv. Hetero-megathic—ordinary and larger flowers ... ..
v. Hetero-gemmous—ordinary and closed buds ... ..	Feather							
		Hyacinth.						
	b. Sexes more or less separated.	{	i. Polygamous — Bisexual, male and female ...	{	α. Monoicous—all on one plant ... ..	Maple.		
						β. Dioicous—on two different plants ... ..	.....	
							γ. Trioicous—on three plants ... ..	Ash.
ii. Diplogamic — Bisexual and male or female			{	α. Monoicous — both on one plant ... ..	{			1. Gynomonoicous—Bisexual and female on same plant ...
						2. Andromonoicous—Bisexual and male on same plant ...		
							β. Dioicous—on different plants ... ..	
				2. Androdioicous—Bisexual and male in different plants ... ..	.....			
					iii. Unisexual—all flowers unisexual ... ..	{		α. Monoicous—male and female on same plant ... ..
				β. Dioicous—male and female on different plants ... ..			Oak.	
			See Errata					

β γ

## CHAPTER XXV.

(2.) *Bisexual Plants.* (a) *Ordinary flowers.*

IN Chapters I. to VI., and also in the eighth chapter of this volume, that contains as a whole only eight chapters, bisexual plants are discussed. No little confusion seems to occur in the minds of young students in connexion with the words "unisexual" and "bisexual." Thus the young scientist is apt to think that unisexual signifies that both sexes are in one individual. The exact converse of that is really what is connoted by the word. A unisexual plant is a plant that has only one sex in each individual flower. The plants to which the largest part of this book is devoted are bisexual—that is, have two sexes in the same flower, and, indeed, this is the most customary arrangement in plants. The study of the forms of flowers met with among those bisexual members of the Vegetable Kingdom comprises the investigation of (a) Normal flowers, that are easy of observation and dissection (b) Cleistogamic flowers, difficult of observation and still more difficult of dissection.

(a) Ordinary conspicuous bisexual flowers. A very large number of the flowers that by their beauty, their odor, their secretion of nectar, and yet other marks indicate that insect agency is necessary for their fertilisation are found on careful examination to have the andrœcia or male organs and the gynœcia or female organs of varying lengths in different flowers. Thus if the common Cowslip be opened flower by flower, now selecting the flowers from one plant and now from another of the species, the stamens will be found in some low down in the corolla tube whilst the stigma of the gynœcium dwells high up within the same tube. In other specimens the conditions will be exactly reversed and the stamens will be found inserted at the top of the corolla tube whilst the short style of the gynœcium has only raised the rounded stigma a little distance

upwards from the bottom of the tube. The first flower has long style and short stamens; the second flower has short style and long stamens. To the Cowslip, and to all other plants whose individual flowers vary in the length of their styles (and of their stamens) the name heterostyled has been given. In the Cowslip there are only two lengths of styles, and two lengths of gynœcia, but in some few plants no less than three different lengths of the sexual organs are encountered. Hence a subdivision of the heterostyled into (a) Dimorphic ( $\delta\iota\varsigma$ , twice,  $\mu\omicron\rho\phi\eta$  = form) where two different lengths are met with, and (b) Trimorphic, wherein three different lengths are encountered. The account of these will be followed by discussion as to the fertility of flowers, the nature of hybrids, the distribution of heterostyled plants, the evolution of these.

(i.) Dimorphic Plants. (a) Their structure. The Cowslip shall be fully described as an example and easily obtainable type of this group of flowers. The root, the stem, the leaves, the inflorescence and calyx present no difference in the two forms of Cowslip. The flowers of the short-styled form open a little earlier than those of the long-styled. The corolla in the short-styled—and therefore the long-stamened—form has a shorter throat or expanded portion near the insertions of the stamens than has the long-styled. The pollen-grains in the short-styled have a greater diameter than those in the long-styled, in the ratio of 100 to 67. They are spherical in shape in this variety; oblong in shape in the long-styled. Of course they are placed high up in the corolla. Still pursuing the study of the short-styled form, equally of course its stigma is low down in the corolla. The stigma is somewhat flattened and not globular, and the little papillæ which render the stigma rough are shorter in the short-styled form than in the long-styled. Lastly the short-styled produces more seed than its fellows. Some of these differences seem to have a significance; to others we are at present unable to attach any meaning. Thus the greater length of throat in the corolla of the long-styled may be connected with the fact that the large and globular stigma with its length of supporting style wants especial room. Again the greater size of the pollen-grains in the short-styled flowers is intelligible, inasmuch as the pollen-grains from the anthers of the short-styled flowers have to fertilise

the ovules of the long-styled flowers. Hence when these grains are placed on the stigma they have a long journey down the long style before them; and it is well therefore that the grains whose pollen tubes have to be of greater length should be of greater size than the grains of the long-styled plant whose pollen tubes have but to traverse the short style of one of the other kinds of flower. Lastly, there would seem to be some significance in the papillæ of the long-styled stigma being of greater size. The pollen-grains coming to that stigma will need some time for the extension of their tubes down the long-style, and during that time are liable to be blown away by the wind. Entangled, however, in the long and large papillæ there is more probability of their remaining in the desired position during all the required time. I sum up the differences between the two forms in a table.

	Short-styled.	Long-styled.
<i>Flowering</i>	Earlier.	A little later.
<i>Corolla</i> ...	Throat small.	Throat expanded.
<i>Stamens</i> ...	Long.	Short.
<i>Pollen</i> ...	Grains larger, spherical.	Grains smaller, oblong.
<i>Style</i> .....	Short.	Long.
<i>Stigma</i> ...	Flattened: short papillæ.	Globular: long papillæ.
<i>Seeds</i> ...	More numerous.	Less numerous.

( $\beta$ ) Their fertilisation. Insects are essential for the fertilisation of the Cowslip, and it is manifest that four possible methods of cross-fertilisation may occur. Thus pollen from the stamens of a short-styled plant may be carried to the stigma of a short-styled plant. There would then be a cross between two similar forms of flower. This union, which has been clearly shown to be disadvantageous as compared with the alternative union, is called by Darwin illegitimate. On the other hand, pollen from the stamen of a short-styled plant may be, and is much more likely to be, carried to the stigma of a long-styled plant. I say "is much more likely," because the positions of the stamens in the first flower and the stigma in the second are identical, and hence an insect visiting the former and carrying away pollen on a particular part of its body, is likely in visiting the latter to brush off that pollen on the stigma. Such a fertilisation is called by Darwin a legitimate union. Yet, again, two

similar cases may occur with the long-styled plant. Thus the pollen from the stamens of a long-styled individual may be carried to the stigma of another long-styled plant. There would then, as in the former case, be a cross between two similar forms of flower. This union is again as disadvantageous as in the former case when compared with the alternative union, and is likewise called by Darwin an illegitimate union. On the other hand, pollen from the stamens of a long-styled plant may be, and is much more likely to be, carried to the stigma of a short-styled plant. I say "is much more likely" because, as in the former case, the positions of the stamens in the first flower and of the stigma in the second are identical; and hence, as before, an insect visiting the former and carrying away pollen on a particular part of its body is likely, in visiting the latter, to brush off that pollen on the stigma. Such a fertilisation is called by Darwin a legitimate union.

Hence, to sum up, four kinds of fertilisation are possible—two illegitimate, where the pollen from a short-styled plant goes to the stigma of short-styled, or where pollen of long-styled plant goes to stigma of long-styled; two legitimate, where pollen of short-styled goes to stigma of long-styled, or pollen of long-styled goes to stigma of short-styled.

( $\gamma$ ) Experiments. Then commence the experiments, innumerable and repeated. The reader feels a sense almost of awe at the patience, perseverance, indefatigable energy of the great experimenter. Hundreds, nay, thousands, of flowers are crossed, first in one fashion and then in another. Many thousands of seeds are counted, many hundreds are allowed to germinate. Measurements of the plants, numbering of the fruits, weighing of the seeds without end. But out of the chaos of facts systematic arrangements spring and generalisations appear. Careful calculations, careful weighing of evidence, carefully arrived at conclusions. From the multitudes of experiments on multitudes of plants, after much toil, certain large general results flow. Thus dealing for a moment only with the cowslip, experiments upon some 240 flowers reveal the momentous fact that if 100 be taken to represent the fertility of the legitimate unions, 69 only will represent the fertility of the illegitimate. These relative fertilities are measured as they were in the experiments described in a former work by counting the number of



fruits and estimating the weight of the seeds in them. Thus one hundred flowers fertilised in legitimate fashion produced 77 capsules, whose seeds weighed 39 grains. One hundred flowers fertilised in illegitimate fashion produced 45 capsules, whose seeds weighed 11 grains. And, moreover, the flowers that are legitimately fertilised have a better physique than those which are fertilised in any other fashion. "Thus, in the spring of 1862, forty flowers were fertilised at the same time in both ways. The plants were accidentally exposed in the greenhouse to too hot a sun, and a large number of umbels perished. Some, however, remained in moderately good health, and on these there were twelve flowers which had been fertilised legitimately, and eleven which had been fertilised illegitimately. The twelve legitimate unions yielded seven fine capsules, containing on an average each 57.3 good seeds; whilst the eleven illegitimate unions yielded only two capsules, of which one contained 39 seeds, but so poor that I do not suppose one would have germinated, and the other contained 17 fairly good seeds."

The advantage derived by dimorphic plants from the existence of two forms of flowers is obvious. By such an arrangement cross-fertilisation is in most cases secured; and we have elsewhere seen, and it cannot be too frequently repeated, that such cross-fertilisation is of advantage in this way. When collision occurs of a male and of a female cell, formed not only in different flowers of the same species, but in flowers differing from one another in certain minute points, such as the lengths of the sexual organs, there is greater likelihood of the resulting offspring possessing more force than would be present in an offspring resulting from the collision of two similarly circumstanced cells. And, further, with such collision of dissimilarly circumstanced reproductive structures there is greater likelihood of the variation which is so essential for all evolution.

Other species of *Primula*, as *P. elatior*, *vulgaris*, the common primrose, *Sinensis*, *auricula*, *Sikkimensis*, *cortusoides*, *involutrata*, *farinosa*, are then considered; in all nine species. And the whole genus *Primula*, as thus investigated, yields the following result, that if the fertility of the two legitimate unions, where pollen from the short or long stamen has passed to stigma of short or long style, be taken as 100, the fertility of the two illegitimate unions, if judged

by the production of fruit, is 88.4, and if judged by the average number of seeds per capsule, is 61.8. The first chapter closes with an account of a series of experiments with *Hottonia palustris*, an aquatic member of the order Primulaceæ, and of *Androsace vitaliana*. Both these plants are heterostyled, both are dimorphic, and in both cases the illegitimate unions are far more fruitful in their results than the legitimate.

(δ) Hybrids. The second chapter is devoted to a discussion as to the relationships between the Cowslip, Primrose and Oxlip, and the decision is arrived at that the Cowslip and Primrose are good and true species, that is they present sufficient differences of structure and function to be placed in separate divisions under the same genus. Here, as everywhere throughout his writings no teleological meaning is attached to the word "species," and assuredly there is no conception of the impossibility of species passing one into the other. The term is simply a convenient label for a set of organic beings possessing certain points in common. But the most interesting part of the chapter is the statement as to the marks of hybrids. It is important to understand clearly in this connexion, as in the study of the origin of species, the meaning of the term "hybrid." The great groups of organic beings called Orders in our essentially artificial methods of classification consist of similar and more numerous groups called genera. Each genus comprises still smaller and still more numerous groups called species, and species are frequently divided into varieties. Thus the order Primulaceæ contains many genera, one among which is named *Primula*. The *Primula* genus again contains many species, one of which is called *P. vulgaris* (the Primrose), and another *P. veris* (the Cowslip), and a third *P. elatior* (the Oxlip); and lastly, each of these is apt to present varieties. For instance, the *Polyanthus* is a garden variety of the Primrose (*P. vulgaris*). If a plant is produced as the result of impregnation of an ovule by pollen from a plant belonging to another genus it is called a Bigener. If a plant is produced as the result of impregnation of an ovule by pollen from a plant belonging to another species it is called a Hybrid. If a plant is produced as the result of impregnation of an ovule by pollen from a plant belonging to another variety it is called a Cross-

breed. If the pollen from one of the genus *Primula* fertilises an ovule belonging to a flower of *e.g.*, the genus *Hottonia*, a Bigener would result. If the pollen from one of the species *P. veris* fertilises an ovule from one of the species *P. vulgaris*, a Hybrid would result. If the pollen from one of the variety Primrose fertilised an ovule from one of the variety Polyanthus a Cross-breed would result.

Later on it will be seen that one of the supposed difficulties in connexion with evolution is due to the nature of hybrids. Hybrid plants are very frequently more or less sterile. This also obtains with hybrid animals. The mule, as is well known, is sterile either in the first generation or the second. In the book now under consideration much of this difficulty is placed on one side by a demonstration of the fact that plants produced within the limits of one species are frequently quite as sterile as hybrids—that is, that cross-breeds are frequently as sterile as hybrids. This important point will be dealt with later; for the present let us state the four marks that show the hybrid origin of any plant.

1. Its occurrence in localities where both parent forms exist.
2. Its character being intermediate between the characters of the two parents.
3. Its greater sterility when crossed with a similar hybrid.
4. Its greater fertility when crossed with one of the parents.

(ε) Other dimorphic Plants. Quitting the order Primulaceæ, the order Linaceæ is next studied. This order includes our own flax with its expressive if cumbersome name *Linum usitatissimum*. Charles Darwin dealt with the exquisite *Linum grandiflorum*, and also with the less beautiful *Linum perenne*. These plants, like the Primrose, are heterostyled and are dimorphic. Pursuing the same method as before, the relative fertilities of the legitimate and illegitimate unions are 100 to 7.

Then follows the narration of experiment after experiment, upon plant after plant. It will only be necessary for us to mention the names of the plants considered, and the numbers that express the results of the experiments. In

each case 100 will be taken as measure of fertility of the legitimate where calculable, and whatever other numbers are given will be the measure of the fertility of the illegitimate unions. The numbers are obtained by the two methods of comparing the number of fruits produced, and also the weights of the seeds produced. It is to be kept in mind that these relative numbers tell us whether the fertilisation of two very similar forms or the fertilisation of two slightly dissimilar forms, the one by the other, is the more advantageous for the plant.

*Pulmonaria officinalis*, 100 to 0.

*Pulmonaria angustifolia*, 100 to 35.

*Polygnum fagopyrum*, 100 to 46.

*Leucosmia Burnettiana*

*Menyanthes trifoliata*

*Limnanthemum Indicum*

*Villarsia*

*Forsythia suspensa*

*Cordia*

*Gilia pulchella*

*Gilia micrantha*

*Phlox subulata*

*Erythroxyton*

*Sethia acuminata*

*Cratoxyton formosum*

*Ægiphila elata*

*Ægiphila obdurata*

*Mitchella repens*, 100 to 20.

*Borreria*, 100 to 0.

*Faramea*

*Sutera*

*Houstonia Coerulea*

*Oldenlandia*

*Hedyotis*

*Coccocypselum*

*Lipostoma*

*Cinchona Micrantha*

The last nine of this list are all members of one botanical order, the order Rubiaceæ, best known to us through the medium of the little yellow or white bedstraw of the country hedges. It is remarkable that this order contains more heterostyled plants than any other. No less

than seventeen of the genera into which it is divided are heterostyled. In connexion with this order and with its genus, *Faramea*, a particularly interesting instance of the transition from one form to another, which the ignorant are so persistently stating is never encountered, presents itself. In *Faramea* the anthers of the stamens in the short-styled flowers rotate on their axes, and in this way the pollen is easily brushed off on to the visiting insect. But the anthers of the stamens of the long-styled form do not rotate on their axes. They open along the inner side. This latter method of dehiscence, or opening, is ordinary in the *Rubiaceæ*. The rotation on the axes of the anthers is extraordinary. The latter movement has been almost certainly acquired much later in time than the ordinary method of dehiscence. As the plant became heterostyled, and the stamens of the short-styled form increased in length, they have gradually become possessed of this beneficial property of rotating on their own axes. But careful examination of many of the short-styled flowers shows that the power of rotation is not completely acquired. Many of the stamens do not rotate fully. Some do not rotate at all. Hence a certain proportion of the pollen is rendered absolutely useless, and it would appear that the evolution of this plant in this direction has not yet reached its maximum. And this is but one haphazard illustration out of multitudes that the careful observation of to-day is constantly revealing of cases where the transition stages that were to be expected on the theory of evolution present themselves and confirm that view.

(ii.) Trimorphic. (a) Their structure. The best illustration of the plants that are not only heterostyled, *i.e.*, with different lengths of gynœcium, but also trimorphic, is the Purple Loosestrife (*Lythrum Salicaria*). If you pluck and dissect flowers of the Purple Loosestrife, you will find the following particulars common to all. A long tubular calyx; distinct, rather crumpled purple petals inserted upon the calyx near its summit; a number of stamens of varying lengths also inserted in the calyx but very much lower down than the petals; a gynœcium with free ovary, a style, and a stigma. But whilst these phenomena are common to all Loosestrifes, there are differences between the individuals. Thus, you may pluck and dissect one flower that has stamens

in two groups, a short set and a long set. When that is the case the gynœcium will be found to be of such length that the stigma is mid-way between the anthers of the short stamens and the anthers of the long. You may pluck another flower and find the stamens in it in two sets, the one set of the same length as the short ones in the first, the other of the same length as the style in the first. And in this second flower the style will be longer than any of the stamens, and the stigma carried far beyond the reach of the anthers. Yet, again, a third will be encountered in which the stamens are in two sets, the one a long set and the other of middle length, and in this flower the style will be short and the stigma far below either set of anthers. Three forms then present themselves. The short-styled, which has stamens of mid-length and of great length, the mid-styled, which has stamens of short length and of great length, and the long-styled, which has stamens of short length and of mid-length. It will be seen that the length of the style is always different from that of either of the sets of stamens, and this will mean difficulty, if not impossibility, of self-fertilisation. For the future we shall name each by the length of its style. The reader must keep in mind that giving the length of the style implies also the length of the stamens. The two sets of stamens in each case are different in length from the length of the style.

The three forms of *Lythrum* differ in yet other ways than in the lengths of their styles or of their stamens. They vary in the size of their pollen-grains, in the size of their seeds, and in the number of their seeds. Thus—representing size by numbers—

Pollen-grains from longest stamens of short-styled form,	9½	to	10½.
"    "    "    "    mid-styled	9	"	10.
"    "    mid-length stamens of long-styled	7	"	7½.
"    "    "    short-styled	7	"	7½.
"    "    shortest stamens of long-styled	6	"	6½.
"    "    "    "    mid-styled	6	"	6.

On looking at this table, it will be observed that the largest pollen-grains are found in the anthers of the longest stamens, and the smallest pollen-grains are found in the anthers of the shortest stamens. If 100 be taken as the diameter of the largest grains, 60 is that of the smallest. Again, in the size of the seeds a similar parallelism obtains.

The largest seeds are met with in the ovaries of the longest styled, and the smallest seeds in the ovaries of the shortest styled. But when we consider the number of seeds produced by individual plants, the parallelism does not continue. The numeration of the seeds in eight carefully-selected, thoroughly-developed fruits, taken from plants growing wild, gave as result the proportional numbers 93 for the long-styled, 130 for the mid-styled, 83 for the short-styled. The mid-styled are, therefore, most fertile. A fine instance of special adaptation that must have required very many years at least for evolution up to the present condition, is shown in the arrangement of the *Lythrum*. The shortest stamens, deep down within the flower, could only be touched by the proboscis and narrow chin of a bee. We find their ends upturned and their lengths varying, so that they stand, as it were, in a narrow file, sure to be touched by the narrow entering proboscis. But the anthers of the longer stamens are nearly on the same level, and at greater distances from each other. As they have to brush, not against the thin proboscis, but against the broad body of the insect, this is the most advantageous arrangement for them.

( $\beta$ ) Their fertilisation. The fertility resulting from legitimate and illegitimate unions between the three forms of *Loosestrife* was first made the subject of multitudinous experiments. A legitimate union will occur when the ovule in a gynœcium, whose style has a particular length, is fertilised by pollen from stamens of the same length as the style.

( $\gamma$ ) Experiments. Some idea of the complexity of the reproductive system of this plant, and of the laborious nature of the experiments will be formed when it is considered that no less than 18 distinct unions must be made before results can be trusted. On each stigma 6 kinds of pollen must be tried, and as there are 3 lengths of stigma that will make 18 unions. 1. The result of the experiments is that if 100 be taken as expressing the fertility of the legitimate unions 33 expresses the fertility of the illegitimate, when the decision is based upon the number of flowers which fruited. If the decision be based upon the average number of seeds in each fruit the proportions are 100 to 46. 2. A further remarkable conclusion is that the greater the difference in length between the gynœcium

whose ovule is being fertilised and the stamen whose pollen is fertilising, the greater is the sterility of the union. Thus if the ovules of the long-styled plant are fertilised first by pollen from mid-length stamens, and secondly by pollen from short-length stamens much better results follow in the former case, than in the latter. 3. And lastly the mid-style form has a much higher capacity for fertilisation than either of the others. Along with that is to be noted the fact that the stamens of the mid-style though not rudimentary are tending in that direction. This is shown by the fact that the pollen grains in the mid-styled form are less in diameter than the corresponding grains produced by the two other forms. We may regard this intermediate form of *Lythrum* as more female in nature than either of the others, and as possibly evolving in the direction of a unisexual female plant.

(δ) Other trimorphic plants. The next genus investigated is the *Oxalis* of the order Geraniaceæ, best known to English botanists by the graceful little Woodsorrel with its delicate leaves, split into three heart-shaped divisions. This is also heterostyled and trimorphic. Further, the difference in size of the pollen grains observed in the *Lythrum* is also seen here.

	Divisions of the Micrometer.
From the longest stamens of short-styled	15 to 16
„ mid-length „ „	12 „ 13
„ longest stamens of mid-styled	16
„ shortest „ „	11 to 12
„ mid-length stamens of long-styled	14
„ shortest „ „	12

The extreme differences in diameter in this case are as 100 to 69. With this genus the most striking differences between the results of the legitimate and illegitimate unions present themselves. If 100 be taken to represent the fertility of the legitimate, that of the illegitimate is represented by 0, as absolutely no flowers, the result of illegitimate union, formed any fruits at all.

One other trimorphic plant is dealt with, interesting as the only member of the great class Monocotyledones that is heterostyled. It is the *Pontederia*, an aquatic plant closely



allied to the Lily order, growing on the banks of rivers in Southern Brazil. The size of its pollen grains:

	Divisions of the Micrometer.
Long-styled form, from the mid-length stamens	13·2
(Average of 20 measurements.)	
Long-styled form, from the shortest stamens ...	9·0
(Average of 10 measurements.)	
Mid-styled form, from the longest stamens ...	16·4
(Average of 15 measurements.)	
Mid-styled form, from the shortest stamens ...	9·1
(Average of 20 measurements.)	
Short-styled form, from the longest stamens ...	14·6
(Average of 20 measurements.)	
Short-styled form, from the mid-length stamens	12·3
(Average of 20 measurements.)	

The extreme differences in diameter are as 100 to 55. As only dried specimens could be obtained by Darwin of course no experiments could be made on this plant.

(iii.) The comparative inferiority of illegitimate offspring. This comparative inferiority shows itself in three principal ways, ( $\alpha$ ) stature, ( $\beta$ ) general constitution, ( $\gamma$ ) nature of the anthers.

( $\alpha$ ) When legitimate plants growing under similar circumstances to their illegitimate companions were compared with them in height the results were that the numbers 28, 29, and 47 expressed the heights of the illegitimate whilst numbers nearly double these expressed the heights of the legitimate, one of which was 77 inches high.

( $\beta$ ) The illegitimate are weak in their constitution. They flower late in the season and sometimes do not produce flowers each year.

( $\gamma$ ) The anthers are often shrivelled, containing brown or pulpy matter without true pollen grains, and in many cases not opening at all. They are called contabascent (contabescere = to waste away). Adding these disadvantages to the lessened fertility that has already been demonstrated over and over again it must be clear that the impregnation of ovules in the illegitimate fashion is of much greater disadvantage to the plant than the impregnation in the legitimate method. And these conclusions are true of all the heterostyled plants upon which the experiments were made.

(iv.) Illegitimate unions and hybrids. In conclusion a striking comparison is made between the illegitimate unions in these heterostyled plants and the hybrid unions between distinct species. It has been shown above that hybrid is the name given to the result of the crossing of two so-called species. All the world knows by this time that there are two opposed views in respect to species. Those who hold, in antagonism to the facts and to the thinkers of modern scientific order, that species are all distinct creations were until recently in the habit of pointing triumphantly to the fact that hybrids were more or less sterile as proof positive of their view. It is to be observed that of late the triumphant tone has been somewhat modified. It is needless to state that the experiments and reasoning of Charles Darwin have mainly produced that modification. To understand thoroughly his reasoning in this connexion it must be remembered that the advocates of the Special Creation view hold that species alone have been thus separately manufactured. They do not maintain that varieties—that is the sub-divisions of species, are special creations. And yet all his experiments go to prove that the same sterility that is encountered when union between two species is effected is met with when mere varieties are crossed. If, therefore, such sterility is an argument in favor of the creation of species, it is an argument in favor of the creation of varieties, and at this last nobody has yet been rash enough even to hint. Reducing the matter to its extreme conclusion we should perhaps be justified in saying that when there was sterility between two individuals of the same variety, as very frequently does occur, we ought to argue from this that those individuals have been specially created. Comparing the hybrid unions between distinct species with the illegitimate unions between forms of the same heterostyled species we find—(a) In both cases every degree of sterility, from slight, through less fertility, to absolute barrenness. (β) In both cases the ease or difficulty of effecting the first union is dependent upon the external conditions to which the plants have been exposed. (γ) In both cases the degree of sterility in plants coming from the same parent is highly variable. (δ) In both cases the male organs are more affected than the female. (ε) In both cases the offspring are apt to be dwarfed and weak. (ζ) In both cases the offspring are profuse flowerers. Small

wonder therefore that Darwin ends this part of his subject with phrases such as these.

“It is hardly an exaggeration to assert that seedlings from an illegitimate fertilised heterostyled plant are hybrids formed within the limits of one and the same species. This conclusion is important, for we thus learn that the difficulty in sexually uniting two organic forms and the sterility of their offspring afford no sure criterion of so-called specific distinctness. The sterility of their illegitimate unions and that of their illegitimate offspring must depend exclusively on the nature of the sexual elements and on their incompatibility for uniting in a particular manner. And as we have just seen that distinct species when crossed resemble in a whole series of relations the forms of the same species when illegitimately united, we are led to conclude that the sterility of the former must likewise depend exclusively on the incompatible nature of their sexual elements, and not on any general difference in constitution of structure.”

(v.) The distribution of heterostyled plants. It is very general. Thirty-eight genera include heterostyled individuals. These genera are widely distributed throughout the world. Thus the three closely allied genera, *Menyanthes*, *Limnanthemum*, and *Villarsia*, inhabit respectively Europe, India, and South America. Heterostyled species of *Hedyotis* are found in the temperate regions of North and the tropical regions of South America. Trimorphic species of *Oxalis* live on both sides of the Cordilleras in South America and at the Cape of Good Hope. Again, the three great divisions of plants founded on the nature of their stem present heterostyled individuals. There are heterostyled trees, heterostyled shrubs, heterostyled herbs. Again, the nature of the habitat appears to be no impediment to the formation of such flowers. Plants dwelling upon alpine summits and in lowland glades, plants dwelling upon the land, plants floating or immersed in the water, or plunged in the stagnant marshes—all these may be heterostyled.

From the general nature of the distribution of these plants it will be anticipated that some advantage accrues to the owners of andrœcia and gynœcia of different lengths. The great advantage clearly is that as all the flowers on the same plant belong to the same form, when legitimate fertilisation takes place two distinct individuals must cross; and

further all the individuals of the heterostyled plant can yield seeds, whilst in the other plants that will come next under consideration where the sexes are separated, only a certain number can yield seed. Of course the heterostyled plants, like the dichogamous and unisexual plants have this advantage over those plants that are liable to self-fertilisation, that the junction of two individuals is essential for fertilisation. Further, the trimorphic plants have a slight advantage over the dimorphic in the struggle for life. For suppose only two individuals of a dimorphic plant, like the primrose, to be side by side in an out of the way part of the world. It is even betting that both will belong to the same form, and in that case the full number of strong seedlings cannot be produced. But if the two plants growing side by side in an out of the way part of the world are trimorphic the betting is two to one that they will not belong to the same form. The odds, therefore, are two to one that legitimate fertilisation will take place and the full tale of strong seedlings result.

(vi.) The means by which plants may become heterostyled. The believer in evolution seeing certain results in the structure and functions of plants and animals is by the nature of his belief compelled to ask himself how these have been brought about. He has not the refuge of the unthinking. He does not avoid all difficulty and confess his own idleness by uttering the formula "It is the will of god." It is impossible, nay it is impious for him to explain the complex structures and relationships which he observes as being in any sense the result of plan or design on the part of hypothetical deity. Recognising the principles that living beings vary, and that only variations that are of use to the living beings are likely to be persistent, it is his honorable duty and difficulty to attempt to reason out the lines along which the variations have passed until they have become permanent. The question of the heterostylism of plants presents a difficult problem for the solution of the evolutionist. Let us see how the greatest of evolutionists deals with it.

(a) The first step towards a plant becoming heterostyled is probably variability in the length of the gynœcium and of the stamens. Without this initial variability in the length of the sexual organs the ultimate result is incon-

ceivable. The plant variable as to the length of its reproductive apparatus would, like all plants, benefit by cross-fertilisation, and probably was at least in some degree self-sterile. So far then we have varying lengths in stamens and gynœcium, self-sterility to a greater or less degree, and the universal fact of benefit resulting from cross-fertilisation. Now natural selection would come into play. The variations in length being infinite at first, are by natural selection reduced to two sets of different lengths in different individuals, and that the long stamens should be associated with the short styles in the same flower would follow from the law of compensation or *balancement*. According to this principle excessive development of one part is apt to be accompanied by lessened development of another, and hence the long stamens would be associated with the diminished style in the same flowers, whilst the converse obtained in others.

( $\beta$ ) Herr Müller suggests that the ordinary plants may have been rendered heterostyled through habit, from continual application of the pollen of one set of anthers to a gynœcium of particular length. He conceives that in time any other method of fertilisation would be nearly or absolutely impossible.

( $\gamma$ ) A third view is that heterostyled plants have specially acquired an incapacity for fertilisation in particular ways. More probable than this, however, is the supposition that the male and female organs in two sets of individuals have become specially adapted for interaction one with another, whilst the sterility resulting from the crossing of individuals of the same form is an incidental and not a directly connected result. By "incidental result" is meant an accompanying result, but not one that is directly traceable to that action to which it is incidental. Probably, therefore, the species which became heterostyled at first varied, so that sets of plants resulted having different lengths of andrœcia and gynœcia, and that simultaneously their reproductive powers were so modified that the sex elements in one set were adapted to act on the sex elements of the other, and hence that the sex elements in the same set became ill-adapted for acting the one upon the other.

## CHAPTER XXVI.

(3.) *Plants in which the sexes are separated.*

(a) **T**HEIR Evolution. Our author commences here with a dissertation as to the way in which plants possessing both sexes may have passed into plants in which the sexes are separated. This conversion can only have been effected upon entomophilous or anemophilous plants. Self-fertile plants would never lend themselves to the development in the direction of separation of the sexes. Next, it is possible that the production of male and female elements by the same individual may have been too great a strain upon its powers. Again, the variations that are so persistently occurring may in some instances have taken the form of the production of large-seeded plants. That is to say, some few individuals may have resulted from variation, individuals that had seeds larger than the average, better supplied with nutriment, and therefore likely to be able to hold their own in the universal battle. This variety with the large seeds would tend to increase and by the law of compensation its stamens would be reduced in size. It would, in short, be moving in the direction of a unisexual female plant. As this particular set of plants would produce less pollen, certain other individuals would have to produce more pollen, and by the law of compensation their female organs would be reduced in size. And thus our first set producing the larger seeds and with their stamens aborted are likely to become unisexual female plants, and our second set producing more pollen with their gynœcia aborted are likely to become unisexual male plants.

Dimorphic heterostyled plants are still more likely to produce unisexual flowers by evolution, for the male and female organ here differ not only in structure, but in function, and one may say that there is twice as much chance in their case of the special development of the one set of organs and the gradual abortion of the other set.

(b) Size of the corolla. In the plants that have their sexes separated, the corollas of different flowers frequently vary in size. It is noticeable that the smaller corolla is always present in the female. Possibly the explanation of this is that the abortion of the stamens which has taken place in the female flower has spread from them to the petals, and this view is strengthened by the fact that in *Rhamnus Catharticus* not only the petals of the female flower have been reduced in size, but the reduction in size has extended even to the sepals. An objection to this explanation is afforded by Darwin himself, after his usual fashion. By the law of compensation the abortion of the stamens ought to have led to increased size of the corolla of the female flower, but perhaps we may argue that the energy saved by the abortion of the stamens has been totally directed to the female reproductive organs, and there has been none to spare for the corolla.

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## CHAPTER XXVII.

(4)—*Cleistogamic Flowers.*

**E**VEN before the days of Carl von Linné, more generally known by his Latinised name, Linnæus, it had been discovered that certain plants produced two kinds of flowers—the ordinary open ones and minute closed ones. Not until 1867 were these latter thoroughly understood, and named by Kühn.

(a) Structure. They are very small, and never open. The petals are rudimentary or absent, the stamens few, anthers small, pollen-grains few, emitting their tubes while still within the anther, gynœcium very small, stigma almost wanting. Flowers that are reduced in circumstances indeed. Everything is upon the smallest possible scale. Fifty-five genera, widely distributed throughout the vegetable kingdom, are known to produce such flowers, and the larger proportion of them, thirty-two out of the fifty-five, are genera whose ordinary blossoms are irregular in shape. The seeds produced by cleistogamic flowers differ neither in their appearance nor in their number from those produced from the perfect blossoms, but the fruits from the cleistogamic develop much more rapidly than those from the perfect. Darwin describes cleistogamic flowers of the following genera out of the fifty-five that show them—*Viola*, *Oxalis*, *Vandellia*, *Linaria*, *Ononis*, *Impatiens*, *Drosera*, *Juncus*, *Leersia*. The cleistogamic flowers owe their structure almost certainly to the arrested development of perfect ones.

(b) Advantages. They would seem to furnish these most desirable results to the plant. (i.) They insure the production of seed in seasons when perfect flowers, owing to climatic conditions, might be able to produce none. (ii.) They produce seeds with very little consumption of matter and very little transformation of motion. A wonderfully small expenditure of pollen is all that is needed for the pro-



duction of seeds as numerous and as perfect as those of the complete flowers. Thus by calculation the whole of the pollen-grains of a cleistogamic *Oxalis* are but 400, of an *Impatiens* 250, of a *Leersia* 210, of a *Viola* 100. Let the reader compare these with the 243,600 grains of a Dandelion, the 3,654,000 of a *Pæony*. (iii.) It must not be forgotten that most of the cleistogamic genera are irregular-flowered; therefore their perfect flowers depend for fertilisation upon insects. Now insects, especially in our strange English climate, are very variable quantities. Hence seasons might occur, and do occur, when, not sufficient insects being present, or an absolute dearth of necessary insects occurring, no seeds would be formed were it not for the cleistogamic flowers. It is not difficult, therefore, to conceive of the gradual evolution of these closed, aborted, self-fertilising, and, on occasion, most useful flowers.

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## CHAPTER XXVIII.

(5) *Personal Characteristics.* (6) *Gradations.*

(5.) IT is now late in the day to call attention to Charles Darwin's enormous capacity for work, but the experiments recorded in the volume whose consideration now is drawing to a close furnish still further evidence of that capacity. Take two special illustrations. In studying *Thymus serpyllum*, one of the gynodioicous plants, he is anxious to ascertain the relative numbers of the bisexual and of the female flowers. Hence he sets to work to examine every plant growing on the edge of an over-hanging cliff some 200 yards in length. As the plants were several hundreds in number, one has here a suggestion as to the amount of patient toil of which our naturalist is capable. Again on page 189 we find the statement that he counted under the microscope over 20,000 seeds of one particular plant before he arrived at certain of his important conclusions. An instance of the notable modesty to which we have had occasion heretofore to refer occurs in the first few lines of the present volume, wherein he states that the subject whereof he is about to speak ought to have been treated by a professed botanist, to which distinction he can lay no claim.

For the benefit and warning of those that talk lightly about the amount of faith which is required in scientific work it is well to quote one little phrase. In speaking of the *Linum* he does once use the expression "I had faith." Doubtless these three words will be quoted by the people who read the works of Darwin and other evolutionists for the purpose of collecting isolated sentences, and hurling them without their context at the heads of the preachers of evolution. But in this case, as in most of their quotations, the context destroys the arguments that have been based upon the particular utterance. "Nevertheless *from my experi-*

ments on *Primula* I had faith." That is the true faith, the faith founded upon experiments.

(6) Gradations. In the study of the different forms of flowers many interesting cases of gradations between forms that would a few years ago have been regarded as created specifically distinct occur. Upon page 291, in speaking of the *Euonymus Europæa* or Spindle-tree our writer states :

"We have a perfect gradation from the female bush (B), which in 1865 was covered with 'innumerable fruits,'—through the female A, which produced during the same year 97—through the polleniferous bush C, which produced this year 92 fruits, these, however, containing a very low average number of seeds of small size—through the bush D that produced only 20 poor fruits—to the three bushes, E, F, G, which did not this year, or during the previous years, produce a single fruit."

Again on page 320, dealing with the various forms of flowers in the genus *Viola*, which is one of the genera presenting cleistogamic flowers, we read :

"It is interesting to observe the gradation in the abortion of the parts in the cleistogamic flowers of the several foregoing species. It appears from the statements by D. Müller and Von Mohl that in *V. mirabilis* the calyx does not remain quite closed; all five stamens are provided with anthers, and some pollen grains probably fall out of the lobes on the stigma, instead of protruding their tubes whilst still enclosed, as in the other species. In *V. hirta* all five stamens are likewise antheriferous; the petals are not so much reduced and the pistil not so much modified as in the following species. In *V. nana* and *elatior* only two of the stamens properly bear anthers, but sometimes one or even two of the others are thus provided. Lastly, in *V. canina* never more than two of the stamens, as far as I have seen, bear anthers; the petals are much more reduced than *V. hirta*, and, according to D. Müller are sometimes quite absent."

Professor Oliver adds that he has seen flowers on *Campanula colorata* in an intermediate condition between cleistogamic and perfect ones.