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THE MAKING OF FLOWERS

THE REV. PROF.
GEORGE HENSLOW, MA.

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BY THE

REV. PROF. GEORGE HENSLOW,

M.A., F.L.S., F.G.S., ETC.

AUTHOR OF "BOTANY FOR BEGINNERS," "FLORAL DISSECTIONS,"
"THE ORIGIN OF FLORAL STRUCTURES THROUGH INSECT
AND OTHER AGENCIES," ETC. ETC.

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CONTENTS.

	PAGE
INTRODUCTION	9
GENERAL OBSERVATIONS	12
THE SUBJECTS OF VARIATION	15
CLASSIFICATION OF PLANTS	21
FERTILIZATION, THE INTERPRETATION OF VARIATION	28
THE ORIGIN OF THE FOUR SUBJECTS OF VARIATION	32
I. NUMBER	32
II. COHESION	37
III. ADHESION	37
IV. FORM	40
ADAPTATIONS FOR POLLINATION IN SE- LECTED TYPES OF FLOWERS	43
CLASS I. DICOTYLEDONS	43
DIV. I. THALAMIFLORÆ	43
,, II. CALYCIFLORÆ	58
,, III. COROLLIFLORÆ	65
,, IV. INCOMPLETÆ	81

	PAGE
CLASS II. MONOCOTYLEDONS	84
DIV. I. EPIGYNÆ	84
„ II. HYPOGYNÆ	88
„ III. GLUMIFERÆ	89
PELORIA	93
MON- AND DI-ÆCISM	95
WIND-FERTILIZED PLANTS	100
FLORAL APPENDAGES	103
HONEY-SECRETING ORGANS	107
THE RECEPTACULAR-TUBE	111
IRRITATION OF THE POLLEN-TUBE	117
THE COLOURS OF FLOWERS	121
EFFECTS OF STRAINS ON STRUCTURES	123
DECLINATE STAMENS	132
THE RELATIVE VALUE OF INTER-CROSSING	135
SELF-FERTILIZATION	141
THE ORIGIN OF SPECIES BY INSECT AND OTHER AGENCIES	149
MORAL CONVICTIONS, OR THE NATURE OF PROOFS ACCEPTED BY ASTRONOMERS, GEOLOGISTS, AND BIOLOGISTS	160
CONCLUSION	167

LIST OF ILLUSTRATIONS.

FIG.		PAGE
1.	Diagram of a typical flower	17
2.	Diagram illustrating the method of change from "opposite" to "alternate" leaves	36
3.	Styles and Stigmas of Pansies	51
4.	Cleistogamous Violets	53
5.	Chickweed	56
6.	<i>Genista tinctoria</i>	63
7.	Stamens of <i>Centaurea</i>	66
8.	<i>Phyteuma</i>	68
9.	<i>Narcissus cernuus</i>	73
10.	Dead-nettle	74
11.	<i>Lamium amplexicaule</i>	75
12.	Thyme	76
13.	Sage	79
14.	<i>Salvia clandestina</i>	81
15.	Monstrous Pear	113
16.	Monstrous Fuchsia	114
17.	Monstrous Rose	115
18.	Conducting Tissues	118
19.	<i>Uncaria</i>	126
20.	Pear	127
21.	<i>Duvernoia</i>	131
22.	Willow Herb	133
23.	<i>Dictamnus</i>	133
24.	Speedwell	134

THE MAKING OF FLOWERS.

INTRODUCTION.

FEW people are without interest in knowing how things are made. Indeed, to be conducted over a manufactory, and to examine the various processes in the construction of any of our common or useful articles, is to take a most fascinating excursion. Similarly, to find out how Nature manufactures her flowers is the pursuit of a branch of knowledge more profoundly interesting still. Unfortunately in most cases the process requires such an extended period, that we cannot easily see how it is done. We may strongly suspect such and such to be her methods, and we may give plenty of reasons for our suspicions; but we cannot quite demonstrate by actual experiment that our ideas are right in every instance. Nevertheless, observations have been so numerous, and experiments so many, that in the opinion of eminent Botánists and other persons the probabilities in favour of our ideas are now so

great, that they amount to the kind of proof with which we are, at all events, quite satisfied when dealing with other and ordinary matters of everyday life ; *i. e.* they approximate to what we call a "moral conviction," or "circumstantial evidence."

It is the object of this book to put forth, as plainly as possible, the line of proof here proposed. And in so doing, I think my readers will discover, whether they be finally convinced or not, how wonderfully interesting a subject it is. I hope, too, that it will at least stimulate them to observe for themselves, and will lead them to take a greater interest in Nature's works than perhaps they have hitherto done.

Instead of adding more upon the nature of the kind of proof offered, which is sufficiently familiar to all students of physics, at least, it will be better to give the reader plenty of interesting facts ; grouping them into a connected series, so as gradually to bring our argument to an irresistible conclusion, if such be possible.

To begin then, What is a flower ? It is a living machine for making seed in order to reproduce the plant and so keep up a succession of its kind. But a flower differs from a manufactory in one way especially ; in that, while man acts upon a machine entirely *from without*, by altering its structure from time to time with the object of adapting or improv-

ing it for whatever need he may have in view ; the plant has the power of altering the flower, so to say, *from within*, slowly for the most part, and only perhaps through a long series of generations, in order to adapt it to its altered needs as the species becomes dispersed, and to fit it for its surroundings, or general environment as it is called. For these are, of course, continually changing as the seeds get scattered over a country, and thence over the world. It is thus that new species arise ; so that a general summary of the lines of argument deduced from observation and experiment will end in the conclusion that all kinds of flowers are the result of a "responsive power" residing in the living "protoplasm" of the plant, acting in concert with the external impulses received from its environment.

The plant in all its parts is, as it were, struggling to keep in harmony with the external world. If it cannot do so, it must succumb. If, on the other hand, it can vary so as to keep its own forces in equilibrium with those of the external world, it lives and thrives, and the new characteristics which it may have developed become hereditary, and thus new species are obtained.

GENERAL OBSERVATIONS.

TO understand how flowers are made it is necessary to know what a flower is. Let us, therefore, take any common plant, as a Buttercup.¹ The blossoms will be found to consist of four distinct sets of parts, or *Organs*.² The outermost are green, and five in number. These are called *Sepals*, and collectively constitute the *Calyx*. The next are larger, yellow ; and there are also five. They are the *Petals* of the *Corolla*. Having removed these, there follow an immense number of bodies called *Stamens*, with thread-like stalks, the *Filaments*, each carrying a sort of double sac, the *Anther*, which bursts at the sides by two slits. The continuation of the filament *between* the *Anther-cells* is called the *Connective*. From these cells of the anther issues a yellow powder called *Pollen*. Carefully removing all the stamens, a small globular green structure is seen in the middle. This is the *Pistil*, and it is composed of a large number of separate little bodies called *Carpels*. Each carpel

¹ I shall endeavour in all cases to select such plants as can be easily procured ; for it is most important that the reader should follow me by examining for himself the living flowers mentioned.

² Any part of a plant which has a distinct office or function is called an "organ."

consists of a roundish bag at the base, or *Ovary*, tapering upwards into a curved sort of beak, the *Style*, which terminates with a rough tip, the *Stigma*.¹ Inside the ovary is a minute little pea-like body, called the *Ovule*, which can generally be readily seen within the ovary, through the walls, by holding a carpel up to the light fixed upon the tip of the knife, or point of a pin. The ovule, after the processes called *Pollination* and *Fertilization* have taken place, will grow into a *Seed* containing an *Embryo* or young plant, the numerous carpels, or collectively the pistil, at that time becoming the *Fruit*.

Now, when we look at a nosegay, we at once see that flowers are not all like Buttercups ; and the first question that arises is, How do they differ ? As in all Nature's works there is an infinite variety arising out of an extreme simplicity ; for all the variations in the structure of flowers only concern a few simple subjects, as I propose to call them ; and when these are once grasped, the interpretation of all the differences in the whole floral world becomes apparent at once. We take the four floral *Whorls*, as the Calyx, Corolla, Stamens and Pistil are called, as our starting-point ; and the *Subjects of Variation*, by which all sorts of differ-

¹ A pocket lens and a sharp-pointed penknife will be found useful for inspecting the minuter parts of flowers.

ences can be introduced, are four, namely, *Number*, *Cohesion*, *Adhesion*, and *Form*. By various combinations of the conditions implied by these four words, *all* flowers are constructed. Thus the parts of one or more of the whorls may vary in number from one to twelve; such numbers being called *Definite*. Or these may be many, as are the stamens as well as the carpels of the Buttercup; such are said to be *Indefinite*. The parts of any whorl may be free, as the petals of a Buttercup, or joined into one piece, as are the five petals of the Primrose. They are then said to *cohere*; but if two or more whorls are united one within the other, botanists call such unions by the term *Adhesion*, to distinguish it from the former. Thus the stamens adhere to the tube of the corolla of the Primrose. Lastly, *Form*. To this there is no limit, the shapes of the petals being infinitely various; and it is especially the origin and meaning of this immense variety which one meets with in Nature, which I hope to be able to explain. Botanists, however, call any whorl which has its parts of the same size and shape, *Regular*. If some one or more parts of a whorl differ from the others, the whorl is said to be *Irregular*.

There is another source of difference, very conspicuous to the ordinary observer, and that is Colour; but botanists do not lay so much stress

upon it when treating of the origins of the floral whorls. However, I will say something about colour in due course.

THE SUBJECTS OF VARIATION.

WE will now consider each of these in detail.

NUMBER.—Of the definite numbers found in flowers, threes, fours, and fives, and less frequently multiples of them, prevail. Thus, a Lily will be found to have two whorls of three petals in each, and six stamens. These also really constitute two whorls of three in each; and there are three coherent carpels forming the pistil. A Fuchsia has a calyx of four coloured sepals, a corolla of four petals, eight stamens, and four carpels. But by far the greater number of flowers have five sepals, five petals, five or ten stamens, and if not five carpels, usually some lower number; because this *numerical symmetry* (as the agreement in number between two or more whorls is called) often fails in the carpels.

We have also seen how the number of parts may be very many or indefinite. On the other hand, any one, two, or even three whorls may be wanting altogether; a flower is then reduced to a minimum of simplicity, and may consist of two stamens

only, as is the case with the Ash-tree and the Sallow Willow, or of even a single stamen, as in the Common Spurges (*Euphorbia*); or of a single carpel, as in Duckweed (*Lemna*).

These facts suggest the idea that we may be able to trace gradually increasing complexities in flowers, from some assumed standard on the one hand, and degradations from it on the other; and this is exactly the case. Our task will be to find out, if possible, how it is that flowers have advanced from a definite number of parts, all being free, to various states of cohesion and adhesion, accompanied by a development of remarkable forms. These, on the other hand, in many cases, have grown more and more simple, losing one whorl, then another, wholly or in part, as well as dwindling in size till there is scarcely anything left but the stamens and pistil wherewith to set the seed.

As five is a prevailing number, I will now give a diagram (Fig. 1) to illustrate the positions and number of whorls which represent an *ideal type*, from which there is reason to believe most flowers have originated. It will be seen that there are *six*, and not four, whorls represented; because, although most flowers, if complete, have only four whorls, yet this number has been probably reduced from six, there having been originally two whorls

of stamens and two whorls of carpels.¹ And even these pairs of whorls have been reduced from an indefinite number of parts, as still exists in the stamens and carpels of Buttercups.

Generally, it may be stated, that “fours” and “fives” prevail in the class *Dicotyledons*, and “threes” in the class *Monocotyledons*.²

Fig. 1.—Diagram of a typical flower.

COHESION.—This term signifies, as stated, that the parts of any whorl may be united. Thus in the Primrose the sepals form a tube, and the petals of the corolla, as well as those of the Foxglove, Potato, and Convolvulus, are also united; while in the Broom and Laburnum all the filaments of the

¹ For the reasons and arguments in support of this statement and others which I may have to make, I must refer the reader to my work, *The Origin of Floral Structures by Insect and other Agencies*, International Scientific Series, Vol. 64.

² For the meaning of these terms see below, p. 22.

stamens cohere, edge to edge, so as to form a tube, which encloses the pod-like pistil, consisting in this case of one carpel only; but the anthers are free. Conversely in the Thistles, Dandelion, and Lobelia, the anthers cohere, but the filaments are free. The carpels are very frequently united, even when the other parts of the flowers are free.

The carpels may be united in two ways. If we take a pea-pod we shall find that it closely resembles a narrow, long-pointed leaf folded down the middle, with the edges in contact. Such is really Nature's method of making a carpel, of course greatly modifying the leaf for its new purpose. The peas, *i. e.* the ovules, are always produced down the united margins in two rows, *i. e.*, one row on each margin. Now suppose we take two or more pea-pods. Place them with their margins in contact, and then compress them so that the *sides* will meet, and imagine them to have thus *grown* in contact. They would then be in a state of cohesion; and a cross section through the ovaries would reveal as many chambers as there are carpels. That is one way. This is well seen in the pistil of the Bluebell. Another may be illustrated as follows:—Take two or more pods, but this time crack them open down the margins where the peas are (but not down the opposite side); half the peas will now be found on one margin and half on the other. Now place

the open pods in a circle, edge to edge, and imagine the edges only to become coherent. There will thus be *one* large chamber, with as many double rows of ovules as there are carpels. The Violet and Mignonette will illustrate this condition.

With regard to cohesions generally, we must distinguish between *congenital cohesion* and *cohesion by contact*. The former signifies that the different parts which form, *e.g.* a corolla, grow up united from the very commencement. In some comparatively few cases the parts are at first free, but become coherent by contact during growth. This is the case with the anthers in the flowers of the large family called *Composites*, such as of the Dandelion and Daisy; for the “flowers” of these plants are really “composed” of innumerable “florets,” each having its own corolla, stamens, and pistil. Linnæus gave the name *Syngenesia*, a word signifying “begotten together,” to signalize this condition; the union, however, is not really congenital, but due to a sort of “sticking together.”

ADHESION.—These are not at all infrequent; thus, whenever the petals *cohere*, the stamens are almost invariably *adherent* within, *i. e.* to the surface of the tube of the corolla; as may be seen in the Primrose.¹ In the Cherry, Strawberry, and Loo-

¹ As rare exceptions in which the stamens are *free* from the corolla, may be mentioned the Heath family (*Ericaceæ*),

strife, the petals are not coherent, but together with the stamens will be found adherent to the circular rim of the calyx.

The question why some flowers have their petals coherent into a tube and others not, brings us to regard the former as being in a more highly altered state than the latter; and with regard to these conditions of union generally, as compared with freedom, botanists regard the latter state as representing a more primitive condition, in that they thus resemble leaves from which they are all undoubtedly derived; so that wherever the petals are regular and somewhat leaf-shaped, they have retained a more primitive character.

FORM.—As freedom of parts is a more primitive condition than cohesion, so regularity of form has preceded irregularity.¹ Both of these conditions may occur with or without cohesion. Thus in the Aconite or Monkshood, and in the Larkspur, the sepals are free but irregular. In the Violet the petals are free but irregular. In the Pea, three of the five petals are free, but two others are coherent. Lastly, many flowers have coherent petals, the corolla being very irregular, as, *e.g.* that of Sage or

which includes Rhododendrons and Azaleas; and the Campanula family (*Campanulaceæ*), or Canterbury Bells.

¹ Reversion from normal irregularity to regularity will be spoken of hereafter under "Peloria."

Salvia, Snapdragon, Foxglove, &c. In fact, there seems to be no limit to the forms of corollas, and no special laws governing their shapes can be detected. Thus, Clematis, Buttercups, Aconite, Larkspur, Columbine, and Pæony, so different from one another in their general appearance, are nevertheless closely allied, and belong to the same family (*Ranunculaceæ*). Similarly Speedwell, Snapdragon, Foxglove, Mullein, and Calceolaria, stand side by side in another but the same family (*Scrophularineæ*). Hence it appears that we seem to want some cause which has thus modified the descendants of the common ancestors of these groups, respectively; which I have merely selected as representative of a great many others.

Besides irregularity in the form of the corolla, it is often found, but to a less striking extent, in the stamens; thus some may be much shorter than the others of the same flower. Sometimes a certain number of the filaments are hairy, the rest being smooth, &c. A careful examination of these minute differences generally reveals the fact that they are adaptations to assist fertilization.

CLASSIFICATION OF PLANTS.

I MUST now explain as briefly as possible how plants are classified, for they are grouped entirely

in accordance with various combinations of the four Subjects of Variation; at least as far as their characters are dependent upon floral structures.

All plants which bear flowers are divided into two classes—*Monocotyledons* and *Dicotyledons*. In the first, as stated above, the number three prevails in the parts of their floral whorls; in the second the numbers four and five. These are not the only characters which distinguish them. Indeed it is an essential feature in the classification of plants, that any group should be recognized by as many constant features as possible. The above names are derived from the *Embryo*, or young plant within the seed. If a Bean, Pea, or Almond be chosen, and the skin removed, the body within is the Embryo; and it will be found to split into two pieces called the *Cotyledons*, or Seed-leaves, as in “split peas.” They are attached opposite each other to a little stem, the *Radicle*, which carries a minute bud at the end, called the *Plumule*.

In many cases the cotyledons soon reveal their true foliar character by appearing above the soil and turning green, as in edible mustard and cress, having previously surrendered to the growing stem a quantity of nourishment in the form of starch, &c., which they at first contained. As there are two cotyledons in the above, they, as well as all other plants which have this number, are called *Dicoty-*

ledons. If there be only one, as is the case in the seeds of Lilies, Palms, Sedges, Grasses, &c., such plants belong to Monocotyledons.

These two classes are divided into groups called *Divisions*, and these are based upon the four Subjects of Variation. Thus all Dicotyledons which have their petals free, and are also devoid of adhesion, are called *Thalamifloræ*. Those in which the petals, while being free amongst themselves, are mostly adherent to the rim of the calyx, the sepals of which are now coherent, constitute the second division known as *Calycifloræ*; while all the plants whose flowers have their petals coherent form a third division, called *Corollifloræ*. Lastly, a fourth division includes a great assemblage in which much degradation has occurred, there being no corolla, often no calyx, and the number of stamens and carpels frequently reduced in number and separated, being situated in different flowers. Hence this division has been called *Incompletæ*.

In Monocotyledons there are similar Divisions, but only three in number. Two have the sepals and petals all alike, so botanists call them collectively the *Perianth*, and it depends upon the condition of the perianth, whether it springs from below and is free from the ovary, when all the plants so constructed are called *Hypogynæ*, or whether they are adherent to it, and so form the

Division *Epigynæ*. The third group has no perianth, but chaffy scales instead, and is called *Glumiferæ*, which is best represented by the families of Sedges and Grasses.¹

Divisions contain *Families*, or *Natural Orders*. All the plants embraced in an Order agree in a certain group of characters ; but if we wish to single out one or two prominent features, we should find that certain numbers would be characteristic of an Order in some cases ; as *e.g.* the *four* sepals, *four* petals, *six* stamens and *two* carpels are peculiar features of the Family called *Cruciferae*, which contains the Cabbage and Wallflower. In other cases certain cohesions are noticeable, as among the filaments of the Order *Leguminosæ*, containing the Laburnum, Pea, and Bean ; and of the anthers in *Compositæ*. Or again, certain adhesions, as that of the petals and stamens on to the calyx in the Rose Family, or *Rosaceæ*. Thus a yellow flowered *Potentilla* is readily distinguishable from a *Buttercup*, to which it has great superficial resemblance.

Orders are composed of *Genera*, and Genera of *Species* : and as is the case with Orders, so a *genus* is known by a collection of constant characters

¹ Further particulars of these Divisions, as well as of the additional group called *Gymnosperms*, must be looked for in any Text Book of Botany.

taken together. We may, however, select one or more prominent features, and we should find that *Number* and *Form* often stand pre-eminent. Thus the genus Bedstraw (*Galium*) differs from Madder (*Rubia*), in having the petals and stamens four in number, while the latter has them in fives. In the order *Scrophularineæ*, each of the different genera mentioned above, as Foxglove, Speedwell, &c., is at once recognized, respectively, by the form of its corolla.

In the preceding brief remarks we have regarded Classification *analytically*: that is, commencing with a single group, namely, all Flowering plants, we divided it into Two Classes. Each Class was subdivided into Divisions, thence we came to Orders, Genera, and Species. If, however, we wish to classify *synthetically*, we begin with Species and Genera; and as the Making of Flowers lies at the foundation of the Origin of Species, it will be as well to explain more particularly how the ideas of a Species and of a Genus have been arrived at.

If we were to collect a number of Buttercups from different fields, roadsides, marshy places, &c., the only difference which might at first catch the eye between the flowers would be their sizes. But a careful examination of the entire plants would reveal a great many more distinctions. Thus one from the roadside might have "runners" like a

strawberry, rooting at the joints ; the flower-stalk would be cylindrical, the sepals spreading under the petals, &c. Comparing it with an early flowering one from a meadow, this latter would be found to have no runners, but a solid ball-like base to the stem called a "corm." It has a fluted flower-stalk, with the sepals reflexed against it, &c. Similarly, those from the waterside or damp ground would have long, narrow leaves, and not outspread or divided into three prominent *segments*, as occurs in the first-mentioned kinds. In fact, each kind or *Species* would be recognized by a group of half-dozen or more characters taken collectively from all parts of the plant.

When, however, we examine the flowers, they all agree in Number and Form, as well as in a total absence of Cohesion and Adhesion. Hence we call them all Buttercups, or in botanical language, the Genus *Ranunculus* : and each species has received a name given to it by Linnæus some 150 years ago, characteristic of some one prominent feature. Thus *repens* is applied to the one having "creeping" runners ; *bulbosus* to that having the bulb-like corm, &c. And as all these characters can be depended upon year after year, they are said to be *constant* to each species respectively.

Each species can, therefore, now be recognized by a *collection of constant characters taken from any*

parts of the plant. Such is a definition of a Species. Similarly a Genus is a collection of Species, all of which agree in some special, but identical combination of the Subjects of Variation in the structure of their flowers.

Now the question arises, if Buttercups have all descended from some common ancestor—and that is the universal belief among botanists—how have the different sorts or species arisen? It is the purpose of the present book to show the grounds for believing that it is to the surroundings or environment, taken in its widest sense, that we must look for the causes of all changes in the structure of plants.

It is not my intention in this book to try and explain how *all* the differences have arisen between various kinds of roots, stems, and leaves ; but only of flowers. And, just as the former are now attributable to various kinds of soils, such as marshy and aquatic, or dry, &c., or again to difference of shade and exposure ;¹ so variations in the structure of flowers are largely attributable, on the one hand, to the visits of insects ; and on the other to degradation, in consequence of their neglect of them ; and thereby, to the absence of any stimulus to development, as will be explained later on.

¹ Some details will, however, be given in a later section of this book.

FERTILIZATION, THE INTERPRETATION OF
VARIATION.

THE interpretation of the differences of floral structures must be looked for in their adaptations to their environment, and especially to the visits of insects. This leads me to say a few words on the importance of Pollination and Fertilization, as the processes are called.

The first question to be answered is—What are the uses of the floral whorls? The calyx is always the first to be developed, and constitutes the protecting cover to the rest of the flower when in bud. As the bud expands, the brightly-coloured corolla becomes in most cases the attractive organ, which insects can see, and by which they are attracted to the flower for honey or pollen for food. The pollen from the anthers of the stamens is the fertilizing substance, and the essential fact to be emphasized is, that this must reach the stigma of each carpel, and the latter organ be thus “pollinated” as it is called; for if it do not, no seed will be “set,” and every part of the flower will perish. The stigmas secrete an adhesive fluid which causes the pollen to stick to it and *to grow*. If we place a little of the powdery pollen in water under a microscope, in order to examine it more

minutely, the minute "grains" swell and often crack, when a little pouch is seen to protrude; or the grains may even burst, showing that they are not solid like shot, but consist of *two* spherical sacs, one within the other, and it is the innermost and more delicate one which protruded. It contains a fluid and granular living matter called "Protoplasm," in which is an important little body, the "nucleus" or sperm-cell. Now when one of the grains sticks to the stigma, the outer sac ruptures and the inner sac protrudes; but now being nourished by the juices from the stigma it grows downwards like a tube closed at the end, penetrating the style. The blunt end of this "pollen-tube" ultimately reaches the ovary, and finally the ovule. Within this latter body is a closed chamber, called the "*Embryo-sac*," in which a nucleus of a peculiar kind, called the egg- or germ-cell, has been prepared. The nucleus within the end of the pollen-tube passes through the membrane of the pollen-tube as well as that of the embryo-sac, and finally becomes absorbed into the nucleus of the latter or egg-cell. This process is called "Fertilization."

The results are most important; for they affect not only the nucleus or egg-cell, but the ovule and carpel as well; so that while the egg-cell now begins to grow on its own account, and

ultimately becomes the *embryo*, the ovule which contained it becomes the *seed* in which the embryo is lodged ; and the carpel develops into the *fruit* containing the seed. Thus, in an Almond, which is a seed, all that is left of the ovule is the brown skin. The white edible body is the embryo or young plant, developed out of the two confluent nuclei. Lastly, the flesh and stone together represent the carpel, which now constitutes the fruit.

The whole and sole object of flowers, as far as the plant itself is concerned, is to set seed and so propagate its kind ; and the innumerable ways by which Nature contrives to secure the placing of the pollen on to the stigma, or to pollinate it, forms one of the most interesting studies in Botany.

The methods of pollination and fertilization have been grouped under three heads—insect, wind, and self-fertilization. We will discuss examples of each method of pollination, discover as far as possible how they have arisen, and estimate the value of each kind of fertilization respectively.

The first class embraces all flowers which can attract insects either by being white or of some conspicuous colour, or by their scent. The colour, though most frequently located in the corolla, may be situated in the calyx, as in the yellow Marsh Marigold and scarlet Anemone ; and even in the anthers, as in the Meadow Rue (*Thalictrum*), and

in the Sallow Willow, which has no calyx and no corolla, but has plenty of honey, and is much visited by bees.

Of course insects do not come to flowers with the intention of pollinating them; but when they search for honey they get dusted with pollen, and on flying to another flower of the same kind (for bees keep very strictly to one kind of flower at a time) the stigma is always so situated as to strike the bee *exactly* on the spot where the pollen has been previously deposited. Hence, the second flower is said to be "crossed" with the pollen of the first. This interchange of pollen between flowers is called "intercrossing."

Now, the remarkable fact concerning such flowers as are attractive to insects, and are intercrossed by them, is the great number of points of detail in the flower which all conspire to the perfect execution of the process of intercrossing. It is quite inconceivable that all these "correlations," as they are called, could have arisen accidentally, and by some chance cause independently of one another, any more than the numerous details in the structure of the human eye could have come about, each item independently and without any causal connection with other items, the final result being such a wonderful construction as is the eye. Similarly, the various and minute points

of structure in flowers which are constructed for insect-pollination, have, according to the theory advanced in this book, arisen more or less *simultaneously*, though gradually, and in correlation with one another through the direct action of the insect upon the flower, as will be more fully explained hereafter.

THE ORIGIN OF THE FOUR SUBJECTS OF VARIATION.

I. NUMBER.—We must now return to consider how the differences implied by these words, Number, Cohesion, Adhesion, and Form, have arisen. First, with regard to Number. I have stated that fours and fives prevail in the flowers of Dicotyledons, and threes in those of Monocotyledons; and the question is, Whence came it that flowers have these different numbers in the construction of their calyx, corolla, stamens, and pistil? This question refers us back to the real origin of all flowers, and that is to a Leaf-bud. For all the parts of flowers are really made out of leaves. Not that they are at first leaves, and afterwards become sepals, petals, stamens, and carpels; but that the same little germ *might* have grown into a leaf or a stamen, according to circumstances.

Such interchanges often occur abnormally, as in the "Green Rose," of which every part appears as a true leaf, though reduced in size. Now when we take an ordinary shoot with green leaves upon it, such as of the Rose or May-tree, it will be found that if any leaf is called No. 1, a spiral line can be traced from leaf to leaf, passing round the shoot *twice* before reaching the sixth leaf, which is the first which will be found to stand directly over No. 1 ; so that *five* leaves constitute what is called a *cycle*. Similarly Nos. 6 to 10 constitute a second cycle ; Nos. 11 to 15 a third cycle, and so on. The position of the leaves of a cycle will be exactly as in the outermost whorl in Fig. 1, p. 17, where the numbers of the sepals correspond to the order and positions of the five leaves of a cycle, supposing them to have been brought down to one and the same level.

Then, as the above arrangement is the commonest among leaves, so "fives" are equally common in flowers, *for cycles of leaves correspond to whorls of flowers.*

A difference, however, must be noted. The leaves Nos. 6, 11, 16, &c., are all over No. 1, when the leaves are scattered spirally along the branch ; but when the cycles are reduced to horizontal whorls, Nature places these whorls, or contracted cycles, *alternately*, so that each cycle or whorl now stands

over the alternate whorl. This is so constantly the case, that it is called the "Law of Alternation," and if it is apparently broken through, one whorl being exactly over or in front of the preceding, it will be found to be due to the fact that the intermediate whorl has been suppressed. This occurs between the stamens and petals of a Primrose; the first or outermost whorl of stamens not being present at all, each of the five existing stamens is now situated exactly in front of one of the five petals.

If now the leaves of the Lilac, Privet, or Sycamore be examined, they will be found in pairs at the same level, each pair standing at right angles to the next pair. Let us imagine two pairs to be brought to the same level at a time, we should then have whorls of four leaves in each.

This is in most cases the origin of whorls of fours in flowers, as in the Fuchsia.

Lastly, a large group of plants have the parts of their flowers in threes, as Lilies, Narcissus, Crocus, &c. In most of these plants it will be found that their leaves are so arranged that the fourth leaf on the spiral line stands over the first, so that three leaves only will now constitute a cycle. This accounts, therefore, for the ternary arrangement so common in the flowers of the class Monocotyledons.

We can thus trace the origin of the various

numbers prevailing in flowers, as threes, fours, and fives, as well as their multiples.

If the number of parts be indefinite, as are the stamens and carpels of a Buttercup, Strawberry, and Blackberry, it is due to the retention of spirals of many cycles, but much compressed ; as may be seen also in the scales of a Fir-cone.

It is thus that Nature uses a leaf-bud and develops it into a branch covered with leaves for one purpose. On the other hand, she shortens the branch and compresses the cycles of leaves into whorls, altering their position and structure, and turns them into floral organs.

We must now take one step further back to account for the existence of spirally-arranged and oppositely-situated leaves on branches. In dicotyledons we start from the two opposite cotyledons, or seed-leaves, in the embryo. The reader might ask, how can these give rise to a spiral arrangement of single leaves ; though it might be easy to comprehend how whorls of fours can be got by suppressing alternate *internodes*, that is the spaces between successive pairs of leaves, in the case where leaves are opposite. The fact is that plants often have both *opposite* and *alternate*, that is spirally-arranged, leaves, situated on the same stem or branch. The Jerusalem Artichoke is a good illustration, and especially useful for the study of

leaf arrangements. If a stem be found having opposite leaves below, and alternate above, to attain this latter condition short internodes are at first developed between the two opposite leaves of two or three pairs; thus separating the leaves of a pair in each case. The leaves at once assume slightly different positions, no longer being strictly opposite. Now it will be found that as soon as the

FIG. 2.—Diagram illustrating the method of change from "opposite" to "alternate" leaves.

upper leaves on the stem stand well apart and singly, the spiral line can be at once drawn through their positions, and the *order* in which the leaves are produced can be detected. It is almost invariably as shown by the accompanying diagram, in which the leaves are placed as if remaining

opposite in pairs, viz. 1 and 2, 3 and 4, 5 and 6, &c. constituting the original pairs. The arrows indicate the order in which they occur up the stem ; and it will be seen that the sixth leaf falls over the first.

It is thus that the numerical arrangement of the parts of most flowers can be accounted for. There are, of course, as in all rules in Nature, some exceptions, but these can always receive their own special interpretations.

II. COHESION ; AND III. ADHESION.—The cohesion of sepals, &c., is an advance upon freedom, and the general interpretation of this condition appears to be to gain strength to support the weight of the insect which alights on the “limb,” or free portions above the tube. We may select flowers which seem to indicate Nature’s progressive attempts, as follows. If we take a Wallflower we shall find that though there is no cohesion among the four sepals into a tube, they are all erect, stiff, and that two overlap the other two, forming a false tube, so to say. Though not united they are rigid enough to keep the slender stalks or “claws” of the petals erect ; the limbs of which form a sort of Maltese cross, which is now firm enough to carry a bee. In the Carnation we find an advance, in that while the form of the petals is just the same as in the Wallflower, the

sepals are now coherent into a rigid tube. If we next turn to a Primrose we see that the petals, while still retaining much the same shape, have their claws united into a tube within the calyx-tube. These latter now give an additional support to the limb.

In certain families the filaments or anthers may be coherent, and the clue to discover the cause of these unions is also the methods by which insects extract the honey from the flowers. Thus in the Pea-family (*Leguminosæ*) we find that in the great majority of cases, as in the Pea, there are ten stamens, the filaments of which are more like ribbons than threads, and are united edge to edge, thus forming a split tube; for there is a single stamen on the upper side which is free; so that the tube is, as it were, split down that side where the free stamen lies. The honey is secreted within the tube at the bottom by a *disk* which surrounds the little support to the single carpel which constitutes the pistil within the staminal tube. The passage to the disk, on either side of the free stamen, thus enables the insect to reach the honey. In Laburnum, Broom, Furze, &c., there is no honey, and the stamens are now *all* united, the passage being closed up by the tenth stamen being coherent with the other nine.

In the family *Compositæ* the anthers are united,

but not the filaments; they thus form a cylinder, supported by the free filaments which are adherent to the tube of the corolla; just as if we took a piece of pipe and supported it erect on five sticks. The pollen falls within the tube, and in order to remove it the style grows upwards within the latter and pushes the pollen out at the top, so that bees when crawling over the head of florets which constitute the ordinary "flower" of a Dandelion, Daisy, &c., get well dusted with pollen. The honey is secreted at the bottom of the little corolla-tubes, which thus get more or less filled with it.

What induces cohesions and adhesions to take place? The best reply to be given at present seems to be that they are the results of local nutrition, due to an excess of irritations. Good illustrations of abnormal unions may be often seen in tropical and other "Orchids" which are cultivated; for it is a very common thing to find one or more petals or sepals coherent or adherent in various ways, other than what is normally the case; and such unions can presumably be only attributable to the artificial treatment the plants receive under cultivation. Again in several members of the cone-bearing family the leaves of adult and vigorous shoots are partly adherent to the branch, but in younger or weaker shoots they are free from it. Such and other instances seem to

suggest *hypertrophy* or excessive nutrition directed to particular places in the plant as the cause. In the case of wild flowers, the extra nutrition has been induced by the irritations applied to certain parts of the flower, such irritations being presumably due to insects which visit them; their weights, pressure, as well as the probing for honey being the irritating agencies, while cohesions and adhesions are the results of the extra flow of nourishment to the parts thus irritated by them. Further illustrations of this process will be given later on. It is, of course, theoretical, but, as will be explained, the theory is perfectly consistent with innumerable facts which together render it highly probable.

IV. FORM.—We now come to consider the feature which is really the main fact which gives rise to the immense variety which exists among flowers. It has already been observed that we must distinguish between regular whorls and irregular ones; or, as it is commonly expressed, regular and irregular flowers. The corolla is usually the most conspicuous feature, but when this is irregular, the calyx and stamens are for the most part irregular too, in correlation with it. The first observation which cannot fail to be made is, that irregular flowers are never terminal, unless they are solitary, like *Gloxinia* and *Violet*; but are situated at the sides of the stems and branches, or laterally, so that

their insect visitors can only enter them on one side, or from the front. Now here we have not one, or a few isolated instances only, but a rule, applicable to innumerable members of the floral world. Moreover, however different the *ground plan* of the flower may be, it is a very common thing to find just the same form assumed in widely different plants. Thus the hood-like sepal of Aconite is imitated by the posterior petals of the Dead-nettle. "Spurs" are found in the Columbine, Violet, Toad Flax (*Linaria*), and *Orchis*, &c. Expanded front petals called "lips" are equally abundant, &c. Similarly "Declinate" stamens, which bend downwards and then turn their anthers upwards, may occur in any flower in dicotyledons or monocotyledons alike.

Again, members of the *Labiatae* resemble some of the *Scrophularineae* in certain particulars. And if the resemblance is wanting in the corolla, certain curious features may be found in genera with no common affinity whatever. Thus the swinging anthers of *Salvia* are found in some species of *Calceolaria* and in the monocotyledon *Curcuma*. Similarly the "jumping" style of *Stylidium*, a dicotyledon, reappears in *Maranta* and its monocotyledonous allies. So too, declinate and uprising stamens occur in *Aconitum*, *Dictamnus*, *Alstræmeria*, &c.

These and other features of irregular flowers,

so often repeated in the flowers of plants having no affinities whatever, all point to some common cause, that cause being apparently the action of the insects themselves, the same or similar kind of insect presumably bringing about the same or similar results in very different flowers.

As the sizes and forms of insects are practically unlimited in number, so are the forms of flowers which have grown in correlation to them. So close is this agreement in many cases, that unless a plant, such as species of Aconite, can receive the visits of some one or very few kinds of bees, it has but little chance of setting seed at all.

Besides the above-mentioned similarities between single organs, entire flowers may strongly resemble one another in form, though belonging to quite different families. Such likenesses have been called Floral Mimicry. Thus, for example, the Pea-blossom is mimicked by *Corydalis*, *Polygala*, *Pelargonium*, *Corydiflorum*, *Collinsia*, &c. Again, *Crocus* closely resembles *Colchicum*; while "bell-shaped" flowers are found both in dicotyledons and monocotyledons, &c. &c.

Such instances of mimetic forms could be multiplied almost indefinitely; and what I would maintain is, that as the use of them is the same, namely, pollination; and as they occur associated with other details, all correlated for one and the

same object, viz. the intercrossing by insects ; so, therefore, one and the same cause has brought them all into existence, namely, the irritations caused by similar insect visitors. The result is that the flowers, within the limits of their own structural possibilities, have grown alike respectively, and become "mimetic."

ADAPTATIONS FOR POLLINATION IN SELECTED TYPES OF FLOWERS.

CLASS I. DICOTYLEDONS.

DIVISION I. THALAMIFLORÆ.

COMMENCING with the Buttercup (*Ranunculus bulbosus*, of the order *Ranunculaceæ*) as a type of a perfectly regular flower, the golden yellow petals are the attractive organ ; each petal has a little honey-pit or *nectary* at its base. This is very easily accessible, so that no less than sixty different kinds of insects have been observed extracting the honey. There is an immense number of stamens spreading in all directions, so that any insect alighting on the flower cannot fail to get dusted on its under side ; and as the stigmas form the most exposed part of the pistil in the middle, it is easy to understand how readily a flower can get pollinated by insects.

It must not be forgotten, however, that as a great part of the pollen is shed just when the stigmas are ready to receive it, it is quite able to set every seed, *i. e.* one in each carpel, without insect aid at all.

Another plant which belongs to the same family or order (*Ranunculaceæ*) as the Buttercup, is the Aconite or Monkshood. This flower has become "irregular" through great modifications, all of which are adaptations to insect fertilization. The calyx has assumed the duty of attracting insects by becoming blue. It consists of five sepals; the "posterior" one now resembles a helmet, and conceals the two petals. These are the only ones left out of five, three being no longer wanted, while the two are converted into structures resembling croziers which secrete honey. The stamens are numerous, and at first hang downwards, to which the bees cling. As they mature successively, their filaments rise up and hold the anthers projecting forwards, so that they must be touched by the bee.¹ The carpels are three in number; their stigmas are so situated that they cannot fail to strike the bee just where pollen has been deposited.

The Aconite therefore furnishes us with a number

¹ Identically similar procedure will be found in other plants, such as *Dictamnus*, *Alstrœmeria*, and Rose-bay Willow-herb (*Epilobium angustifolium*), &c.

of correlations as follows:—A metamorphosed, coloured, and irregular calyx; petals metamorphosed into nectaries; dependent stamens endowed with motion so as to elevate them at the proper time when the anthers are mature; and lastly, stigmas correctly placed for pollination while the insect is extracting the honey from the petals.

With regard to the fertilization of Aconites, so highly “specialized” are they, that no insects other than a few kinds of bees—in some cases only one species of bee—have been seen to visit the flowers; so completely adapted have the flowers become to large kinds of bees alone, that other insects cannot get at the honey, and consequently neglect to pay the Aconite any visit.

It must be borne in mind that the Aconite is by no means singular in this respect; indeed, the rule holds good for all specialized flowers, that the more they are adapted to particular kinds of insects, the less are they visited by others. Another fact of all such flowers is noticeable, that whenever a flower becomes markedly specialized, and is attractive to insects, with a very conspicuous corolla, or calyx, or both, the stamens mature their pollen, and often shed it entirely, before the stigmas are sufficiently developed to receive it. This condition is called “protandry,” a word signifying “stamens first.” Such flowers, therefore, run a great risk, in the

absence of the proper insects, of setting no seeds at all, and therefore may die out altogether.

We will now take the Wallflower, belonging to the order *Cruciferae*. This has four sepals in pairs, two lateral, and two "anterior" and "posterior." They stand erect, the latter pair overlapping the edges of the former so as to form a sort of false tube. The petals are four, with long slender stalks or "claws." If we remove the sepals, the petals instantly fall down, showing the use of the stiff sepals for supporting them. There are six stamens, two shorter than the other four. Now these two bend outwards so as to leave a hollow space or sort of tube from top to bottom, down to the "honey-gland," which is not on the petals as were the nectaries of the Buttercup, but is a swelling on the *floral receptacle*, as the extremity of the flower-stalk is called, round the base of each of the lateral stamens. The lateral sepals will be observed to be somewhat pouched at the base, and are therefore able to collect the honey secreted from the glands. The two tongue-like stigmas are directed towards the back and front of the flower, that is, in the posterior and anterior directions, forming a sort of fork over which the proboscis of the insect passes in its way down to the honey-gland.

Here, then, we have every facility for an insect to transfer the pollen from one flower to another ;

and the several correlated points of structure are, the honey-gland on the floral receptacle ; the bag or pouch-like sepals to collect the honey ; the tube-like arrangement of the sepals ; the "cruciate" or cross-like corolla formed by the brightly-coloured limbs of the petals, forming a landing-place for the insect ; the anthers standing erect close to the "tube" ; and the flap-like stigmas ready to remove the pollen from the proboscis of the insect as it glides over it.

Let us compare this flower with that of the Shepherd's Purse. This plant, which belongs to the same family, or "Crucifers," from the cross-like petals, is so inconspicuous as never to be visited at all. There is no honey-gland, no honey, and no scent. The stigmas, instead of spreading, form a globular head ; and the anthers are placed close in contact with it. Both anthers and stigmas mature together, and it is perfectly well able to set its own seed, which it does in abundance, so that it is one of our commonest weeds. Hence a clear gain is secured by its not being dependent upon insects at all ; for the sole object of plant life is to set seed, and so keep up a succession of its kind.¹

¹ It was formerly thought that this process of "self-fertilization," as it is called, was in some way injurious to a plant ; and that if the kind or species was never "crossed," it would die out. It is now known that this idea was based on an altogether erroneous inference. The fact really is that habitually self-fertilized plants are the most prolific.

Such small-flowered, self-fertilizing plants are among the most widely dispersed of all flowering plants ; and another remarkable feature about them is, that they often become far more abundant and grow to a much greater size when transported to foreign countries, than is the case in their own country. Indeed even small plants in England have become formidable opponents to the native vegetation, from their size or rapidity of multiplication. Thus the Water-cress grows twelve or more feet long, and nearly an inch in thickness in the rivers of New Zealand ; and the Knotgrass (*Polygonum aviculare*), and others of our English weeds will cover many square yards.

There is a considerable number of species of the order *Cruciferae*, with very insignificant and unattractive flowers, all of which are habitually self-fertilized, and mostly very common, several being widely dispersed, such as the Bitter-cress (*Cardamine hirsuta*), Hedge-mustard (*Sisymbrium officinale* and *S. Alliaria*), Vernal Whitlow grass (*Erophila verna*), Watercress (*Nasturtium officinale*), Shepherd's Purse (*Capsella Bursa Pastoris*), Wart-cress (*Senebiera Coronopus*), &c. They nearly all agree in the minuteness of their petals, the globular stigma, the absence or reduced size of the honey-secreting glands, general unattractiveness, and, on the other hand, in the abundance of their seed.

The presence of the corolla and the structure of the flowers, being on the same plan as in the conspicuous flowers of the Wallflower, Stock, Cabbages, Radish, Honesty, Dame's Violet, and others, reveal the fact that these little flowers have been derived from ancestors which were formerly attractive to insects, but that their existing descendants are now "degraded" or "degenerated," as botanists say. These words do not imply anything injurious to the flowers, but, as the words simply imply, "a step downwards," or "down from the genus"; and, as we see, so far from suffering in consequence, they gain enormously in the one and sole object of flowers, namely, propagation by seed.

Let us now examine the Pansy. Like the Aconite, this is an irregular flower. It belongs to the family *Violaceæ*, which derives its name from the genus *Viola*, which includes both Pansies and all kinds of Violets.

All the parts of the flower, excepting the three carpels, are free. To begin with, the flower is reversed in position, for what appear to be the upper petals are really the lowermost. A similar reversal is found in the spotted and other species of *Orchis*, in which the ovary which in this case supports the flower, is twisted. I would attribute this feature to the weight of the insects, and to the weakness of the support. An interesting fact,

which seems to bear this out, was observed by H. Müller, who says—

“I have observed very numerous bees visiting a handsome, large-flowered variety of Pansy, which is not uncommon on sandy soil at Lippstadt. *Apis mellifica* (the honey bee) always sucks in a reversed position, with its head downwards; it often alights in the usual position, and then turns round. Humble bees usually suck hanging back downwards to the flowers, which are bent down by their weight.”¹

Now, I think this reversal of position carries a very significant fact with it. An irregular flower, as the Snapdragon, always has the lowermost or “anterior” petal enlarged if it have to carry the insect, thus forming the so-called “lip,” or “labellum”; but if the flower be reversed, as of the Pansy and *Orchis*, it is really the “posterior” petal which now lies on the anterior side. It is this petal which supports the insect, and is now enlarged accordingly. This is true for the genera mentioned, and for *Ophrys* and others; whereas it is, as is the rule, the anterior petal which forms the labellum in other genera of *Orchids*, e. g. *Listera*, or the Tway-blade.

The importance of the foregoing observations lies in their testimony to the ease with which any

¹ *The Fertilization of Flowers*, p. 118.

part of a flower can become adapted to insects, in whatever way it may happen to grow.

Thus with regard to the Pansy and Violet, the posterior petal having become the lowermost, is prolonged into a tube, closed at the end, called a "spur." Two of the five stamens, which are immediately over the spur, are provided with honey-secreting appendages, which lie within the space which collects the honey. The five anthers form a hollow cone round the ovary of the pistil. When an insect alights on the lower petal, it is guided to

Fig. 3.—Styles and Stigmas of two forms of Pansies, (*a*) that of the larger and intercrossing; (*b*) that of the self-fertilizing form.

the orifice of the honey-bearing spur by means of streaks of colour, which are called "guides," or "path-finders." There is also one on the style (Fig. 3, *a*, *g*). It passes its proboscis down the tube, forcing the anthers asunder in its passage. It thus gets dusted with pollen. On entering another flower, the stigma (Fig. 3, *a*, *st*), which projects beyond the anthers (forming a sort of mouth with an extended tongue (*t*), on a globular head), now

receives the pollen. In order to ensure this, the style is bent just above the ovary, and thus forms a spring (*spr*), which tends to keep the stigma down upon the front petal, so that the tongue-like stigma (*t*) cannot fail to scrape off the pollen from the proboscis when forced under it.

The stigma, moreover, has two fringes, one on either side, and these keep the pollen back just at the entrance to the spur, so that none can reach the stigma in front. Consequently the Pansy is unable to fertilize itself, and fails to set seed unless visited.

There is a very small flowered variety, of a pale yellow colour, common in corn-fields, in which these hindrances to self-fertilization are wanting (Fig. 3, *b*), so that it is quite independent of insects, and consequently sets abundance of seed.

In the Violet, which is another species of the same genus (*Viola*) to which the Pansy belongs, the flowers are very similarly constructed, and, strange to say, practically never set seed at all in this country, though they do so in warmer climates, as Liguria. After a plant has done flowering in spring, the leaves begin to grow, and if they be lifted up, runners will be discovered which produce a succession of minute flower-buds at the joints. These never open, and are of very different structure from those which produce the ordinary flowers.

The corolla is usually quite arrested, or else the petals are minute and greenish (Fig. 4, *a*), the stamens have no honey-secreting appendages (Fig. 4, *c* and *f*), and the style is very short with a truncated end, which forms the stigma (Fig. 4, *d*). The

Fig. 4.—Cleistogamous flower of the Violet (*Viola odorata*): (*a*) petals; (*b*) spur only of a petal; (*c*) stamen; (*d*) pistil.

anthers lie over it, so that the pollen tubes enter it while the grains lie within the anther cells (Fig. 4, *g*). As these buds (4, *e*) never open, being protected by the sepals, they are called “cleistogamous,” a word

(*e*) Cleistogamous flower-bud of *Viola canina*; (*f*) stamen; (*g*) stamens, with anthers over the stigma, uplifted by the swelling ovary.

signifying “concealed unions.” They set seed abundantly.

There are several facts which seem to point to temperature as playing an important part as well as nutrition in the production of these little buds.

Thus the common sweet-scented Violet does not produce them in some countries, where the conspicuous form of flower is perfectly fertile. On the other hand, they are produced by Violets in all parts of England.

Of other species, *Viola nana* bears ordinary flowers in its native home in India, but only cleistogamous ones in England. Again, *Viola palustris* bears only the larger flowers near Paris, which are perfectly fertile, but when it grows on mountains it bears cleistogamous flower-buds. Lastly *V. Roxburghiana* had abundance of cleistogamous, but no perfect flowers, in Mr. Darwin's hothouse; and it bears the perfect flowers in India "only during the cold season, and these are quite fertile. During the hot and more especially during the rainy season, it bears an abundance of cleistogamous flowers."¹

From these facts it will be seen that, assuming that the conspicuous flowers have been formed through the agency of insects, the cleistogamous buds contain adaptations for self-fertilization, and are degradations² from the former kind, brought about by climatic and perhaps other conditions furnished by the environment.

¹ Darwin's *Forms of Flowers*, p. 320.

² That they are really derived from the conspicuous flowers which are adapted to insects, may be seen in the fact that in strong growing garden plants the "spur" may sometimes be found without the "lip" to the front petal (Fig. 4, *b*).

The next flower to be examined is the Clove Pink (*Dianthus Caryophyllus*, of the order *Caryophylleæ*). This has petals with long claws like those of the Wallflower; but in order to support them, Nature has, so to say, advanced a step, for now the sepals are coherent into a perfectly rigid tube, and not merely overlapping as in that flower. The stamens are so strongly protandrous, that the anthers have generally shed their pollen some time before the two long stigmas are ready to receive it. The flower being attractive both by colour and scent, is therefore almost entirely dependent upon insects. When, therefore, experiments were made by Mr. Darwin, he was often obliged to take pollen from other flowers of the same plant, instead of using pollen from the anthers in the same flower as the pistil to be experimented upon—that is, to secure self-fertilization. By this means the time between the maturation of the anthers and stigmas was reduced; so that after the third generation, plants were raised quite capable of fertilizing themselves. Moreover, the colour of the petals changed, becoming of a lighter or brick-red tint, instead of being a dark crimson. This experiment is interesting, for it shows that flowers *can* become self-fertilizing which are usually not so. As so many flowers—indeed the majority—though they may be often crossed by insects, as the Buttercup, can readily

fertilize themselves, it is presumable that complete self-fertilization could be in all cases easily recovered, as it has, indeed, been under experiment not only with the Clove Pink, but with many others, which normally are quite incapable of fertilizing themselves.

Another plant belonging to the same family as the Pink, well illustrates an intermediate condition which is very common in flowers, as *e.g.* in certain kinds of our Wild Geraniums. The Greater Stitchwort (*Stellaria Holostea*), so common in our hedges in early summer, has rather a large white flower with two whorls of stamens, containing five in each.

Fig. 5.—Chickweed: (a) closed flower-bud; (b) expanded, showing petals reduced in size : stamens, three only ; anthers closely adpressed on the stigmas.

One set, the outermost, sheds its pollen *before*, the other set does so *during*, the time that the stigmas are mature. So, if the flower were not visited at all it can set its own seed by the second whorl of stamens. Its relative, the Chickweed (*Stellaria media*), has very insignificant little flowers. The corolla is similar in form, but much reduced in size. Instead of ten, there are generally five or even only

three, stamens (Fig. 5, *b*); which, instead of spreading *away* from the pistil, as is so commonly the case with flowers visited by insects, are now closely adpressed against it, bringing the anthers in direct contact with the stigmas (Fig. 5, *b*), as is the rule with regularly self-fertilizing flowers. The stigmas are much shortened, so that they are in contact with the anthers. They mature together, and so the flower is regularly self-fertilized. It is only in bright sunny days that the flower is fully expanded. In dull weather, and even throughout the winter—at least when snow is not on the ground—this little but vigorous weed continues to set seed, even within the buds, which under such circumstances do not open at all. Hence the conclusion is suggested, that it has degenerated from some more conspicuously flowered form of the species by continual self-fertilization consequent on the neglect of insects. And, as a usual result we find this species to be cosmopolitan in its range. It is a very variable plant. Some specimens from South Europe have quite a large corolla and ten stamens, and are called the variety “grandiflora”; others have the petals exceeding the sepals in length, the stamens being five in number; others, again, have a smaller corolla with three stamens; and lastly, some have no corolla at all, and never open the calyx; such are strictly cleistogamous. This variety is very

abundant and the only one in Egypt. Hence this species is interesting as furnishing a complete series of gradations between a large flower attractive to insects, and minute cleistogamous buds without any petals at all.

As in Crucifers, so in the present order *Caryophyllæ* there are a certain number of species with very conspicuous and attractive flowers, such as several kinds of Pink, the Soap-wort (*Saponaria officinalis*), Catchflies (*Silene*), Campions (*Lychnis*), and Corn-cockle (*Githago segetum*); while, on the other hand, there are many "weeds," with very insignificant flowers, and, as may now be anticipated, highly self-fertile—such as the Chickweed (*Stellaria media*); several kinds of the Mouse-ear Chickweed (*Cerastium*); Sand-worts (*Arenaria*); Pearl-worts (*Sagina*)—one species of this last has been degraded so far as to lose its corolla altogether, and is called *apetala* in consequence; Spurry (*Spergula arvensis*); and lastly, *Polycarpon tetraphyllum*—this name, "Much-fruit," given to it by Linnæus, is an unconscious witness to the advantages of self-fertilization!

DIVISION II. CALYCIFLORÆ.

In this division the petals are always free, and together with the stamens adherent to the border of the calyx.

The first family of importance to be mentioned is the *Leguminosæ*, already referred to, which includes Peas, Beans, Clovers, Vetches, &c. The blossoms have been called "papilionaceous," from some fancied resemblance to a butterfly on the wing ; while the petals have received special names as follows:—The large one at the back is called the Standard, the two at the sides are the Wings, and the two coherent in front constitute the Keel petals. The general structure has been already described.

Though the flower of the Common Pea is well adapted for intercrossing, it is perfectly well able to set seed of itself ; indeed, it is rarely visited. Although it secretes much honey and affords much pollen, Mr. Darwin said that he had observed the flowers for thirty years, and in all that time had only thrice seen bees of the proper kind at work, such as were sufficiently powerful to depress the keel. This is a case, therefore, of a plant with a highly specialized flower having either retained or reacquired perfect self-fertility in a foreign country.

The White or Dutch Clover (*Trifolium repens*) of the order *Leguminosæ*, is constructed like the Sweet Pea, and is visited by the hive-bee and a few other insects. When insects are excluded by means of a fine net only one-tenth of the usual quantity of seeds is produced. So infertile is it that when it was first

taken to New Zealand, where our hive-bee is not a native, but little seed was set. The difficulty was overcome by introducing the bee into that country. The Red Clover (*T. pratense*) differs from the White in having all the petals coherent into a tube—a very exceptional condition in the Pea family—which exactly fits the tongues of the humble-bees, which are apparently the only kinds which can properly fertilize it. Consequently in wet seasons, when not many bees are about during the flowering period, but little seed can be saved by the farmers. To show how intimately one thing depends upon another in Nature, Mr. Darwin observed—that as field-mice devour the comb of the humble-bee, it would be advantageous to sow clover in fields near to habitations where there were plenty of cats, so that they might keep down a superabundance of field-mice. In that case humble-bees might multiply, and consequently cats would thus indirectly benefit the farmer in securing a good crop of clover seed !

With regard to the fertility of the Red Clover, Mr. Darwin found by experiment that a hundred flower-heads on plants protected by a net did not produce a single seed ; while a hundred heads on plants growing outside which were visited by bees yielded sixty-eight grains weight of seed.

Like the Pea in England, but apparently unlike the Dutch Clover, the Red Clover proved to be

perfectly self-fertile, both in New Zealand and Victoria, before the humble-bee was introduced for the purpose of fertilizing it.¹

Although there is a general resemblance in the structure of flowers of the Pea family, and they are all fertilized much in the same way by insects—if they be not entirely self-fertilized, as is the case with several minutely flowered species—yet there are peculiar differences in certain genera, which are not uninteresting. In the majority of cases the stamens and included pistil lie horizontally within the boat-like keel petals, and are only exposed by the weight of the insect depressing the latter, when they rise up and dust the bee on the under side. In the common Bird's-foot Trefoil (*Lotus corniculatus*) as in the Lupins of our gardens, the keel tapers upwards to a point like the prow of a gondola. Within this the pollen accumulates. The filaments swell just below the anthers, so as collectively to form a block below the mass of pollen. When an insect alights, it forces down the keel-petals, and the pollen is consequently exposed. This has been called the piston-action ; but this expression is more applicable to the process in a Daisy or other members of the Composite family ; for while

¹ Syme, *The Modifications of Organisms*, p. 113: K. Paul and Co. A writer who accepts the theory advanced in this work.

in that case the pistil acts like a piston in a steam-engine, and drives the pollen out of the cylinder composed of the coherent anthers ; in the Lupin it is the cylinder of petals which is forced backwards, and so the pollen becomes exposed.

I have already described two species of Clover, but there is another (*Trifolium subterraneum*) which is remarkable, not for its method of fertilization, which is probably "self," but for the curious way in which it buries its fruit. After flowering, the little "head" of flowers bends downwards till it reaches the ground, the stalk growing, if need be, to elongate it. The head consists of about one to three flowers which form pods ; the rest on the top are abortive. As the pods enlarge they bend backwards upon the stalk, *i.e.* downwards, while the abortive flowers form a small sharp-pointed cone in the middle ; the point penetrates the earth. The abortive flowers merely consist of a rigid calyx ; the five free portions of the sepals now spread out like claws and dig up the earth, piling it over the pods behind them, not unlike the way a mole digs out the earth and pushes it aside. Now the calyx is provided with hairs, which are capable of absorbing nourishment from the earth, which they convey to the fruit ; and it is found that if perchance pods do not succeed in getting buried, the seeds within them do not ripen. It was in consequence of this peculiar

habit that Linnæus gave it the name *Trifolium subterraneum*.

In the Dyers' Greenweed (*Genista tinctoria*) and other species of the same genus, the wings and keel petals are in a high state of tension when the flower is mature (Fig. 6, *a*). Their little stalks or claws are horizontal, but the moment the flower is touched they curl downwards, thereby flinging the petals down with a sort of explosion (Fig. 6, *b*, *c*), the stamens darting upwards simultaneously; so that if an insect alight upon the keel, it cannot fail to be well dusted.

In the Medicks, such as Lucerne (*Medicago sativa*), there is a similar explosion, but it is effected by the stamens, and not the petals, being in a state of tension. As soon as the flower is visited by a bee the stamens cease to be horizontal, and suddenly spring upwards and become semi-circular, while the anthers strike the bee on the under side.

Fig. 6.—*Genista tinctoria*: (*a*) before; (*b*) after explosion; (*c*) claws of keel petals.

It is a remarkable fact that the power of self-fertilization is sometimes wanting in a species, while another so closely resembling the former that some botanists would not hesitate to call it a "variety," may fertilize its own flowers with the greatest ease; just as closely allied species will sometimes cross with great difficulty, while species so far differing from each other that some botanists would call them by different generic names, will cross readily. All this means that "morphological" differences, seen in the "forms" of parts, do not always run parallel with "physiological" differences, only revealed by the results of experiments; species being made by botanists, as explained above, solely on their morphological characters, *i.e.* differences in their visible organs, roots, stems, leaves, flowers, &c.

The French Bean (*Phaseolus vulgaris*) and the Scarlet-runner (*P. multiflorus*) illustrate these remarks. The former is regularly self-fertilized, and consequently it is this plant which is so often "forced" in winter when there are no bees about. On the other hand, the Scarlet-runner is largely dependent on bees. This explains the fact that writers in the Gardening Journals have from time to time complained of the failure of the crop, for at least half a century; as nothing was known till lately of the importance of the agency of bees.

The construction of the flower is curious. The keel-petals which enclose the pistil are bent at right angles, just above the upper end of the ovary; they are then twisted spirally, so that the extremity looks like a small snail-shell. The anthers and stigma are, of course, within the coiled-up extremity; the wings grip hold of the keel by means of depressions which fit upon corresponding knobs on the keel. When a bee alights on the *left* wing (as seen from the front), its weight pulls the keel down, the brush-like stigma sweeps past the anthers and becomes exserted from the orifice of the "helix," and deposits the pollen on the bee; and at the same time receives the pollen caught from a flower previously visited. By taking hold of the left-hand wing-petal and moving it up and down, it will be readily seen how the stigma comes out of, and retires back within the orifice.

DIVISION III. COROLLIFLORÆ.

In this division the corolla is always in one piece, in consequence of the cohesion of the petals. It contains many orders, including those which botanists regard as the most highly differentiated, or which have advanced furthest from the primitive and simple type, as seen, for example, in the Butter-

cup. Many have regular corollas, but several orders are characterized by irregularities.

The first order to be noticed is the *Compositæ*. The flowers of the plants of this family are "composite," *i. e.* they consist really of innumerable florets, each being capable of setting its own seed. The calyx is either wanting, as in a Daisy, or reduced to minute scales or hairs, the so-called

Fig. 7.—Stamens of *Centaurea*: (a) anthers closed; (b) open, with style and stigmas protruded.

"down" of Thistles, Dandelions, &c.—botanically it is called the "pappus." The corolla is a little tube which holds the honey secreted at the base by a little ring or cup in which is the style (Fig. 7, *a*). The filaments, as stated, spring from the inner side of the corolla-tube, and support the united and closed-up anthers.

The style passes up the middle of these, forces their tips asunder, and ultimately appears out above them with its two spreading stigmas (Fig. 7, *b*), or coiled back like miniature ram's-horns, as in the Dandelion.

The tubes of the corolla vary much in length in different species, and are consequently visited by different insects.

Dr. Herman Müller, who observed all the insects which visited Composites near Lippstadt in Germany,

records no less than 546 species of insects in the following average proportions:—*Lepidoptera* (Butterflies, &c.), 15 per cent.; *Apidae* (Bees, &c.), 41 per cent.; and *Diptera* (Flies, &c.), 27 per cent.; other short-tongued insects, 17 per cent. Bees, therefore, proved to be the chief visitors. This is almost invariably the rule; the only species mentioned by Müller in which short-lipped insects surpass the *Apidae* in number is the Ox-eye Daisy (*Chrysanthemum leucanthemum*), in which the honey rises into the widening throat of the corolla, and is therefore easily accessible.

Contrasting this with *Centaurea Jacea*, which has a corolla-tube more than three times the length of that in the Ox-eye Daisy, the *Lepidoptera* now rise to 27 per cent.; *Apidae*, about 59 per cent.; while *Diptera* sink to nearly 12 per cent.; and other short-lipped insects are only 2 per cent.

The *Compositæ* thus well illustrate the fact that corolla-tubes are proportionate in length to the highly-specialized insects, a universal feature seen in all other orders as well. The enormous number of species and wide diffusion of the *Compositæ* are proofs of the advantages accruing to it from the peculiar structure of the flowers.

On the other hand, as elsewhere, the self-fertilizing forms are very and particularly widespread. Indeed it is probable that few "heads" cannot be

fertilized by the pollen from the same. Though this is strictly crossing flowers on the same plant, the physiological state of any two florets of the same head is probably the same ; so that it would be practically equivalent to self-fertilization. In the common Groundsell (*Senecio vulgaris*), how-

Fig. 8.—*Phyteuma* ; corolla showing congenital cohesion below ; cohesion by contact above.

ever, the stigmas often fail to escape from the anther-tube ; so that such florets are strictly self-fertilized, and I need hardly remind the reader of the abundance of this troublesome weed.

In the order *Campanulaceæ*, which includes the Hare and Canterbury Bells as well as Lobelias, there is one plant which is interesting as having both kinds of cohesion mentioned above exemplified at the same time. It is *Phyteuma*, a plant with heads of small blue florets, not uncommon on the Chalk Downs of Kent. The lower portion of the corolla consists of congenitally united petals ; but the five portions of the limb cohere *by contact* at the apex, and so form a tube which collects the pollen shed into it by the five free

anthers which are included within the corolla-tube (Fig. 8). They thus form the "cylinder" for the "piston" action of the pistil, the style of which continues to grow, and so sweeps out the pollen beyond the extremity of the tube, just as it does from the syngenesious anthers of the *Compositæ* and *Lobelia*.

The order *Primulaceæ*, which contains many species of *Primula*, such as the Primrose, Cowslip, Oxlip, Auricula, &c., as well as many other genera, as the *Cyclamen*, Pimpernel, Money-wort, &c., may be taken as a good type with regular flowers. I have already alluded to the Primrose as illustrating the tubular structure in the corolla, which affords such an increase of strength in comparison with the complete freedom in the Buttercup.

The chief peculiarity of the majority of the species of *Primula* is the different lengths of their stamens and styles, which have given rise to the word "Heterostylism." It occurs, however, in other plants of very different orders. Thus it is found in a St. John's-wort (*Hypericum ægyptiacum*), in the Wood Sorrel (*Oxalis*), in the Purple Loostrike (*Lythrum*), and Buckwheat (*Polygonum Fagopyrum*), as well as other plants of different orders. The two kinds never occur on the same plant, and the rule is that more seed is set when stigmas are fertilized with pollen from stamens of the same length as the styles which

bear them, than when they are of different lengths. Consequently the first are called "legitimate" or "homomorphic," *i. e.* "like-formed" unions; the second "illegitimate" or "hetero-morphic," *i. e.* "other-formed" unions.

The differences are easily observable, for in one, the "short-styled" form of Primrose or Cowslip, the anthers are visible at the entrance of the tube, the style of the pistil being very short. In the other kind, the "long-styled" form, it is exactly the reverse; the globular stigma now protruding, while the anthers are situated low down within the tube. On comparing two such flowers, the stigma of the short style is found to be on precisely the same level as the anthers of the short stamens of the other. Now when pollen of the one is artificially placed on the stigma of the other, or *vice versa*, more seed is found to be set than when the stigmas are pollinated by the anthers of stamens of a different height. An insect flying from one kind of flower to the other would convey the pollen to the stigma, as its proboscis would be dusted at a point exactly suited for pollinating the pistil of the next flower.

The idea was, in consequence, maintained that Nature had so arranged and constructed the flowers *in order* to intercross them, and so *prevent* self-fertilization. And *if* bees would pollinate flowers

as carefully as Mr. Darwin and others have done in their experiments, the same results would probably follow in Nature.

Unfortunately, however, Nature cannot depend upon insects always crossing them in the legitimate way ; nor, indeed, upon their crossing them at all. The consequence is, that it is generally only those flowers with the short stigma upon which some pollen can fall from the anthers above them that manage to set any considerable quantity of seed. Such is the case with the Cowslip at least ; and of the four kinds of union possible, this was found by experiment to be the least fertile. Consequently, although this contrivance of heterostylism may *seem* to be admirably constructed for intercrossing, yet, when the flowers are left to Nature and the capricious visits of bees, &c., or else in their absence altogether, we find they have to be contented with the least fertile method.

We shall see hereafter what the "good" of intercrossing is ; but at present I only want to emphasize the fact that, coupled with these arrangements for crossing flowers, there are certain, not to say serious disadvantages to the flower itself.

Although the heterostyled condition is pretty constant in Nature, it is found that under cultivation the short style can sometimes grow up so as to bring the stigma up to the level of the anthers,

as is not infrequently the case in Auriculas, when highly nourished. On the other hand, the long style can be partially arrested in growth, so that its stigma may be on the same level with the short stamens in the same corolla-tube. This is often the case with *Primula Sinensis*, the Chinese Primrose, probably when allowed to be insufficiently nourished. In both cases self-fertilization ensues, which then proves to be a more fertile process than when they are correctly crossed in the heterostyled condition.

This power of fluctuating in the relative lengths of the filaments and styles would seem to give us the clue to the origin of heterostylism. For example, I have noticed many differences in the lengths of the stamens of *Narcissus cernuus* (Fig. 9), which is not a regularly heterostyled plant. The flower stalk or *peduncle* always bore the same kind of flower on each of the *pedicels* of the *umbel*. Thus there were mostly three flowers to each peduncle, as in Fig. 9, (*a*, *b*, and *d*); one specimen of *a* and one of *e* had only a single flower, and one of *c* had two flowers. In *a*, *b*, *c*, *d*, the three short stamens, as well as the three long ones, were all of the same height respectively; but in *e* one of the shorter set was taller than the rest.

Recognizing this instability of the stamens and pistil, it is reasonable to assume that it may be due

to varying degrees of nutrition, which can readily bring about such changes, a relatively strong vegetative vigour elevating the stamens in the one case, while a slight tendency to degeneration with lessened vital vigour tends to suppress the pistil in the other. Insect agency I take to have been the cause of heterostylism, through irritation with a consequent flow of nutrition. It has at the same time *fixed* the heights of the stamens and styles,

Fig. 9.—*Narcissus cernuus*.

so as to render them permanently dimorphic for legitimate fertilization. By "*fixed*" I mean that as only those stigmas would be dusted with pollen which came from stamens of the same height, a process of selection by the bees would go on; the plants which did not get fertilized would die out in time from setting no seed.

Other families with regular flowers in this division, *Corollifloræ*, are the Heaths, Gentians, Periwinkles,

Convolvulus, Borage, Potato, &c. None are without some special peculiarities, but they exhibit nothing which calls for particular note on the present occasion.

The first order with irregular corollas of the Division *Corollifloræ* to be noticed is the *Labiata*, or "lipped" flowered plants, of which the common White Dead-nettle (*Lamium album*) is a good type (Fig. 10).

The calyx is tubular and strongly ribbed, or

Fig. 10.—Dead-nettle ; corolla in section to show position of stamens and style.

otherwise provided with strengthening tissue to support the corolla, for the tube of this is very slender at the base, much widening above, with a three-lobed lip to support the insect. Plenty of honey is secreted by a disk at the bottom of the tube surrounding the four-lobed ovary, from which the slender style rises, terminating above with its two tongue-like stigmas. There are four stamens ; the fifth, on the posterior side of the corolla, being suppressed, the two filaments which spring from

the anterior side of the tube bend backwards, then rise up so as to bring their anthers just above the pair on the hindermost pair of filaments.

The observer will see at once how fitly everything is prepared to enable the bee to extract the honey, and be dusted with pollen simultaneously on its thorax, while the projecting stigma can remove what has been previously deposited there.

Another species of *Lamium*, not uncommon as a corn-field weed, is *L. amplexicaule*. This is peculiar for having cleistogamous flower-buds in early summer, but fully expanded flowers later on. They are simply undeveloped flower-buds; but while the corolla remains closed, the anthers and stigmas mature, so that it can set seed. Figure 11,

Fig. 11. —*Lamium amplexicaule*: (a) cleistogamous flower-bud; (b) vertical section; (c) pistil.

shows the structure of the bud, and how the style continuing to grow as if it had to extend beyond the flower, becomes crooked under pressure.

Taking *Lamium album* as a type, there are several modifications in different genera to suit

their particular visitors. Thus while the stamens are erect and arching *over* the bee in the Dead-nettle, they are horizontal and *lie under* the bee in Lavender, and some others.

In Mint and Thyme the flowers are minute

Fig. 12.—Thyme ; corolla and stamens (the style is concealed within).

and too small to be individually entered, or to support a bee ; but being crowded together they can collectively carry it, while it thrusts its tongue first into one flower then into another, just as in Composites and many other plants which have these flowers in "heads." The stamens are, nevertheless, of unequal length, and four only in number ; but they have lost the fixed arched position just as the corolla has become reduced in size. The stamens now standing up erect, or spreading out of the flower, the bee gets dusted in a less definite position. These flowers, therefore, indicate some degree of degradation from the very specialized flower of the Dead-nettle.

A genus with a still more highly specialized flower than that of *Lamium*, is *Salvia*. There are many species of this genus, one being the Garden Sage (*S. officinalis*), but they all agree in the way in which the flowers are crossed, though minute differences exist in each species in accordance with its adaptation to special insects.

With regard to the general structure of the flower, in the first place, the sepals cohere and the petals also, the one strengthening the other as in other cases. There are only two stamens, for the two hindermost have now become rudimentary. The corolla has a broad lip composed of the single anterior petal. This forms the landing-place. The two posterior petals together form a hood which conceals the anthers. Such are the general features; but a few more details will be advisable. The calyx is "two-lipped," that is to say, three of the sepals, easily recognized by three points, form the back part, while two points are seen on the front. They give the idea of the three and the two having been partly *wrenched asunder*. Now as each sepal is a sort of leaf, it has a cord running down the middle, corresponding to the "mid-rib" of a leaf. Hence one can count five mid-ribs in the calyx; but the observer will find several more, which do not occur in ordinary leaves at all. As the tube of the corolla is, so to say, an invention of

Nature's to gain strength to support the weight of the insect which alights on the lip, so the tube itself is supported by the tubular calyx. And to strengthen this, several additional cords are run up the tube along the lines of the margins of the sepals where they are coherent. The accompanying

diagram shows their positions—*d* standing for *dorsal* cords or mid-ribs; *m* for *marginal*; *s* being a supernumerary cord. We now see how cunningly the calyx-tube is strengthened, and how Nature can add one or more cords wherever any special strain is felt, and which must be met. The weight of the insect is all in front over the position of *s*. It is here where the greatest stress or tension lies. The centre of gravity not being in a vertical line directly down the tubes, the weight has, as it were, pulled the flower forwards and stretched the calyx; this necessitates the extra cords at the sides and back, as at *m*, *m*, and *m*, *s*, *m*, in front.

Now let us look at the corolla. One can scarcely

credit the fact that this is composed of five leaf-like parts, but so it is. The large flap in front is only one petal, the hood is composed of two, and the remaining pair are minute, rudimentary, and situated one on each side over the gaps in the calyx. Similar rudimentary lateral petals are seen in *Lamium* (Fig. 11).

Next let us investigate the nature of the stamens. There is reason to believe that the ancestor from which *Salvias* have descended had a regular flower,

Fig. 13.—Sage ; corolla, in section to show the position of stamens and style.

with five regular and coherent petals, with five stamens alternating in position with them. Of these, one at the back of the flower has entirely disappeared, two have become reduced to useless rudiments (Fig. 13, *r, st*), which are still present, and two only have remained effective ; but an extraordinary change has come over them.

If we examine the stamen of the Buttercup, it will be seen that the filament runs up *between* the anther-

cells. This part is called the *connective*. In *Salvia* it has a very remarkable form, like a curved rod (Fig. 13, *con.*), so that the two anther-cells are widely asunder, one at each end, as seen in Fig. 13 (*an*; *ab*, *an*).¹ The two connectives oscillate on their very short filaments (*fil.*), swinging in a vertical plane. If the lower anther-cell (which is generally abortive and devoid of pollen) be struck, the upper cell which contains pollen swings downwards in front; and if a bee be on the lip and has, in searching the tube for honey, struck the lower anther-cell and forced it downwards, then the upper one comes down and hits the bee on the thorax or back, depositing a packet of pollen. On retiring from the flower, the connectives swing back again within the hood; and when the bee repeats the process in another flower, it will be found that the stigma strikes her exactly where the pollen has been previously deposited. Such is the remarkable mechanism of the flower of *Salvia*, and all the details collectively conspire for one end, namely, the fertilization of the flower by insect agency.

I have already observed that it is a very general thing to find some species of a genus well adapted

¹ The separation of the anthers will be seen to have, so to say, commenced in *Thymus* by a thickening of the connective (Fig. 12, *con.*).

for insect fertilization, as that of the *Salvia* just described ; while other species of the same genus are specially fitted to secure self-fertilization. Even if the flowers have not degraded so as to become actually cleistogamous, all kinds of adaptations have arisen for securing it. Thus while *Salvia Verbenaca*, a not uncommon English species, is constructed as described, *S. clandestina* is a variety which is perfectly self-fertile. The pollination is secured by the stigmas, which are of great length and curl backwards, lying between the two anther-

Fig. 14.—*Salvia clandestina*: (a) corolla ; (b) stamens ; (c) style and stigmas.

cells, so that fertilization can easily take place. The corolla is extremely small, often inconspicuous, and probably rarely or never visited by insects. On the continent it is one of the commonest of species of *Salvia*.

DIVISION IV. INCOMPLETÆ.

I WILL now select a few examples from the fourth division of Dicotyledons—the *Incompletæ*. A large proportion are wind-fertilized, and although

all, I should say, without exception, are degradations from some ancestral state in which the flowers were adapted to insects, yet several have become again attractive, and are, so to say, revisited. Thus of the Dock Family (*Polygonaceæ*), the Docks (*Rumex*) are all adapted for being pollinated by the wind. Two species, the Sorrel (*Rumex Acetosa*) and Sheep's Sorrel (*R. Acetosella*), have stamens and pistils not only on different flowers but on different plants. Another genus (*Polygonum*) has twelve British species, of which the Bistort (*P. Bistorta*) and the cultivated Buckwheat (*P. Fagopyrum*) are attractive, and much visited by insects. This is in consequence of the calyx having become coloured or white—there being no corolla in any of these flowers; this organ, as in all other members of the *Incompletæ*, has disappeared altogether. Moreover, honey-glands have been formed, which are entirely wanting in the other species, which are self-fertilizing, such as Knotgrass (*P. aviculare*) and the Black Bindweed (*P. Convolvulus*).

With regard to the first two species, besides an attractive calyx, differences exist in the stamens, in that, while the Bistort is strongly protandrous, the Buckwheat is dimorphic and heterostyled, like the Primrose.

Of the wind-fertilized species, besides the Docks may be mentioned the Goosefoot, Orache, the

Salt-wort, Spurges, Dogs' Mercury, Box, Stinging Nettles, Hop, Elm, Willows and Poplars, Oak, Beech, Nut, Birch, and Alders.

A few Spurges and the Sallow Willow (*Salix Caprea*) are about the only ones which have recovered the power of attracting insects. In Spurges, especially some foreign species, the leaves or bracts surrounding the minute flowers have become coloured, being yellow or scarlet; and it is these which are conspicuous, and doubtless invite the insects to visit the plant; and as the coloured leaves all cluster round the flowers in the middle, they would be readily found. Perhaps the reader is familiar with the scarlet-leaved *Poinsettia*, an allied plant often sold as a table decoration in winter.

When a flower has degraded, and become wind-fertilized, but re-acquires some attractiveness, it never seems able to reproduce the characters of its ancestors. Thus in many of the *Incompletæ*, the calyx has become coloured; but the lost corolla is rarely, if ever, restored. Honey-glands are re-developed, which in all probability had been lost, as in Willows and *Polygonum Fagopyrum*.

These re-acquisitions all tend to show the ease with which flowers can respond to insects, as soon as the insects find something to attract them in flowers otherwise inconspicuous.

CLASS II. MONOCOTYLEDONS.

DIVISION I. EPIGYNÆ.

I WILL now pass on to the second class of Flowering Plants, or Monocotyledons, and select a few types from the first division, *Epigynæ*. A family remarkable for the great irregularity of the flowers is called *Orchideæ*, from the genus *Orchis*.

Of all flowers most specialized in their adaptations to insect fertilization, this family stands pre-eminent. The reader is referred to Mr. Darwin's work entitled, *The Fertilization of Orchids*, for full descriptions of several kinds. The peculiar feature in many is the total incapacity to set their own seed, in consequence of a projection called the "rostellum," upon which the pollen is rigidly fixed, until it be removed by insects. This is the case with the species of *Orchis*. But it must not be overlooked that here, as elsewhere, self-fertilization occurs normally in many genera, both in conspicuous flowers as well as in cleistogamous buds. There are several ways by which this is brought about. Thus Mr. Darwin describes the "Bee-ophrys" (*Ophrys Apifera*), in which the "pollen-masses," though fixed, can swing backwards on to the stigma. Hence this species sets an abundance of seed, and is very common. In some foreign

species the rostellum appears to be dwarfed, consequently the pollen can readily fall into the "stigmatic chamber."¹ This has given rise to cleistogamy in certain species. And it is just those species which are self-fertilizing that are most abundant, and the most widely dispersed.

Moreover, it has often been observed in Orchids, as with Violets, that although the flowers are very conspicuous and well adapted for insect visitors, the proportion of pods formed to the flowers previously borne by the plant is extremely small.

From what has been now said, the reader will see the need of caution, lest we should be too hasty in our judgment as to the use and value of these marvellous contrivances by which insects are enabled to cross flowers. Or again, that *because* they exist, therefore we *must* infer that they are necessarily of some important value to plants. The only way to discover the use is to examine large numbers, and ascertain to what extent seed is naturally secured by them—for this is the sole object of flowers in nature; and how far the species maintains its existence over the world, *i.e.* what is its distribution. Having done

¹ As this is not a text-book of botany, the reader is recommended to refer to Oliver's *Lessons in Elementary Botany* (Macmillan) for any further particulars on the structure of flowers. Remarks on the degeneracy in Orchids will be made later on.

so, the rule will be found to be that self- and wind-fertilizing plants are by far the most prolific and also the most widely dispersed. On the contrary, plants which bear flowers the most specialized in adaptation to insects, set comparatively the least amount of seed, and are, as a rule, most limited in their distribution over the globe.

We will now take the Iris Family (*Iridaceæ*). The three genera, *Iris*, *Gladiolus*, and *Crocus*, though so different in their general appearance, or *form*, all agree in the fundamental details of their flowers. They have only three stamens instead of six, the usual number in Monocotyledons. The style branches into three divisions, which generally flatten out below the stigmas, and being coloured resemble three additional petals, hence they are said to be "petaloid," or petal-like.

In the Iris, one stamen is found under each arching petaloid style; and the anther overhangs one of the outer reflexed petals, popularly called the "falls." The honey is secreted at the bottom of the filament. Lastly, the stigma is a little semi-circular ledge or flap on the underside of the petaloid style, which thus resembles the tip of the bowl of a spoon held downwards. A bee alighting on the "fall" petal, probes the little passage on either side of the filament, the anther conveniently bursting *outwards* instead of *inwards*, dusts

the bee on the thorax. On flying to another flower the spoon-like stigma scrapes the pollen off her back, which thus gets lodged upon the little stigmatic ledge.

It is clear that as there are three "falls," three stamens, and three stigmas similarly arranged, three different visits can be paid to the same flower.

In *Gladiolus* the flowers are arranged in a long "spike," consequently they can only be visited from one side, or in front. As in all other cases of a similarly lateral position, the flowers have grown irregularly; they have become "lipped," while guides are formed on certain petals only. The two hindermost stamens rise up, become arched with the anthers looking downwards, the anterior stamen crosses over, and so places its anther parallel to the others, just as in *Lamium*. Now it is easy to see that a bee entering the flower gets dusted by all three anthers at once on its thorax. And if the reader will compare the above description with that of the Dead-nettle (Fig. 10, p. 74), he will see that with a different set of materials a similar result is obtained, the process of pollination being exactly the same.

Lastly, in the *Crocus* we get quite a different method. The flower stands erect, and is consequently regular; the three stamens, together with the style, with its tufted extremity and stigmas,

form a column in the middle. When a bee comes it alights on the stigmas,—the contracted base of the perianth prevents its resting upon it,—the bee then crawls head downwards, grasping the stamens with her legs ; and since the anthers burst outwards, she gets well dusted on the underside, and not on the thorax. Flying to another flower, the brush-like stigmas sweep off the pollen as soon as she alights upon them.

These three genera are therefore interesting as showing how nature has adapted each to a different method of pollination ; yet each has its own set of correlations, admirably fitting it for intercrossing.

DIVISION II. HYPOGYNÆ.

ALL the preceding belonged to the division *Epigynæ*, because it will be noticed that the perianth is *upon* the ovary ; the next division is called *Hypogynæ*, because it is *below* it. Of this the great Lily family (*Liliaceæ*) is the best type : the flowers are regular, and call for no special remarks, except perhaps to observe how the Meadow Saffron (*Colchicum autumnale*) closely resembles the true Saffron (*Crocus sativus*). The structure is, however, quite different, though the method of pollination is the same. So that just as *Gladiolus* resembles the Dead-nettle, so *Colchicum* resembles *Crocus*.

There is one plant which is worth noticing, the Feather Hyacinth (*Bellevallia comosa*). It has long been cultivated, and is very common in fields of Mediterranean regions. It carries a long raceme of small purple bells ; the lower ones are perfect, but the flowers become more and more abortive upwards ; the uppermost being quite barren. Under cultivation not only have these latter disappeared altogether, but *all* the flowers on the raceme are totally arrested ; but now, the flower-stalks or little pedicles have become hypertrophied, they grow out and branch, the whole producing a violet-coloured feathery process, consisting of flower-stalks only.

DIVISION III. GLUMIFERÆ.

JUST as we saw that in Dicotyledons there are a large number of plants the flowers of which have degenerated and become wind-fertilized, as the Willows, Oaks, &c., so in Monocotyledons the Division *Glumiferæ*, or "Chaff-bearers," contains an immense quantity of plants, namely, all the Grasses and Sedges, the characteristic feature of which is their adaptations to be fertilized by the wind. They are in all probability degradations from ancestral conditions when the flowers were conspicuous and intercrossed by insects ; for there remain

rudiments of a perianth, as well as other facts which appear to warrant the idea.

Lastly, in a few of the aquatic plants of this class the water is the medium for conveying the pollen. This is the case with the grass-like plant often washed up on our shores called the Grass-wrack (*Zostera marina*), in which the flowers are reduced to the very minimum of simplicity.

We have thus arrived at the end of the two great groups of Flowering Plants, and the question may arise, What is the common origin of them both? That this common ancestor was derived from some member of the Flowerless plants seems certain; but it was so long ago that the links are lost. There are, however, certain plants called Club-mosses (*Lycopodium*), and a creeping moss-like plant often seen in conservatories called *Selaginella* which give us the clue. They have no flowers, but they possess organs corresponding to the stamens and ovules, if not pistils; and certain details in the fertilization very closely resemble what takes place in Fir-trees and their allies, collectively called "Gymnosperms," or "Naked-seeded" plants, because they have no pistil, but only naked ovules. This group and the preceding were some of the earliest of Nature's efforts at terrestrial plant life, and botanists consider that there are sufficient grounds for thinking that

Gymnosperms form the link between Flowerless plants or "Cryptogams" and Dicotyledons. But whence came Monocotyledons? Links are here sadly wanting; but there seem to be sufficient indications to lead us to strongly suspect how they arose.

When we examine the structure of the stem, say of a Palm-tree or Asparagus, we find no indication of the "rings" of wood we see in any branch or stem of an oak, but only isolated "cords" of wood. Now, when dicotyledons grow in water, there is a tendency to imitate this structure, as well as resemble monocotyledons in several other points. In other words, the vegetative system of monocotyledons betrays degradations; and such as are brought about or at least often imitated in dicotyledons by an aquatic habit.

When we pass to the seeds, fresh degradations are observable. Thus the embryo has lost one cotyledon, as well as the power to develop a main central tap-root, like that of a carrot.

Having only one seed-leaf, as soon as the embryo grows, the second leaf assumes only one of two places—either directly opposite, or at an angular distance of 120° . In the first case the leaves are arranged in two ranks; in the second in three ranks. As the latter prevails, so a ternary arrangement has become fixed in the floral whorls, as explained above.

There is a considerable amount of evidence other

than what I have just stated ; but I think this is enough to support the hypothesis that monocotyledons arose at a very early period in the world's history from dicotyledons, primarily through an aquatic habit. Many have retained this, and are still aquatic ; but a large number have become terrestrial ; but they, nevertheless, retain various structures in their stems and leaves which are characteristic primarily of plants living in water.¹

In the geological history of plants their remains are necessarily very badly preserved in the rocks ; and so perishable are they that many of the world's successive floras have entirely disappeared. What we do know, however, indicates that flowerless herbs, shrubs, and trees, were the first terrestrial plants the world saw ; then Gymnosperms came, and the two kinds flourished together for lengthened periods, and have supplied us with coal ; but when the first dicotyledons appeared, as well as the first monocotyledons, is at present utterly unknown ; so that we shall, perhaps, never advance further than a hypothesis or speculation as to their real origin.

¹ In support of the contention that the characteristic anatomical features of aquatic plants, which are now hereditary, have been actually caused by a watery environment, M. Costantin and others have grown normally terrestrial plants in water. As soon as new growths appeared, such *at once* began to assume the aquatic type of structure. These experiments therefore verified the inference already drawn from many similar instances.

PELORIA.

WE must now consider some special features which may occur in any member of the floral world. The first to be described is known as *Peloria*. It is a peculiarity which often occurs with plants bearing irregular flowers, that they may at any time produce perfectly regular flowers as well.

Plants, however, which have regular flowers normally, never suddenly produce irregular ones.

The regular flowers which are borne by plants having ordinarily irregular ones are always at the ends of branches, whereas it will be remembered irregular flowers are always lateral in position ; so that insects can only enter the latter in one way, *i. e.* from the front ; but the regular ones can be approached from any point of the compass. It is the belief of botanists that all irregular flowers are descended from regular ones, and when such appear, as they not rarely do, that they are reversions to an ancestral state. As examples of plants which are particularly liable to bear them, are Snapdragon, Foxglove, *Calceolaria*, Horse-chestnut, *Pelargonium*, &c. Another form of acquired regularity is obtained by the multiplication of the irregular part. Thus *Linaria*, or Toad-flax, has only one petal with a spur ; but sometimes every petal is spurred so

that a regularity is acquired ; but it is not exactly a restoration to the primitive type, which presumably had no spur at all. Linnæus observed this kind of regularity, and called it "Peloria," which signifies "monstrous."

There are several plants cultivated by florists which are naturally irregular, but under cultivation they tend to become regular, and it is the aim of florists to complete the regularity, and so restore them as nearly as possible to the primitive condition. Pansies, Azaleas, Pelargoniums, and Gloxinias are cases in point. The last-mentioned plant has a drooping and strongly lipped flower, with four stamens, but the regular form is erect, the border of the corolla symmetrical, and there are five stamens. The restoration of the lost stamen affords another indication of reversion.

As long as insects can come to the flowers of Gloxinias in their natural home, these have presumably become and remained adapted to them, *i. e.* drooping in consequence of the weight of the insects, with a spreading lip to aid in their support, the position of the anthers being such as to secure pollination, &c. But under cultivation, though florists often cross them to raise new varieties, yet the flower is never visited by the right insects. Their irritations have ceased, and no responsive action takes place to keep up the normal form, by

directing the flow of nutriment unequally so as to develop an irregular flower. Consequently the flower now tends to revert back to the primitive and regular condition, the flow of sap being equally distributed in all directions.

Here, then, we have cases which indirectly support the theory herein advanced; *viz.* the appearance of regular forms amongst irregular flowers is due to the absence of insects, with a consequent reversion to the ancestral, regular form. At the same time it is shown why no regular flower ever suddenly becomes irregular, simply because to do so requires a long period during which the same kind of insect has constantly visited it, as well as, it may be, the flowers of several generations.

MON- AND DI-ÆCISM.

IN nearly all the plants hitherto referred to, there were both stamens and pistil in every flower, though in some cases, as Pinks, the stamens mature so long before the stigma is ready, that self-fertilization could rarely take place at all. Now in many plants the stamens and pistil are in different flowers, either on the same plant, which is then called "Monœcious," as the Cucumber and Oak-tree, or on different plants, "Diœcious," as the common night-

flowering Catchfly, Nettle, and Yew-tree, and the Sorrels already alluded to. In all such cases self-fertilization is of course impossible, and the aid of insects or else of the wind is indispensable. The Oak, Nettle, and Yew, as well as nearly all Grasses and Sedges, are instances of wind-fertilized plants. It is not uncommon to find most of the species of a genus with the stamens and pistil in the same flower, yet one or two species of the same genus may be diœcious. This implies that this separation is a subsequent arrangement. And as any such flower may suddenly have the missing organ restored, we see in this fact another instance of reversion.

One might imagine that plants dependent upon the wind for fertilization would run a great risk of not receiving the pollen at all; but it is one of the many remarkable facts in Nature, that such plants appear to be fertilized with extraordinary ease: and as I have mentioned, it is, as a rule, only wind- and self-fertilizing plants which have a cosmopolitan distribution.

If these plants have descended from perfect flowers, the question is how have they arisen? Probably several causes have been at work. But in point of fact, the origin of the various conditions which exist amongst stamens and pistils is an extremely obscure subject, and would require a

volume to treat of their evolutionary history properly. Nevertheless, there are some well-known facts which supply hints, or but little more, as to the conditions which are associated with, if they be not the actual cause of, the occurrence of monœcism and diœcism.

The first point to be noticed is, that it often happens that the anthers and stigmas do not mature together. If the former are mature first, the flower is called protandrous; if the stigmas do so, it is protogynous. Now, other conditions associated with these are in the first case a larger corolla, the complete number of stamens, and a full proportion of pollen, together with plenty of honey, thereby rendering the flower highly attractive to insects. In consequence of this heightened vigour in the outer whorls, the pistil is checked in its development. On the other hand, protogynous flowers are mostly very small and unattractive; the corolla is greatly reduced in size. There is generally a diminution in the number of stamens and quantity of pollen, and no honey may be secreted. This arrest of development of the outer whorls, then, enables the pistil to gain the ascendancy. As the former group of flowers are visited by insects, so the other is not; and we see at least a coincidence between these two facts. Moreover, as by further observations it becomes a broad gen-

eral rule, we may suspect some cause and effect; that is to say, insects act as local irritants when they rest on flowers and search for honey, stimulating the development of the outermost whorls especially, which thus tend to drain the nourishment away from the pistil, and so retard its development. If, on the other hand, they cease to visit the flower from some cause or other, equilibrium is more nearly established between the stamens and pistil, so that they mature very nearly or quite simultaneously; or, as is often the case, the pistil gains a slight ascendancy, and matures its stigmas first, and the flower becomes protogynous.

Now this shows that it is possible to recognize a sort of compensating process of growth between the two organs, *i. e.* if one be vigorous, the other may be poorly nourished.

As another illustration of such coincidences, it is found that in herbs and trees which have the stamens and pistil separated, that pistilate flowers are associated with a relatively greater vital vigour in the branch which bears them, and staminate with lessened vitality. Again, if the seeds of dioecious herbs are sown very thickly, and are consequently more or less impoverished when they germinate, a greater proportion of staminate plants are produced than when sown thinly. Trees, as the Ash, may produce only staminate flowers in one

year and pistilate in another. These and other facts show that protandry and protogyny, as well as even the existence of stamens and pistils respectively, may be dependent on a variety of causes, such as nutrition, temperature, soil, &c., as well as hereditary influences which tend to reproduce whatever the parent had. It is not possible, therefore, to give in each case the precise cause or causes of the arrest of the stamens on the one hand, or of the pistil on the other, which has separated them, and so brought about a monœcious or diœcious condition. Enough, however, is known to point clearly to the external conditions or environments as influencing the plant, and thence the structure of the flowers, so that the separation has become a fixed condition in many cases.

Heterostylism may be mentioned as probably another cause; for experiments show that the "long-styled" form is mostly the more fertile of the two forms, indicating a first tendency to the separation; and although Primroses can be crossed any way, and are more or less fertile, yet in several genera of the order *Rubiaceæ*, to which the Coffee, Cinchona, and Madder belong, certain heterostyled plants have become quite diœcious as well.

WIND-FERTILIZED PLANTS.

THE consideration of diœcism leads one to speculate upon the condition of the first flowers that existed. Reasons are forthcoming which lead one to entertain the suspicion that the first flowers were probably wind-fertilized, and with stamens and pistil separated. I have already remarked that Fir-trees, Yews, and their existing allies, are the modern representatives of the earliest plants which bore flowers, as far as we know and can discover from geology. Excepting perhaps *Welwitschia*, in all the genera which are now extant, the stamens and ovules (for they have no true pistils, and are therefore called *Gymnosperms*, or “naked-seeded”) are separated, being either on the same tree as the Fir, or on different trees as the Yew. There is no true calyx or corolla, but only minute *bracts* or scales protecting the stamens or ovules in bud.

All existing trees and shrubs of this group are wind-fertilized, and it is extremely probable that there were no flower-loving insects in existence when gymnosperms first appeared upon the scene of life.

When, however, we look for links between the gymnosperms and dicotyledons which most

nearly resemble them in any way, we are at a loss ; for we cannot fix upon any existing or extinct plants whatever with any degree of certainty as connecting the two groups. In the dicotyledons of to-day all three methods of pollination are abundantly exemplified. The great group *Incompletæ*, in which is collected a vast number of plants which display various degrees of degeneracy, as we have seen, has many which are wind-fertilized, such as Nettles, Docks, Spurges, Elms, Willows, Poplars, Oaks, Beeches, Birches, &c. In the structure of the flowers of these plants one often notices peculiarities which suggest some ancient affinities with members of the other sections of dicotyledons, viz. Thalamifloræ, Calycifloræ, and Corollifloræ, respectively ; so that we are led to believe that they have become degraded from such through various causes which cannot now be traced. One, however, is presumably the neglect or absence of the proper insect-fertilizers. In no case, however, can we recognize amongst them what may be called any primitive wind-fertilizing type at all ; much less any individual closely akin to the gymnosperms.

When plants degenerate, the process of pollination runs either in the direction leading to self-fertilization, or else to wind-fertilization. We have already noticed the conditions of the former, which

collectively indicate many points of arrest of structure, so that such flowers are more like buds which do not or cannot develop into widely-expanded flowers; the anthers of the stamens, *e.g.* remaining clustered over the stigmas. With regard to wind-fertilized flowers, the stamens and pistils are situated in exactly opposite conditions to the preceding. The anthers and stigmas are often turned away as far as possible from each other; the latter being often feathery or enlarged, thereby offering facilities for more readily catching the pollen blown to it by the wind. In Nettles the filaments are highly elastic, springing up and outwards as soon as the sepals open, so that they fling the pollen into the air. In other cases the anthers are suspended so slightly that they swing upon the filaments, and so disperse the pollen readily, as in Grasses.

Though wind-fertilized flowers are without much doubt degradations from a previously insect-fertilizing condition, yet in a few cases they have re-acquired an attractiveness, and are again visited by insects. Thus the Common Sallow Willow has flowers which consist of two stamens only, yet they are so numerous and crowded together that the yellow anthers become very conspicuous; moreover, a large honey-gland is formed in each flower which is highly attractive, so that the

“catkins,” or collections of flowers, are much visited by bees. The genus *Plantago*, or Plaintain, illustrates reversionary changes from an anemophilous (“wind-loving”) to an entomophilous (“insect-loving”) state. *P. lanceolata* is visited by pollen-sucking insects, and can be fertilized either by insects or the wind. *P. media* illustrates transitions in point of structure, as the filaments are pink, the anthers motionless, and the pollen-grains aggregated, and it is regularly visited by humble-bees (*Bombus terrestris*). On the other hand, the slender filaments, oscillating anthers, powdery pollen, and elongated style with a protogynous stigma, are features of other species indicating anemophily; while the small dry and degraded corolla points to an ancestral state of entomophily.

With regard to the origin of anemophily, if a flower had been originally protogynous, with, as is customary, “long-lived stigmas,” then this protogyny associated with other degradations due to neglect has ended with anemophily.

FLORAL APPENDAGES.

IN many flowers adapted to insect fertilization, while the construction of the various parts conspires to render every facility to the proper insect for

pollination, it is a very common thing for the flower to be able to exclude small insects which would rifle it of its treasures, but which cannot transfer the pollen from one flower to another. Dr. Kerner, in his interesting work entitled *Flowers and their Unbidden Guests*, has described and figured a large number of instances of the forms of flowers, in which various outgrowths from the sepals, petals, and stamens, and occasionally the pistil—which he calls “wheels,” “tangles,” &c., composed of hair or wool—tend to stop the ingress of ants and other small insects. In some cases there are sticky secretions which effect the same end.

Many of these extra productions I would suggest to have resulted from the irritations set up by insects; so, as a consequence, they occur just and only where they are wanted; and while they form no hindrance to the larger and stronger insects which have presumably caused them to be developed; they, however, may effectually prevent the smaller ones from entering.

As a few examples:—It is not uncommon to find the entrance to a tube of a corolla surrounded by a “wheel” of hairs if the flower be regular, as in Gentians, but in Honeysuckle and Speedwell (*Veronica*), which are irregular, the hairs are all on one side. In *Amaryllis Belladonna*, Kerner describes and figures one-sided flaps growing out of the

perianth, and so overlapping one another as to furnish a very small orifice for the entrance of a proboscis. There is no such growth on the anterior side, but only on the posterior, which is probed by the insect, the latter being supported by the declinate stamens.

In a genus allied to Gentian, the honey is secreted in pits in the corolla ; each pit is protected by a tangle of hair.

In *Monotropa glabra* and *Daphne Blagayana*, the stigma is large, and nearly blocks up the tube ; and while in the former the irritation set up by the proboscis of an insect has presumably given rise to a glutinous secretion, in the latter it has caused a development of hair.

Now in observing a great number of these various kinds of obstructions, such as Dr. Kerner has described and figured, similar coincidences are at once seen to occur between their positions and the ways by which the flower is pollinated by insects. Thus in the garden "Nasturtium" (*Tropæolum*), the three anterior petals are fringed, but not the two posterior. In the irregular flower of Speedwell the front of the tube only has hair, but in the regular Gentian they are all round the tube. And as I have often shown, it is the innumerable coincidences which lead us to see a cause and effect behind them,

If we look for analogous cases, where epidermal cells are made to grow out into hairs in consequence of some excitement from without, we find many such. Thus in those plants, such as Orchids and Ivy, which climb by adhesive roots, we find that the contact with the wall or flower-pot is quite sufficient to cause the cells to elongate.

Again, hairs are extremely common within and without the surface of Galls. In these, as on the Oak, Willow, &c., the presence of the maggot causes hypertrophy of the tissues, which thus swell into the Gall, which may be clothed with long or short hairs, as the case may be. Lastly, the growth of the pollen-tube actually causes hairs to be formed down the hollow passage of many styles, and within the ovary.

These and other instances are sufficient to show that there are various kinds of external stimuli, which, when brought to bear upon the skin or epidermis in several places, can bring about, through the responsiveness of the protoplasm, the production of hairs. Hence, it is not without collateral evidence that we may attribute such production to the irritation of insects in search for honey.

HONEY-SECRETING ORGANS.

I HAVE had occasion often to allude to the honey in flowers, and it will be as well to make some further remarks.

Bees visit flowers either for honey or pollen, both of which constitute important articles of food. When we examine the localities where honey-glands are situated, we find no rule to guide us beyond the fact that they are invariably where those insects which visit the flower can most easily reach them. As examples, they are most commonly in the floral receptacle, as in the Wallflower and Geranium. If instead of forming separate glands the secretion takes place all round, the thickened structure is called a disk, as occurs in the Maple, Cherry, and Blackberry. The glands are occasionally borne by the sepals, as of the Lime, each sepal being boat-shaped, and carries a quantity of sweet juice within the hollow. Buttercups have the honey in a pit at the base of the petal. In Aconite and Hellebore the petals are completely changed into honey-bearing structures, having quite lost their petaline character. In Anemone, of the same family, there is no honey, but bees come to it, as they do to the St. John's Wort, Rose, and Laburnum, none of which have honey, for the sake

of the pollen. In the Violet two stamens, as mentioned above, have tail-like processes which secrete the honey. One stamen of *Penstemon* does the same. Several stamens in *Atragene* bear honey. Lastly, the pistil frequently produces it; as *e.g.* by the sides of the carpels of the Marsh Marigold, the base of the pistil in *Rhododendrons*, and many others.

Hence no rule can be established as to the places where one would be likely to find the honey on any *à priori* grounds. Thus, for example, in the order *Ranunculaceæ*, we find the glands on the petals, or stamens, or carpels, or wanting altogether.

With regard to the origin of honey-bearing organs, or "nectaries," as botanists call them, there are many reasons for inferring their existence to be due to the direct and irritating action of insects themselves when searching for juices as food or otherwise.

That a merely mechanical irritation may cause a flow of nutrient fluid to the spot, so that the tissues may increase in size by the development of cells which would not otherwise occur, is abundantly evident. It is seen, for example, in the growth and development of Galls, which are due to the puncture of an ovipositor and the insertion of an egg; hence the inference that hypertrophy may occur whenever an insect's proboscis can irritate

the floral organs, is by no means without foundation.

One of the most remarkable cases is the process called "caprification," by which the cultivated figs are enabled to develop embryos and ripen by the aid of insects bred in the pistils of the "Caprificus," or wild fig. They have been supposed to convey the pollen from the stamens within the latter to the cultivated varieties ; but Dr. Cunningham, who has lately studied the process in *Ficus Roxburghii* at Calcutta, has arrived at the startling conclusion, that although the insects enter the figs, they carry no pollen with them ; but that by uselessly "pricking" the ovaries, for they cannot penetrate them so as to lay eggs, they induce not only a flow of fluid within the figs, but the irritation thus set up is actually the cause of the development of embryos as *buds outside the true embryo sac*, in which no *true* embryo is produced !

Similarly in the case of nectaries the flow of honey may perhaps have originated as a pathological phenomenon, which has become fixed and hereditary, for pathological conditions often determine a flow of gum, as in Cherry-trees, &c., and it is impossible to draw any hard-and-fast line between a pathological and varietal state ; as, for example, in closing the scar after the fall of the leaf, the fibro-vascular bundles are sometimes stopped by gum—

a process which, in this case, might be regarded as normal, and not pathological, as in the former.

Similarly, while the surface of most trees is protected by dead cork, a feature which could not be called abnormal, or pathological; yet a potato if injured will convert the cells exposed to the air into cork, and thus protect the underlying tissues. Such a case leads one to regard the superficial cork of trees as being a direct result of surface exposure.

If a particular locality be perpetually irritated, so to say, for generations, all analogy shows that the effect may become permanent and hereditary; at least, as long as the irritation is persistently renewed year after year. And, on the contrary, the theory is equally supported by the negative evidence of the disappearance of the honey-glands whenever the whole flower degenerates and becomes regularly self-fertilized, or else wind-fertilized. In these cases, in unison with the degradation in size and colour of the corolla, or else its entire loss, the nectaries tend to, and generally, vanish entirely; as may be seen in the Knotgrass (*Polygonum aviculare*) as compared with the Buckwheat and Bistort.

The simple origin of nectaries, then, according to my theory, is that insects, having been attracted to the juicy tissues of flowers, by perpetually withdrawing fluids, have kept up a flow of the secretion

which has become hereditary, while the irritated spot has developed into a honey-secreting organ. Consequently these spots occur exactly wherever the prevailing insect found it most convenient to search.

THE RECEPTACULAR-TUBE.

THERE is a peculiar structure in many flowers to which I have not yet alluded, but which has caused a good deal of controversy as to its real nature. It was at first called the "calyx-tube," but now more generally the "receptacular-tube." A few examples will best illustrate it. If the blossom of a Cherry be examined, there will be found to be a cup lined with honey-secreting tissue, upon the edge of which are the sepals, petals, and stamens; the single carpel standing freely at the bottom of the cup. It is this cup which is the organ in question. It was supposed to be formed by the coherent *bases* of the sepals, the upper portions being free; hence the term "calyx-tube." In the Raspberry it forms a sort of expanded dish, the honey-secreting tissue being a little circular trough, between the stamens and the pistil. It is much the same in the Strawberry. In the Rose it forms the ovoid swelling under the sepals, and

which becomes scarlet in the Dog-rose, and constitutes the "hip" when ripe.

In all these cases it will be found that the pistil is perfectly free, either above it, as in the Blackberry, Raspberry, and Strawberry, or concealed within it, as in the Cherry, which has only one carpel, and in the Rose which has several.

If now we look at the flower of the Apple, Pear, Medlar, Hawthorn, or Quince, we see a swelling below the calyx, not unlike that of the Rose; but on cutting through any one of these as soon as it begins to enlarge into a fruit, the carpels are found to be plunged into a mass of soft tissue, and constitute the "core" of an Apple, and the stones of a Medlar and Hawthorn. The solid tissue is the "tube," which in these latter cases has become adherent to the carpels.

If the carpels are *free* from the "tube" they are called "superior," and the calyx is said to be "inferior." If the tube is adherent to the ovaries of the pistil, the latter are said to be "inferior," and the calyx is called "superior." This is the condition of the last-mentioned fruits—the Apple, &c.

Now it has been thought that this tube is not formed from the bases of the sepals, but from the flower-stalk itself growing up round the pistil, till it reaches to the top of the ovary; but it goes no further. Hence the term "receptacular tube," as

being formed by the outgrowth from the "floral receptacle."

The truth is that it is probably sometimes formed by the calyx, sometimes by the receptacle, and sometimes both take part in it.

In an Apple, if cut through vertically, the carpels

Fig. 15.—Pear with hypertrophied and united petioles.

are seen to originate at the end of the flower-stalk, the fleshy part being the basal parts of the calyx. The best reason for coming to this conclusion is supplied by a "monstrous" state of the foliage of a Pear-tree in which the leaf-stalks were fleshy and more or less coherent, as shown in Fig. 15.

If, however, a Pear be cut vertically, it will be found that the flesh tapers down to a point on the stalk considerably below the place where the carpels arise. Hence the lower part of a Pear is certainly stalk, or as botanists say "axial," to distinguish it from "foliar." Similar monstrous flowers of Fuchsias (Fig. 16) sometimes occur in which the

Fig. 16.—Fuchsia, with foliaceous sepals and petals. (*After Masters.*)

sepals appear as leaves, the stalks of which separate, and at the same time reveal the origin of the tube; the ovary being "inferior" in that flower. Hence, while the Fuchsias and Apples appear to have constructed their tubes out of the stalks of sepals, a Pear has utilized both calyx-stalk and floral receptacle.

In the Rose the tube appears to be wholly axial, for the sepals represent leaves; and in monstrous states they become more leaf-like than usual, and occasionally bear "stipules" (Fig. 17, *st.*) at their bases, on the summit of the tube. In the figure given, there will be seen an extra leaf growing out of the side of the tube, another indication that it is axial, that is stem-structure and not foliar.

Fig. 17.—Monstrous Rose, with a leaf-bearing receptacular tube.
(*After Masters.*)

The use of the tube appears to be, in its simplest form, a honey-secreting organ, as in the Raspberry and Cherry, just as it is in the Pea family, for it is a small cup-like process, which really secretes honey; and if we compare the blossom of the Maple with those mentioned above, we see how a thick honey-disc surrounds the style in the flower

of this tree ; so that this honey-disc may perhaps be, as it were, the beginning of the tube ; we thus pass from a small "rim," to a sort of "dish," and thence to a "cup"—the final condition being attained by the adhesion of the cup or tube to the surface of the ovary. When that stage is arrived at, the honey can now be only formed on the summit of the tube or ovary. Such is the place where it is secreted in the May, Willowherb, Carrot and Parsnip family (*Umbelliferæ*), and Daisy family (*Compositæ*).

What has been the origin of the tube ? As there is no such thing as a tube in leaf-buds, which are the origins of flowers, nor are they associated with the more simple flowers like Buttercups, we must regard the calyx- or receptacular-tube as a subsequent development ; and I think the same interpretation will apply as given for other floral appendages, and that is hypertrophy of the tissues primarily induced by the irritations of insects. These, as explained, are believed to be the direct cause of the secretive tissues, or honey-glands ; and I regard the tube as a structure correlated with the gland which secretes the honey. Finally, we see the two successive conditions, the tube being at first quite free from the ovary ; then, secondly, it becomes adherent.

It may be added that flowers with normally in-

ferior ovaries, that is, like the Apple, or those which have them encased by the tube, will sometimes be developed quite freely, the tube being totally absent. Such unusual cases throw light on the origin of it, as they are reversions to a more simple and ancestral type of flowers.

The presence of an inferior ovary, therefore, in such degraded flowers as the Nut, Beech, Oak, &c., which are wind-fertilized, and entirely devoid of corolla, honey-scent, or anything attractive to insects, may be taken as an indication that their ancestors were insect-fertilized plants; but that they have now degraded to the present inconspicuous condition, and are entirely dependent upon the wind for pollination.

IRRITATION OF THE POLLEN-TUBE.

OF the many agencies which can influence a plant from without, and thereby cause to be developed certain tissues in response to them, the pollen-tube is one which is peculiarly remarkable for its action on the interior of the style and ovary, apart from its fertilizing action on the ovule.

The first effect produced by the development

of the pollen-tube, is the formation of the so-called "conducting tissue," or layers of specialized cells, which nourish the tube in its downward growth. They become highly charged with nutritive and saccharine matters, which would not have been produced had no pollen-tubes ever descended the styles of flowers. It is exactly comparable to the tissues of Galls. In these also, unquestionably as an indirect result of the presence of the grub—which may so far be compared to a

Fig. 18.—(a) Section of conducting tissue of Fumatory; (b) of Blackberry; (c) section of ovary of a Crucifer. (*After Capes.*)

pollen-tube—there is an accumulation of nourishing matters upon which it feeds.

In some cases the conducting tissue consists solely of an altered epidermis; in others, the underlying cells are concerned in its formation. Thus Fig. 18, *a* shows the canal in the style of Fumatory, the epidermis lining it being charged with sugary matters, three pollen-tubes being seen in section. Fig. 18, *b* shows the formation of conducting tissue

at the angle of the inflected carpellary edges of *Rubus*. Fig. 18, *c* is a section of the ovary of a crucifer in which the central "false-dissepiment" forms the conducting tissue.

Now, if the theory advanced in this book be true, that no present structure exists which has not been brought into existence through some foreign action upon one previously existing, then the existence of this specialized tissue would never have arisen had it not been for the irritating action of the pollen-tubes.

Besides the analogous influence of an egg or grub within a Gall, parasitic fungi cause a similar flow of nutriment to the point of attack, which often causes a leaf to become of a darker green, and exhibit a more vigorous growth in the neighbourhood, for a time.

But, perhaps, the most remarkable effect of the pollen-tube has been noticed in Orchids ; for it has been observed that the influence was twofold, in that it actually determined the growth of the ovary and the formation of the ovules *before* the process of fecundation had taken place. At the time of flowering the ovules are in a most rudimentary condition, and there is no conducting tissue at all. As soon as pollination has taken place, the spaces within the ovary between the rows of ovules become covered with hairs filled with a granular

substance. As soon as the pollen-tubes are formed, the ovules begin to grow. The embryo sac and its contents then begin to develop, and finally it is not till after a month that everything is ready. Five weeks after that fertilization is completed.

Similar processes have been observed in other plants, such as the Mullein (*Verbascum*).

It may be added, that the production of hairs as a result of the action of the pollen-tube has been noticed in many plants, such as Willows, &c.

The significance of the above details lies in the fact that external influences, both mechanical and physiological, can bring about changes in the epidermal and sub-epidermal tissues, with a determination of a flow of fluids of a specific character to those specialized tissues. Hence by analogy I infer the possibility of insects having caused the secretive tissues of honey-glands and the tufts of hairs forming appendages over them.

Perhaps the pulp of an Orange or Lemon may be due to the same cause; for every one of the spindle-shaped cells full of juice arises from the inner surface of the ovary, and is attached by a long or short stalk, according as it has to occupy a space remote from or near that surface. They are in fact swollen and juicy *hairs* compacted together.

COLOURS OF FLOWERS.

I MUST now say something about the presence of colour in plants, which tends so materially to enhance their beauty. Although we cannot say exactly why some colours prevail, or what is the direct cause of the presence of any particular tint, we can detect certain principles which enable us to get a clue to their interpretation.

Green is the general and almost universal colour of the "vegetative organs" of plants, as *e. g.* their leaves; and when we regard the flowers of such types of the earliest of plants which we now possess, we have strong reasons for suspecting that they are but little altered from the primitive but extinct forms of early geological periods. I allude to the cone-bearing trees. In these there is no calyx and no corolla, but only stamens and ovules. The former are yellow, and this seems to have been the primary colour of petals when they were first developed, probably out of stamens. The next colour to be evolved appears to have been red, and lastly came blue. Now it is highly probable that different colours have arisen indirectly through the irritating action of insects.

When we search for the immediate cause of colour, nutrition is clearly an important one. Various soils

will affect it, as also the air or climate generally. Thus the same plant grown in high latitudes or altitudes, as in Alpine situations, has much brighter flowers than when it is grown in opposite conditions.

The crossing of flowers is much practised by florists as a means of enhancing the variety of tints. The interpretation is, that crossing is a stimulating process, and provokes the petaline energy to a high degree. These and other causes derived from the environment act upon the colours of plants; but there are certain features in the distribution of colours on the petals which can only be correlated with insects. Thus, when coloured flowers are regularly visited by insects, and thus intercrossed, the colours are usually bright and vivid; but when flowers have become insignificant and regularly self-fertilizing, the tints are paler, and often go altogether. Such appears to be one condition of degradation which such flowers have undergone, from a more conspicuous ancestral form.

A particular feature of corollas attractive to insects consists in what are called "Guides." These are streaks or spots of a different colour distributed on certain petals only, if the flower be irregular, but on every petal symmetrically if it be regular. They are invariably so situated that the nectary or honey-gland is in their immediate neighbourhood and below them. Hence if an insect directs its

proboscis down the flower along the guide, it is sure to be rewarded. Here, again, we have an invariable coincidence, and as it occurs in flowers from all parts of the vegetable kingdom, we are again justified in looking for a common cause. Now, as stimulus is seen to intensify colour, so is it reasonable to think that local irritations set up by the insects themselves have been the starting of the difference in colour of these particular places. Beyond such coincidences, and the presumed cause and effect behind them, we cannot at present go.

It may be here mentioned, that the order of development of colour appears to be first yellow, then red, and finally blue, while white may occur in any normally coloured flower, just as albinos are found amongst most animals.

EFFECTS OF STRAINS ON STRUCTURES.

I HAVE intimated that insects have largely concurred in bringing about the present forms of floral organs, conspicuously so of the corolla. We must consider now the grounds of this belief. First let us call to mind the broad distinction between the regular and irregular flowers with regard to their positions on the plant. All terminal flowers are regular, and many which are attached to the

sides of a main stalk, as the little bells of the Lily of the Valley, are regular; but in such cases the flower can be visited from any direction. Irregular flowers, if there be many on one common stem, are situated very close to the stem, and can only be visited from the front. And if it so happen that the flower be solitary, and extends *outwards* instead of *upwards*, then it is often irregular, as the Violet and garden Nasturtium (*Tropæolum*), and many orchids. Here, as always occurs, it is not a single or few instances only, but an universal rule, which is applicable to flowers from all parts of the vegetable kingdom, and we consequently look for a common cause to effect it.

The question, therefore, arises, if we assume that a regular flower can become irregular by its living protoplasm responding to the mechanical impulses of the insect, that it can form a tube out of separate petals to gain strength, that it can expand the anterior petal to form a lip or landing-place; or, if there be no petal there, that it can develop the filaments so as to acquire the strongest possible condition, as when they are declinate; if, I say, we assume such possibilities in flowers, can we discover that other parts of plants are capable of responding in this hypothetical manner? The answer is that such is the case, not rarely, but very frequently.

A few of the more striking cases may be

worth mentioning. Let us take our first illustration from climbing-plants. Many climb by means of their leaf-stalks or "petioles," others by tendrils, and in various other ways. Now, if a leaf of a Clematis be examined, nothing peculiar will be perceptible; but let it come into contact with a stick and remain so, it will be found in a few hours to have coiled round it. If its tissues be examined before, and again some weeks after contact, an extraordinary development of woody tissue will be observed to have taken place. The result is, that instead of falling off in autumn, as it would have done if left alone, the leaf-stalk now remains permanently entwined around the support. Next let us examine the tendrils of the Virginia Creeper (*Ampelopsis hederacea*), and of its Japanese ally (*A. Veitchii*). The tendrils of the former are at first very slender and thread-like, terminating with little hooked tips. As soon as one of its branches has secured a hold by catching some little roughness on the wall, the effect of the contact is to cause the tip to swell into a little adhesive pad, the fine tendril becomes greatly thickened, and instead of remaining straight, is more or less curved and twisted. Lastly, instead of falling off, as the branches of the tendril do which have not succeeded in fixing themselves to the wall, they remain permanently adherent.

In the Japanese species the little pads are already in process of formation *before* any contact has taken place, but complete their development and become adhesive as soon as they touch the wall. In this case, therefore, we see that the effect of contact, which only produces the pads in the former, has become hereditary in the second species, as they are partially developed in *anticipation* of the mechanical irritation produced by contact with the wall.

As another case, that of a peduncle acting as a

Fig. 19.—Climbing Peduncle of *Uncaria*; (a) thickened after catching a support. (After Treub.)

climbing process, may be mentioned the *Uncaria*. In this plant the flower-stalk is at first slender and curved. If it catch nothing it remains so; but if it succeeds in “hooking” itself to a support, it thickens enormously, as may be seen by comparing the two peduncles in Fig. 19.

Many other instances of different kinds might

be given, but these few illustrate a general property of protoplasm, of *responding to external and mechanical* irritations.

An experimental proof that growth may be regulated by merely mechanical means was made early in this century, by fixing parallel bars one on either side of a young tree, so that it could only oscillate in one direction. The tree grew elliptically, instead of having a circular stem, the long axis of a transverse section being parallel to the

Fig. 20.—Diagram of the end of a Dr. Jules Guyot pear.

bars. Similarly the thick fleshy stem of a Cactus was submitted to certain strains, and woody tissue was specially formed to meet them. We are all familiar with the fact that as fruits are formed their stalks grow far stronger and thicker than what they had when they were only required to carry a flower; and a curious instance of growth in response to resist strains is seen in many pears which have a one-sided hump near the stalk end.

The accompanying figure (Fig. 20) will explain the cause of this.

Pears which are thus lop-sided—for the extra growth is more or less continued all down one half of the fruit—always have their stalk attached obliquely to the stem; and as the pear increases in weight it tries to hang vertically downwards. Now it is easy to understand, that while the weight acts in a vertical line (w), the tension (t) along the stalk is not directly over the centre of gravity of the pear, *i. e.* in the same vertical line. Consequently, just as one breaks a stick across one's knee, so these two forces acting at an angle tend to wrench the pear from its attachment to its stalk. The hump grows out on the opposite side to strengthen the weakest part, and resist the strain (r) to which it is thus subjected.

Of the preceding examples, we see how sensitive leaf-stalks can be; and in the case of many tendrils, as of the Pea, the metamorphosed blades; in others, as the Virginia Creeper and Vine, they are metamorphosed flower-stalks with which they climb; and I might have added illustrations of the way in which roots respond to gravitation, to contact with impediments in the soil, and to mechanical touch when utilized as climbing organs. Again, we see how the stalks of flowers can thicken to resist the weight of the fruit. We have,

therefore, abundance of evidence from all parts of plants to warrant the belief that parts of flowers may be quite as sensitive as well. And when we come to examine them we find this to be the case. The petals of many flowers are highly irritable, and move in various ways the moment they are touched. Thus in *Genista* the flower spings open, a *Masdevallia* (orchid) flings its labellum upwards, &c. ; and it has been noticed that if the flower of a *Stanhopea* or *Coryanthes* (orchids) be tied up so as to prevent the usual expansion, at the moment when they are about to open, the farther development is suddenly stopped, so that such flowers "kept fresh three times as long as they would have done on the plant." In this experiment we have a remarkable illustration of the extreme sensitiveness to a merely mechanical touch of the thread which bound it.

Numerous instances of irritable stamens are known, as of the Barberry, in which they spring forwards on receiving a touch at the base of the filament. In the common Rockrose (*Helianthemum vulgare*) they bend outwards if gently compressed. In Lucerne (*Medicago sativa*) and other species of Medick, they spring up violently, &c.

Similarly in the pistil, both slow and rapid motions are common. In *Stylidium* and *Maranta* and its allies, the style dashes across the flower

when irritated. In the common Musk the two flap-like stigmas, which at first lie extended, close up and are pressed together as soon as they are touched.

One of the most curious instances of alteration due to irritation occurs in a species of *Clerodendron* (allied to our garden Verbenas), which grows in Australia. A small caterpillar takes up its abode within the flower, but seemingly does not feed upon the tissues. The effect of its presence is to cause hypertrophy of the corolla and stamens, which now assume a regular instead of the normally irregular one, while the filaments and style are likewise affected, becoming much thicker than usual.

The above cases will be enough to show how widespread is the phenomenon of irritation and its effects. They give us a basis for inferring like possibilities in the parts of flowers when visited by insects in search of honey.

The facts are, that thousands of adaptations to insects exist on the one hand, and abundant evidence on the other of the irritability of protoplasm and its responsiveness to external stimuli. We are thus enabled to draw a conclusion based on innumerable probabilities, which is practically equivalent to a demonstration.

The theory is immensely strengthened by the

fact more than once alluded to, that the correlations between the structures of flowers and insect agencies are not confined to one organ, as the corolla, alone, but every organ contributes to the process.

Take, for example, the case illustrated by the flower of *Duvernoia* (Fig. 21). Looking at *a*, and supposing we knew nothing of the intercrossing effected by insects, we might well ask, What is the

Fig. 21.—*Duvernoia adhatodoides*.

use of this great irregularity? Why and how has it come into existence? No answer is forthcoming. Now, turning to *b*, we can at once see its adaptations. The weight of the bee must be very great; but the tubular structure of the base, and the curious shape of the lip of the corolla, with its lateral ridges firmly gripped by the bee's legs, is evidently not only an excellent landing-place, but is so con-

structed as best capable of supporting the weight of the insect, which can thus secure an excellent purchase while rifling the flower of its treasures.

Besides the corolla, the anthers and stigmas arch over the orifice, and are so placed as to strike the bee on the thorax at the same spot. Moreover, the honey is secreted just where the bee can get it most readily, while the anthers are depositing the pollen upon it. Lastly, the calyx-tube strengthens the base of that of the corolla just where it would be likely to bend under the weight of the bee.

DECLINATE STAMENS.

WE have seen that in the case of the Violet and *Salvia*, and many others, as the Pea, Snapdragon, Orchids, &c., the front or anterior petal is enlarged so as to form a landing-place for the insect when searching for honey and pollinating the flower. This enlarged petal was presumably due to the strain required to support the insect. But in many cases the petals are so arranged that no one stands in the front, though all may be present. The stamens then form the landing-place. When such is the case they either hang downwards, so that the bee clings to them, as in the Rose-bay Willow-herb

(*Epilobium angustifolium*) (Fig. 22) and Aconite (see p. 44), or else they take the form called “de-

Fig. 22.—Willow Herb.

clinate.” In some cases there is an anterior petal, but the rule is that when present it is not enlarged,

Fig. 23.—*Dictamnus*, with moving and declinate stamens.

or else it is smaller than the others, and not infrequently it is suppressed altogether, as in the Horse-chestnut.

As examples of these conditions may be mentioned Azaleas, Rhododendrons, and some Lilies. In these flowers the stamens are declinate, but they lie over an interval between two stamens, and the largest petal, instead of being in front, is on the posterior side. The same rule applies to the garden Pelargonium, excepting the "Scarlets" and "Zonals," which follow the usual rule, the stamens not now supporting the insect. In the Germander Speedwell (*Veronica Chamædrys*) (Fig. 24) the flower has four petals, the smallest being

Fig. 24.—Speedwell.

the anterior ; there are only two stamens which are situated laterally, and when an insect alights it clings to the filaments, which it drags under its body, so that they together with the style form the support.

Lastly, in the Horse-chestnut the number of petals should be five ; and if the terminal flowers of several bunches be examined, one or more will be found to be regular with five petals ; but in all the laterally situated flowers four only are present,

for the anterior or fifth is entirely suppressed, the declinate stamens occupying the place.

In some instances, instead of suppressing the fifth, the position of the lowermost petals has become, so to say, shifted just as if they had been pushed aside to get them out of the way; *Epilobium* (Fig. 22). *Dictamnus* (Fig. 23), *Godetia*, and *Clerodendron*, &c., are so constructed.

Now the significance of the above observations lies in the fact that they are not single instances, but can be multiplied indefinitely from all parts of the floral world; and that they constitute invariable rules wherever the structure of the flower is such as to require the insect to be supported by the stamens and not the corolla. Hence the argument rests upon the abundance of coincidences, which collectively imply some causal relationship between the two; and that relationship, I maintain, is that the stamens have assumed their present form and position through the presence of the insects themselves, and in response to them, while the petals have altered as above in a corresponding manner.

THE RELATIVE VALUE OF INTER-CROSSING.

HOW are all these minute correlations to be accounted for, unless by some common cause

which has brought them into existence *simultaneously*? Which is most probable, that the flower has spontaneously varied in, at first, a purposeless manner in the directions we now see it, and by *one item at a time*, or has it grown into the form we now see in exact response to the strains and irritations set up by the bee itself and *all together*? Considering the many points all conspiring to one end in the flower, and that as there is an infinitude of insects, so is there in the forms of flowers; and again, that in every case we find a similar collection of characters all minutely correlated to the insects, the conclusion is forced upon one, that the probabilities are all in favour of the latter suggestion rather than that of the former.

A few more of these correlations may be mentioned with certain numerical calculations, which the late Dr. H. Müller has recorded, as to the number of species which visit differently constructed flowers. Generally it may be maintained that open flowers with exposed and readily accessible honey have the largest number of visitors. Short-tubed flowers have fewer, and are visited by short-tongued insects; while flowers with long and slender tubes are almost entirely confined to the Lepidoptera, Butterflies and Moths alone having sufficiently long proboscides; the Orchid *Angræcum sesquipedale* of Madagascar having a spur often more than

twelve inches long, and therefore, as far as is known, capable of being visited effectually by one insect alone, having a proboscis of the same length.

Hence a complete parallel exists between the number of insects and the degrees of facility with which the honey can be extracted from the flower. The more exposed the more easily is it secured; and the more highly modified the flower may be, the greater the concealment of the honey, the more restricted are the species of insects which visit it.

Now when we remember that the setting seed is the sole object of flowers, we at once perceive that, as far as this purpose can be fulfilled, the more specialized a flower has become, so in the same proportion does it run risk of setting less seed, or even none at all.

What, then, or wherein lies the "good" of all these wonderful constructions in adaptations to insects? Is there any use in them to the plants themselves?

The first impression one entertains is, that surely Nature would not have made them without some good to the plant; and many persons thought we were justified in assuming such to be the case without asking more. But Science is never satisfied with what are called mere *deductions*, that is, inferences, without testing them in every way possible; *verifying* them, especially by experiment if one can;

if not, by accumulating abundance of instances, till the *probabilities* of the inference being right are so numerous as to preclude any other. Now this is the line of evidence we are following; and the reader will now see how I have first *inferred* that the origin of floral structures is due to the irritation of insects; and not being quite able in all cases to verify it to the extent one could wish by experiments, I have brought forward a number of positive facts which meet their explanation satisfactorily, and *without exception*, as far as I know, on the assumption that the inference was a true one. In other words, I am accumulating the probabilities till they will amount to a *moral conviction*, which is a sufficient verification of the deduction with which we started.

Now to return to the inference that inter-crossing *must* be beneficial, and the converse inference that self-fertilization *must* be injurious, both of which were at once but too hastily accepted, for no one made any attempt to *verify* either the one or the other. When, however, we begin to collect facts from Nature, regardless of both these inferences, we begin to discover that neither are strictly true!

It is, of course, necessary to start with some definite notion as to what is of advantage to a plant, and what is not. If Nature requires a species to live, it must itself thrive, and before it dies, must

leave plenty of healthy offspring ; for the struggle for existence, during the germinating period especially, is intense for all plants. Fortunately, every individual plant as a rule makes far more seed than can possibly grow to maturity. Hence no plant has more than two "ends" ; one being its own health and vigorous growth ; the other is seed. Now the evidence from Nature, and the experience of florists both agree in this—First, that the flowers adapted for insects, and which are frequently crossed, are not the most prolific ; but it is the insignificant weeds, and from a florist's point of view, the worthless plants, which seed the most abundantly. Secondly, if we trace the dispersion of plants over the globe, the rule is that the conspicuously flowering plants are much more limited in their range than the self and wind-fertilized, which are often cosmopolitan.

Mr. Darwin has described an elaborate series of experiments to test the effects of crossing and of self-fertilization. He has recorded them in his work called *Cross- and Self-Fertilization of Plants*. His experiments showed that in most cases the "crossed plants" grew taller, were more vigorous, as shown by comparative weights, and sometimes even more fertile at first, than a corresponding number of self-fertilized plants. These results *appeared* to corroborate the inferences which I have mentioned.

But he unfortunately did not experiment with plants *habitually self-fertile*, like Chickweed and Shepherd's Purse, but almost solely with plants normally adapted for inter-crossing, most of which, however, were also naturally self-fertile.

Secondly, the remarkable fact was discovered in his experiments, that when self-fertilization was artificially persevered with for a few generations, the subsequent offspring became much more highly fertile than the original parents, which were markedly adapted for inter-crossing, and in some cases were incapable of setting seed at all without the aid of insects, as described above in the case of the Clove Pink. Consequently we can now see that both inferences were not altogether sound. The fact is, that crossing has simply a temporary stimulating effect, especially with regard to the vegetative organs, but it enhances the corolla as well. Consequently our florists make great use of the process to "improve" flowers; but they find that after crossing a particular plant for a few generations, they derive no further "good," *i.e.* what a florist calls an improvement, and have to begin again along some new line.

Mr. Darwin was, therefore, misled in regarding mere *vegetative vigour*, which is the most conspicuous result of inter-crossing, as a "good." And it is so to a certain extent, *i.e.* it benefits the

individual, but not the *species*. This latter can be only said to derive any good from inter-crossing when plenty of seed is left by the parent, so that the *race* may thrive and be perpetuated, though the individuals may rapidly die.

It is clearly no special benefit to a race of plants that members of it should be large if they cannot hold their own nor disperse themselves widely ; and it is not, as a rule, the larger, more conspicuous plants and flowers, but the smaller, the humbler weeds, little self-fertilizing annuals, which are all over the world wherever climatal conditions are suitable.

What, then, are the structures of such flowers that they can so readily pollinate themselves? Having seen and considered several difficulties which lie in the way of self-fertilization in flowers adapted for inter-crossing, our inference would be that their structure would be the exact opposite ; and such is precisely the case. I will now consider them, therefore, more particularly.

SELF-FERTILIZATION.

IN flowers which are adapted to insects, it very often happens that the anthers are nowhere near the stigma, but are so situated that they strike the

bee successively on the same spot, as described in *Salvia* and *Primrose*. In many flowers, however, they are in contact, or nearly so, yet the stigmas cannot be fertilized, as they have not matured simultaneously with the anthers, which may have shed all their pollen before the former are ready to receive it. Lastly, as mentioned in the case of *Orchids* and the *Pansy*, even if the pollen were ready together with the stigma, a mechanical obstruction prevents pollination in the same flower.

Hence the rule may be formulated, that when flowers are adapted to insects, there is a greater or less difficulty in their being properly pollinated at all, if the right insects do not visit them.

Nevertheless, notwithstanding the fact that a large family like the *Orchids*, and several other plants, as *Salvia*, *Pansy*, &c., cannot fertilize themselves, yet by far the greater majority of plants whose flowers are adapted to insects can, nevertheless, effect self-fertilization to some degree, though it may be with more or less risk of failure.

If now we turn to regularly self-fertilizing flowers, we find Nature runs no such risk, by placing the anthers in immediate contact with the stigmas. We have seen how this is the case in cleistogamous flower-buds, as of the *Violet* (Fig. 4, p. 53); and the figure of the *Chickweed* (Fig. 5, p. 56) illustrates the same fact. Similarly, while in

Mallows with large flowers, as the Common (*Malva sylvestris*), and the Musk (*M. moschata*), both of which are strongly protandrous, it is not till a later period that the pink stigmas grow up and spread out like a brush far above the now empty anther-cells; on the other hand, in the small-flowered species (*M. rotundifolia*) the stigmas mature simultaneously with the anthers, curling in and about them so as to be readily pollinated.

It is interesting to compare allied species of the same genus, one of which may have all its parts adapted for inter-crossing, while the other is quite as carefully adapted for self-fertilization. Thus, of our Wild Geraniums, the large-flowered *G. pratense* is in every way attractive. It secretes honey, and is protandrous with late-maturing stigmas; whereas the minute-blossomed *G. pusillum* matures its stigmas simultaneously, or even slightly in advance of the anthers. It has no honey, is unattractive, but perfectly self-fertile. The Buckwheat (*Polygonum Fagopyrum*) is dimorphic, being heterostyled; has attractive flowers, and secretes honey. Its ally, the Knotweed (*P. aviculare*), has minute, inconspicuous, unattractive flowers, no honey-glands, the anthers adpressed to the stigmas, and it is an abundant seeder.

We will now sum up the main characteristics of self-fertilizing flowers, which will be at once seen

to be just those features in which the conspicuous flowers are wanting. In other words, they represent undeveloped or arrested conditions, which only meet with their full development in the regularly inter-crossed flowers. Self-fertilizing flowers are thus "degradations" from a previously more conspicuous state. The word implies nothing derogatory, or anything injurious to the plant; rather the reverse. Thus, though the number of anthers and quantity of pollen are generally reduced, as too much is made than is really required in flowers that are crossed, for a small quantity has been proved by experiment to be amply sufficient.¹

1. In the first place, the flowers are inconspicuous even when fully expanded.

2. The calyx and corolla are often only partially expanded, or not at all.

3. The corollas are white or of pale colour; while specially coloured streaks, specks, "guides," and "pathfinders," peculiar to inter-crossed flowers, are more or less reduced, if not absent.

4. The corolla is partially or totally arrested.

5. The mature stamens of the expanded flower retain, in many cases, the incurved, *i. e.* an arrested, position, which they had in bud; the anthers thus remain in contact with the stigmas.

¹ The following facts are taken from my paper *On the Self-Fertilization of Plants*.—TRANS. LIN. SOC. BOT., 1877.

6. The stamens are often reduced in size and number, and the pollen in quantity.

7. The pollen-tubes may often be seen to be penetrating the stigmas, either from grains still within the anther-cells, or evidently derived from those of the same flower.

8. The styles are shortened, and the stigmas are situated appropriately for direct pollination from the anthers of the same flower.

9. The partial arrest of the corolla and stamens in their rates of development allows the pistil to mature with comparative rapidity.

10. The stigma is consequently early matured, so as to be ready before or simultaneously with the dehiscence of the anthers.

11. There is little or no scent.

12. The honey-glands are smaller or totally absent, with corresponding little or no secretion of honey.

Dr. Hermann Müller, who was one of the greatest observers of the details of flowers, gives a number of modifications of what he describes as "the countless ways in which plants revert to self-fertilization in default of sufficient insect visitors."

Now, the interpretation of all such flowers is, as I have observed, degeneracy. Let us trace certain stages, and consider the pistil first. The number of carpels is generally less than five, even when the

other whorls retain that number. Thus, in the large Pea family, or Order *Leguminosæ*, while the sepals and petals are five, the stamens ten, and excepting one solitary genus, all members of it have but one carpel. In all flowers with coherent petals there are rarely more than two carpels. When we ascertain the number of seeds per carpel, Nature has adopted two methods, either to produce many, or else very few, or even only one. It is a remarkable fact that of the largest Orders, the Composites and Grasses, the flowers individually never produce more than one seed. Comparing the Order *Labiataæ*, to which the *Salvia* and *Dead-nettle* belong, no flower produces more than four seeds, and often less; while *Scrophularineæ*, which contains *Fox-glove*, *Snapdragon*, *Speedwell*, and many other plants, and like the *Labiataæ* has only two carpels, bears an indefinite number of seeds in each carpel. This Order contains 1900 species, while the former has 2600. This shows that a large number of seeds is no special gain to the race. It is simply that all the more seedlings are destroyed before they come to maturity.

Besides this diminution in the number of carpels or seeds in the highly specialized flowers of the above two Orders, actual degeneration may set in, and the ovules, though numerous, never come to maturity. This is the case with *Orchids*, perhaps

the most highly specialized of all flowers adapted for insect fertilization. The ovary is degenerate, and the ovules remain very rudimentary. Indeed, as stated, they, as well as the ovary itself, require the stimulating effect of the pollen-tube before they can grow sufficiently to be benefited by it. The embryo never grows to maturity, even when fertilized ; and out of tens of thousands of ovules in a single plant, only an infinitesimal quantity ever germinate, whether in the wild condition or under cultivation.

One may well ask, What is the advantage of their wonderful adaptations to insects, when of 40,000 blossoms counted on one plant of *Dendrobium speciosum*, well exposed in its native land to insects, one single pod only was observed to have matured ? On the other hand, the many self-fertilizing Orchids, some being cleistogamous, set seed abundantly and are widely dispersed.

The fact is, I repeat, that our previous ideas were all wrong, and *we must reverse them*. The most conspicuous flowers and regularly (if at all) fertilized by insects are not the best off ; *but they cannot help themselves*. The responsive power within them is automatic, so to say, and not volitional. Whatever an insect does to them, they must yield to it, and grow in adaptation to it ; but while they are thus being stimulated to become what *we* may choose to call finer flowers, and handsomer plants with larger

leaves, and so on; yet all this is secured at a sacrifice of fertility. They neither set seed in anything like the proportion that "weedy" plants produce, nor can they hold their own so well when they find themselves transported to distant countries. And as all plants struggle for their own existence, and care nought for that of anything else, those which cannot have plenty of well-nourished seeds, and moreover are dependent upon insects—perhaps upon one or two kinds only—will ultimately die out and disappear altogether.

The degeneracy of the pistil, as described above as taking place in flowers adapted to insects, appears at first to reach a point which under the circumstances appears advantageous; that is to say, the reduction of the number of carpels and the numbers of seeds does not appear to lessen the amount of individuals which survive to maturity; for it would seem preferable to have a few vigorous seeds than a large number of weaklings out of which a few only can survive. But Orchids seem to show that degeneracy may go too far, in that the ovules being impoverished and arrested in growth, far too few are capable of surviving the struggle for existence.

If now we turn to the insignificant self-fertilizing weeds, we find that their flowers show degeneracy as well, but it is not in the pistil so much as in the external whorls. The consequence is, that although

the stamens may be reduced in number, as *e. g.*, from ten to three in Chickweed, and the quantity of pollen proportionally diminished, an ample supply is left for all practical purposes, and as a resulting fact, enormous fertility is secured. Indeed I know of nothing in self-fertilizing plants at all comparable to the degeneracy of the ovules in Orchids ; but the points of degradation enumerated above are all immaterial as regards the purpose of all flowers ; namely, the setting of seed.

THE ORIGIN OF SPECIES BY INSECT AND OTHER AGENCIES.

ASSUMING my theory to be true, that all the numerous adaptations to insect fertilization have arisen through the applications of the insects themselves to flowers ; and remembering that those same structures are the very ones which botanists take note of as distinguishing species and genera ; the conclusion is arrived at, that all species and genera of flowering plants which are conspicuous for their form, size, colour, scent, &c., or whatever features they may possess which render them attractive to, or adapted to, insects, have actually come into existence through the aid of insects.

That is to say, the living protoplasm of the plants has responded to the irritations set up by the insects and the flowers have grown in adaptation to them ; though, of course, not all at once. No important change might probably appear, it may have been, for several generations ; but the final issue is, that the forces *within* the flowers have secured equilibrium with those *without* ; and the existing forms of flowers are the result.

The reader may perhaps have read Mr. Darwin's book, *The Origin of Species by Natural Selection*, and wonder why natural selection has not been mentioned in the present work. The fact is that Natural Selection means simply that the majority of the offspring of a plant die, and the few survive, or are thus metaphorically "selected" ; and geology tells us that nearly all species of plants and animals ultimately die out altogether, their places being taken by new species which have been "evolved" out of the preceding. Whenever an individual lives to maturity it is usually presumed to be "the fittest that survives" ; but if we ask why, of a hundred seeds dropped by a plant, a few only are thus selected and come to maturity, the causes are many. The first is, that the strongest or best nourished seeds will gain the mastery in the struggle. That form of selection might be called "constitutional." Then those seeds which fall on the outskirts of the

crowd may survive, not having to struggle at all, though they might be in themselves seeds of inferior quality. On the other hand, the very best seeds may fall on stony ground, and consequently perish. Hence, what we popularly call "luck" has something to do with the survival of many.

Having mastered the struggle for existence during infancy, or the germinating period, the few are thus "selected," and come to maturity and blossom. It is not till then that the specific or even generic characters can in many cases be discovered; as, for example, in a field of grasses, or a garden of bulbous plants, &c. Now suppose that our selected plants of a particular species be all in blossom together, and ready to receive the visits of insects; and let us imagine that some particular species of insect comes as a *new* visitor. A number of flowers of the same species will therefore be visited. The flower is supposed to be not in perfect adaptation to the new-comer, but according to the theory, it will *begin* to respond to it. The flowers set seed. Next year the process is repeated, the responsive action is again excited, and a further degree of adaptation is reached; and so on for several generations, till at last from being a slightly perceptible *variation* from the original form, the modifications increase so much that new *specific* characters are acquired: in other words, a *new species* has come into existence.

Now let us suppose that from some accident, certain plants of the same original kind have been overlooked, and were not visited by our new friends. They have, we will suppose, been self-fertilized instead of being crossed. Their seeds have fallen, we will imagine, mixed with those from the crossed flowers, within the same limited area. Mr. Darwin has shown us what may possibly happen. He made numerous experiments with plants selected for their conspicuousness, and probably more or less crossed by insects in Nature. He sowed an equal number of seeds of those he had artificially crossed, as well as of those he had artificially self-fertilized with their own pollen. The rule was that the seedlings derived from the crossed flowers, having been stimulated by the process of crossing, were "constitutionally" stronger than the self-fertilized, gaining the mastery over them in the preliminary struggle for existence, when both kinds were planted crowded in the same flower-pot.

These experiments proved that inter-crossing is a *stimulating process*—at least for a time. It is true that Mr. Darwin showed also, that when the two processes were continued for a few years, the plants derived by successive self-fertilization in a few generations not only recovered themselves, so to say, but sooner or later surpassed in fertility the descendants of plants successfully inter-crossed for the

same number of years. But when it is *first* done, and the stimulus can take its full effect, then the seedlings of the crossed flowers proved to be stronger than those of the self-fertilized.

Now this would seem to be exactly what is wanted to allow the plants *just beginning* to vary in adaptation to some new insect visitors to start on their evolutionary career. There would be so many seedlings, the flowers of which would be approaching adaptation to the new insects, that if many were destroyed in the early struggle, there would be enough to continue the evolution of the new species.

I have theoretically demanded the visits of some new insects. It is more probable that the plant will travel to the insect, rather than the reverse; though this might be possible. In other words, migration is a very important, and probably almost always a preliminary, step to the evolution of a new species. The rule in Nature is, that different species of the same genus are found in different localities, though certain species may be very widely dispersed, or even cosmopolitan. Even if several species are found within a square mile, they have mostly different habits, as mentioned in the case of Buttercups; and this reminds us that while the adaptations in flowers may be attributable to the insects themselves, we must give the credit of a

large number of differences in other parts of the plants to the changes in the environment. Just as when wild flowers are cultivated, even if they are not crossed at all, but simply left to their own resources, it is found that after a few years all parts of the plant frequently become modified, and such changes can only be attributed to their environment, *i. e.* soil, humidity, heat, &c. Hence, to start a new species, *two* things are generally wanted—a new locality, and a new insect.

On the other hand, those kinds of flowers which habitually fertilize themselves, and are never visited by insects, as well as wind-fertilized plants, have presumably arisen through the neglect of insects, and in some cases are due to a more inclement climate. Both kinds have originated by slow degradation from insect-fertilized flowers, as described above.

A theory may be often supported by analogous instances, and this is the case with the one I am advancing in this book; for although I am only concerned with the Making of Flowers, yet the making of roots, stems, and leaves has been—I think there is no doubt—by analogous methods, by which each species has become adapted to its environment.

One first observes, just as with flowers, not merely a single instance, but numerous coincidences,

of the same kind, all conspiring to lead one to the conclusion that they are not mere accidents, but imply a cause and effect. Observations of a kindred character may be made both on wild and cultivated plants. First with regard to wild ones. They do not vary much within any given time ; allowing for exceptional genera, Buttercups of to-day are deserving of the same names that Linnæus gave them ; and although some genera, such as the Hawkweeds (*Hieracium*), have produced very many varieties, yet when their distribution is studied, they are found to be correlated to their environment. Thus Sir J. D. Hooker observes—"Variable as the genus is, the sequence of its forms is so natural as to have been recognized by all botanists. This sequence represents, to a considerable extent, the spread of the forms in altitude and area in the British Isles."

Similarly, species of Buttercup can be, so to say, "localized"—*R. repens* frequents waste ground, *R. acris* and *R. bulbosus* meadows, *R. Flammula* damp ground, and so on. Similarly, the many forms of *R. aquatilis* form three groups, such that some have two forms of leaves, the submerged being finely divided, the floating being entire ; secondly, if none arise to the surface they are all dissected ; thirdly, if the plants grow on mud, none are dissected.

Now when we extend our observations we find similar floating and submerged leaves appearing amongst widely distinct species and genera of aquatic plants. Hence we cannot fail to see that these associated conditions between the plant and its environment begin to bear a significance which would not be suggested by a single and simple coincidence.

Another class of phenomena is seen in what are called Representative plants. These are plants which are either different species of the same genus, or of different genera of the same or even of different Orders, growing in different countries, which have approximately the same physical conditions and climate. Such plants retain their own peculiar *floral* structures, but their vegetative systems are closely similar; thus Cactuses of Mexico *resemble* the Euphorbias of Africa; the vegetative growth of both being just like that of *Stapelia* (*Asclepiadaceæ*), these three being of three different Orders. Again, Aloes of the Lily family strongly resemble the Agaves of the Amaryllis family; the former being African, the latter American. Besides the remarkable *fleshiness* of the above genera, an adaptation to dry situations where rain only falls for a short time in the year, a spinescent character is not uncommon under the same conditions in many plants which have

nothing else in common, as occurs in the deserts of Egypt.

Parallel series of phenomena occur under other conditions. Thus when we find similar and peculiar anatomical structures in parasitical plants of widely different orders, we are bound to recognize the peculiar habit of growing upon "host" plants as the cause ; the effects being degeneracy in various directions and degrees. In many, all green matter is suppressed, and the leaves are arrested. In most, the ovaries, ovules, embryos are arrested in various ways. A similar series of facts can be shown to prevail in "Insectivorous plants," which partially live on insects which they catch. Here, again, coincidences are so numerous as to justify us in concluding that the insectivorous and parasitic habits have brought about the existence of the anatomical structures which are associated with those habits.

If we now turn to the results of cultivation, which may be regarded as experimental verification, we shall soon see how conclusive the argument is. Take, for example, the races of the Cabbage (*Brassica oleracea*). This grows wild on our chalk cliffs of Kent, but as long as it is in its native condition it never makes any attempt to form anything like our garden Cabbages and Cauliflowers. Yet under cultivation we have raised innumerable forms.

It would be ridiculous to say that they have not arisen in consequence of their changed conditions ; or that they were not due to the responsive power of protoplasm to the artificial environment to which they were subjected.

What is true for Cabbages is true for all kinds of cultivated plants, of which the peculiar characters are now hereditary.

Various experiments have been made with roots, stems, and leaves of plants, in which it was found that by placing them in unaccustomed conditions, they at once began to grow similar to those which are habitually subject to those conditions. Thus, when stems normally aërial are made to grow underground or in water, the tissues subsequently become different from the aërial type ; and what is significant about the new growth is, that the new tissues produced closely resemble the normal structure of subterranean and aquatic plants respectively. There is no *à priori* reason why they should not have grown quite differently ; but comparing the result of the experiments with the anatomy of normal subterranean and aquatic stems and roots, the conclusion is forced upon one that we have a distinct cause and effect.

Again, the tissue on the upper side of leaves is different from the lower side ; but if leaves are made to grow reversed, the tissues will in many cases become more or less reversed.

Similar observations on different parts of plants are so numerous as to establish the fact, that by subjecting parts to certain conditions to which they are not accustomed, we can induce them to assume structures characteristic of plants which normally grow under such conditions. What conclusion *can* we arrive at, but that such structures as are normal have resulted from the responsive power of protoplasm to the conditions in which they have grown?—and that such structures have become permanently established by *heredity*, until a new set of external conditions compels them to change again?

Two more illustrations may be given. Many maritime plants have fleshy leaves; this is *presumably* due to salt. By experimenting with ordinary plants watered with salt-water, the fleshiness is artificially induced, thereby verifying the deduction.

Again, that spiny processes of plants growing in arid districts is due to the dryness, is an inference drawn from many similar instances. And when the Barbary was grown in a perfectly dry air, it produced no leaves (after the first two or three), but spines only; conversely, when grown in a saturated atmosphere, it produced no spines, but leaves only, the spines being really metamorphosed or rather arrested leaves. This experiment, like the preceding, verifies the deduction.

MORAL CONVICTIONS, OR THE NATURE OF
PROOFS ACCEPTED BY ASTRONOMERS, PHY-
SICISTS, GEOLOGISTS, AND BIOLOGISTS.

BIOLOGISTS who demand experimental verification as being in their eyes the sole kind of proof that is acceptable in the animal and vegetable kingdoms, ought at least to remember that this is not the only kind accepted outside the biological sphere.

Before, however, showing that astronomers, physicists, and geologists are perfectly contented with a less exact kind of proof, it will be as well to restate this kind a little more fully.

When a single coincidence occurs, it would be very rash to infer that there must be some causal relationship between the two events which happen together. When, however, the same coincidence happens two or three times, one "naturally" begins to suspect some link. When the same coincidence is repeated over and over again, we then accept a causal relationship as proved, though we may not as yet be able to trace the action. When we can so arrange the suspected circumstances as to bring about the same coincidence artificially, we consider that we have demonstrated the causal connection by verification. Thus, if a pair of dice fell with the sixes uppermost, we

should regard it as a mere coincidence ; if we threw them not only once, twice, or thrice with the same result, but several additional times, we should begin to suspect they were loaded. When we discovered that however often we threw them they always fell in the same way, we should be “morally convinced” of the fact ; and such an experience is *now* equivalent to a demonstration. If we then took a pair of ordinary dice, loaded them on the side of the ace, and found we could produce exactly the same results, we should have then verified our deduction. In many cases we cannot verify in this way and so demonstrate the truth of the hypothesis, inference, or deduction ; but the proof is accepted, nevertheless, when the probabilities accumulate and attain a very high order. They then amount to a moral conviction, or “circumstantial evidence,” which is universally accepted as being practically equivalent to a mathematical demonstration.

Before Galileo’s time the prevalent idea was that the sun, moon, and stars revolved round the world in twenty-four hours, producing day and night. When, however, the distance of the heavenly bodies were found to be far greater than was previously supposed, and that the same results would follow if they were at rest and the earth alone to revolve on its axis, the previous notions were reversed ;

but let us observe their opposites cannot be verified. The argument is this:—It is infinitely more probable that the earth should revolve, than that the sun, at a distance of more than 90,000,000 miles, and *à fortiori* the stars, whose distances may be measured by billions, should revolve through *six times their distance* from the earth in twenty-four hours.

It is sometimes said that the pendulum verifies the rotation of the earth; but it is only a corroborative evidence; it is no proof in any other sense. If a pendulum be swung in the direction of the north and south poles, provided it can swing a sufficient time, it will soon swing in a north-east and south-west direction.

Now we *believe* the earth revolves; and *if this be true*, we can easily account for the change of direction, because meridians are not parallel. But had this experiment been tried before the time of Galileo, astronomers would undoubtedly have suggested some other and totally different cause for the variation in the direction of oscillation. The conviction, therefore, that the earth revolves is based on probabilities (each one of itself affording no demonstration) of a very high order. Of course, other phenomena tend to corroborate the conviction, such as the greater diameter at the equator than through the poles, &c.

Similarly, physicists do not hesitate to accept coincidences as identities if they accumulate so that the probability becomes a certainty. Thus, when what is called the absorption band, known as D in the solar spectrum, was found to occupy the same position as the monochromatic yellow band of light due to vaporized sodium, it was a remarkable coincidence, and nothing more ; but when other substances agreed with other lines in the spectrum, and many additional coincidences rapidly accumulated, some relationship appeared certainly to exist. The consequence is, that it is now accepted as an established fact that all absorption bands traceable to the sun indicate the existence of corresponding substances. Now it is obvious that these coincidences cannot be verified by analyzing the matter of the sun. Hence, this is a case in which verification by experiment is out of the question. The conviction is established solely in multitudes of coincidences of the same kind.

Lastly, geologists, including palæontologists, have no other evidence whatever on which to establish their convictions. When fossils were first noticed they were regarded as curious resemblances to living organisms, or *lusus naturæ*, or else the Creator was supposed to have purposely made them just as they are ; while the distribution of the strata was thought to have been due to the Deluge,

&c. &c. When, however, facts were more accurately ascertained, and parallel series of phenomena were seen to be now produced by the existing forces of nature, the coincidences were too striking not to suggest similar causes. Thus "lacustrine" strata with only freshwater or terrestrial fossils in them, were *presumably* formed, just as rivers now carry mud into lakes. "Igneous" rocks were *presumably* formed by volcanic or other heat-action. The distribution of boulders of a character peculiar to mountains far away, were at first *presumably* deposited by "waves of translation" until the phenomena of glaciers and icebergs was studied, when geologists changed their opinion, and now the present positions of boulders is *presumably* due to the transplanting power of ice, as being a far more probable hypothesis. Thus were the convictions now entertained by geologists accumulated; old ones abandoned or modified; new ones being accepted in proportion as *probabilities* were strengthened.

But, just as physicists cannot get a portion of the sun to analyze it, so geologists cannot make the world retrace its steps, and go through the process of rock-building again. Their convictions, therefore, cannot possibly be verified by experiment. They are based solely and entirely on coincidences and resemblances which have accumulated by

observations till any other hypothesis is now unthinkable.

The evidence accepted by palæontologists, who study the fossils found in the rocks, is of identically the same kind. So that when a single bone of a particular kind was shown to Professor Owen, he at once pronounced it to be that of a gigantic bird, the entire remains of which were subsequently found, which verified his deduction.

Lastly, the great Doctrine of Evolution itself is based upon the same class of evidence. If all species were sharply separated from one another, as a cat from a lion or tiger, Evolution would very possibly have never been thought of, and "special creations" would have been accepted till now. But it is just because that whenever a considerable quantity of fossils of similar kinds have been found, they invariably merge more or less into one another, and the links increase till the idea of a special creation for each and every minute variety becomes unthinkable. Every evolutionist knows how the conception once received, obtains innumerable corroborations by multitudes of significant facts, of little account when considered singly ; but collectively have very great weight, such as the many facts of Embryology, the presence of rudimentary organs, &c.

As long, therefore, as a few facts only were

known which seemed to point in the direction of some continuous descent with modification, it remained as a "working hypothesis" only; but as a vast accumulation of coincidences and probabilities were secured, any other hypothesis is at the present day absolutely inconceivable, just as is the idea of the sun travelling round the world in twenty-four hours.

Similarly, to return to our particular subject, the evidences for the fixation of characters in plants—originated through the responsive power of protoplasm to external influences—*i. e.* the proof that they become permanent by heredity, provided the influences be continuous through several generations, is of the same kind, and is equally acceptable. In Nature they take place more slowly, and are therefore not easily seen in progress. Under cultivation, just like animals under domestication, the responsiveness is more easily excited, variations are set up more rapidly, and are more easily rendered permanent, and thus breeders and florists can soon establish "races" which come true by seed or breeding.

CONCLUSION.

I HAVE now, I trust, written enough to prove my contention that Flowers have been moulded into their existing forms by the agency of insect-visitors; that the living, sensitive protoplasm is endowed with a power of responsiveness to external stimuli—including nourishment, as in insectivorous plants; mechanical irritations, as in climbing plants; and in many other ways; that Flowers are equally endowed with this power; that they have to exert an effort to support the weight of the foreign body; that the sepals, petals, and stamens can in time grow in response to the weights, strains, thrusts, &c., put upon them; that as these are continually kept up, so in time the results of the effort becomes hereditary; and that all the innumerable and often minute correlations which are to be found in a flower, are in view of attaining one and the same end, have in this way come into existence.

Let me conclude with a hypothetical origin of a flower, which afforded the original subject for the manipulations of the insects, to which we are indebted for all the Floral World as we now have it.

All that seems necessary for us to assume as the origin of a flower with a conspicuous corolla or perianth, is a leaf-bud of which some of the members have been already differentiated into carpellary,

others into staminal, organs, the outer appendages being simply bracts, like, we will say, those surrounding the stamens and ovule of the Yew.

As insects often come for pollen alone—as to the honeyless flowers of Laburnum, Poppies, St. John's Wort, Roses, &c.—and then pierce the juicy tissues for moistening the honey, as they have been seen to do in Anemones, Hyacinths, *Orchis*, &c., we may, I think, infer with some probability that they did the same with the primitive flowers.

Having once attracted insects to come regularly, then a multitudinous series of differentiations would follow. The corolla would in all probability be the first to issue out of the stamens by their metamorphosis into petals, as occurs normally in the Water-lily—or perhaps out of the bracts—as being the next whorl to the stamens, and as a result of stimulus; other changes, described under the Principles of Variation, would follow by degrees and in different combinations; but in every case they would be due to the responsive action of the protoplasm, in consequence of the irritations set up by the weights, pressures, thrusts, tensions, &c., of the insect visitors.

Thus, then, do I believe that the whole Floral World has arisen.

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