



Tuffen West sc.

W. West imp.

The Fertilization of Plants.
(illustrating Dr. Sgale's article.)

THE FERTILISATION OF VARIOUS FLOWERS BY
INSECTS. (COMPOSITÆ, ERICACEÆ, &c.)

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[PLATE LIX.]



A VERY short time ago it was considered a sufficient explanation of the various colours and forms of flowers to say that they were devised to please the eye of man by their brilliancy and their variety. This no longer satisfies us. For we have learnt from Mr. Darwin, that every detail of structure in an organism exists purely and solely for the sake of that organism itself, or because it was of use to the ancestors of the organism, and has been derived from them by inheritance. If anyone bear this general law in mind, and examine by its light a number of different flowers, he will, I think, be led inevitably to two conclusions. Firstly, he will be convinced that the purport of a nectary is to attract insects, and that those flowers which possess one require the visits of insects for their due fertilisation. A second conclusion will be this: That any notable irregularity of the corolla is also—if not invariably, yet usually—connected with the visits of insects, and has, like the nectary, for its ultimate object fertilisation by their agency. The manner in which the irregularity acts is not always the same. One very common result of it is to compel the insect to visit the nectary in some particular direction by barring up all others, that particular direction being such that the insect is made to impinge in a useful way upon stigma or upon anthers, as the case may be. Another very frequent purport of the irregularity is to compel the insect to alight on a particular part, where its weight causes certain mechanical effects by which the pollen is transferred to the body of the insect and is then carried off to the stigma, perhaps sometimes of the same, but more frequently of some other, blossom.

This view of the purport of irregularity throws light on a fact noticed in manuals of botany, but hitherto, so far as I know, un-

explained, viz. the manifest connection which exists between the presence of nectaries and irregularity of the corolla. "It is to be remarked,"* says A. de Jussieu, "that the development of a nectary on any particular part, stands frequently in intimate relationship with the irregularity of the flower, and seems to determine irregularity on that side where it is situated." This intimate connection of two structural peculiarities becomes perfectly intelligible if it be admitted, as urged above, that the two have one common object, viz. the promotion and utilisation of the visits of insects.

I have already in two former numbers of this Review† given sundry illustrations of the preceding remarks. To those illustrations I would now add some others. Combining these with the former, I shall, I think, have shown reasons for concluding that nectaries and irregularity have for their final cause the promotion of intercrossing, and that the same purpose is often subserved by other structural peculiarities which might at first seem matters of indifference. Such, for instance, are the coherence of the anthers (e.g. *Gesenria*, *Composita*); their irregularity in form (e.g. *Erica*, *Salvia*), in number, length, or general arrangement (*Didynamia*); their mode of dehiscence (e.g. *Vaccinium*, *Arbutus*, &c.), its period (e.g. *Digitalis*), and the direction of their dehiscent surfaces (e.g. Thyme, &c.). Such also are the set of the flowers on the stem (e.g. *Melampyrum* and *Pedicularis*); their mode of inflorescence (capital); the distribution of their colouring (*Pelargonium*), and perhaps even the size of the calyx (*Pedicularis*).

I have already pointed out‡ how in Thyme and Marjoram intercrossing is much facilitated by the close crowding together of the flowers, in some of which the stigmas, in others the anthers, are alone mature: because a bee, crawling over the flowery surface, must inevitably convey pollen from blossom to blossom. The still closer crowding of the capital and the *umbel* may perhaps have a similar result. If it be so, we are furnished with the *raison d'être* of these modes of inflorescence.

As far, at any rate, as regards the capital, facts, I think, justify this supposition. If we examine a flower-head in any of the thousand composites, we find as follows: Firstly, in each individual hermaphrodite flower the pollen ripens and is exposed before the stigma is mature. Secondly, the different flowers in the same head do not expand simultaneously, but the expansion begins with those of the circumference and extends centripetally. There are thus collected together flowers in every stage. Some in the centre, not yet open: outside these a ring of others, in

* "Botanique," ninth edition, p. 312.

† See the July number of last year, and the January number of this year.

‡ P. 53.

which ripe pollen is exposed, while the stigmas are yet immature: still more externally, flowers in which the stigmas are mature and exposed, but from which the pollen has mostly or altogether vanished, having been carried off by insects. It is evident how the different periods of pollen and stigmas in each blossom hinder self-fertilisation, and how, on the other hand, the close crowding of flowers in different stages, favours intercrossing.

The common Feverfew will serve as an example. Here each disk-flower is furnished with both pistil and stamens. The five anthers are united so as to form a tube, closed at the upper end (fig. 1), and they dehisce on their inner surface, that is, inside the tube. In this latter is lodged the style, which in the yet immature flower is only so long as just to reach into the lower end of the tube with its upper extremity. This extremity is bifid, but the two segments are held in close contact with each other, there being no room in the tube for them to diverge laterally. The stigmas are bends on the borders of the inner surface of these segments, and are therefore not exposed to any great extent, so long as the two segments are in close contact. At the upper end of each segment is a tuft of hair-like papillæ, which are so set that the whole style, while it is in the tube, somewhat resembles a besom with the handle downwards and the twigs uppermost. When the flower first expands the pollen is already ripe, and lies in that part of the closed anther-tube which is above the hairy summit of the style. The style, however, continues to grow, and as it lengthens the broom-like end sweeps out the pollen cleanly from the dehiscent cells, and, forcing it upwards, makes it break open the closed end of the tube and overflow on the surface in a confused mass (fig. 2). Hence it is soon removed by the insects which crawl over the flower head, and by the time that the style itself protrudes from the tube, all or most of it is usually already gone. The bifid style now itself emerges, and its two segments soon separate from each other and expose their stigmatic surfaces (fig. 3). To these a bee can scarcely fail to convey pollen from the close adjoining flowers, which lie next towards the centre and are less mature. Doubtless, also, it will not rarely happen that some of the flower's own pollen will still remain scattered over the petals, and that some of this will be conveyed to the stigma and self-fertilisation occur. But most of this, and often all, as already mentioned, has already gone; whereas the pollen of the more central flowers is yet undiminished in amount. The flower also itself is but one, while its less mature neighbours are several, so that the chances are largely in favour of intercrossing. This, therefore, and not self-fertilisation must be the rule.

To speak of the tufts of hair-like papillæ as collecting pollen

for the fertilisation of the flower is clearly erroneous. Their position shows that their use is the very opposite. They serve to sweep the pollen out of the way, and prevent it from reaching the stigma. It would be better, then, to call them *poils expulseurs* than *poils collecteurs*, by which latter title they are known in French manuals.

As the expansion of the flowers begins at the circumference, and thence extends towards the centre, it is plain that the pollen of any given flower must be used to fertilise another placed more towards the periphery than itself. What, then, of the most peripheral of all? Their pollen can be of no use to flowers in the same capital, for none lie outside them. It is intelligible, therefore, that these flowers should cease to produce a comparatively useless product; and accordingly we find the ray-flowers destitute of stamens, though still provided with a pistil. As there are no stamens there is again no necessity for a brush to sweep out the pollen, and accordingly we find that the hair-like papillæ are quite rudimentary in the style. It is the saving thus effected that enables the ray-flower to produce a large corolla; and this again we may conjecture to serve, by the brilliancy it gives to the capital, to attract insects.* The disk-flowers by this arrangement are free from any obligation to produce a showy corolla, and so have more material at their disposal for a plentiful production of pollen.

This view of ray-function is in harmony with the fact that, as a rule, in non-radiate capitals the individual florets are larger and more conspicuous than the disk-flowers of a radiate. They have to perform for themselves the duty which in the other case falls almost exclusively on the ray. It harmonises also with the fact, that when either there is an exception to this rule, or when in radiates the ray is so small as to add but little to the brilliancy of the capital, other means are usually adopted to increase the attractiveness. Thus a number of the inconspicuous capitals may be massed into a corymb or a panicle, which, in virtue of increased size, appeals more fully to the eye. Such, for instance, is the case with *Eupatorium*. Or the flowers may be endowed with a strong aromatic odour, as in *Artemisia*, and insects be thus allured through another sense than sight. Or both plans may be combined, as is the case with Tansy. Again, what function has the ray, if not that here assigned to it? Perhaps it may be said that it has none; that it is nothing more than the inevitable but useless consequence of the staminal suppression; that the primary object of Nature was to produce a monœcious condition, which is of known advantage;

* That the ray serves to attract insects was held by Sprengel, as I learn from "Origin of Species," p. 145. Mr. Darwin "does not feel at all sure that the idea is so far-fetched as it may at first appear."

and that the production of the ray was merely a secondary result of this, the spare material necessarily appearing in some shape or other. But this view is irreconcilable with the fact, that in some capitals (e.g. *Centaurea Cyanus*) the suppression includes not only stamens but pistils. Here there is a large unhandsome ray, and yet no monœcious condition. What possible interpretation can be given of such a ray of neutral flowers, excepting that it is intended to attract insects?

We have seen that in such flowers as Feverfew self-fertilisation must not be an infrequent occurrence, though less frequent than intercrossing. In some other nearly allied flowers—for instance, in the Marigold—it is altogether prevented. For here, not only do the ray-flowers cease, as in Feverfew, to produce pollen, but the disk-flowers develop no stigmas. It is curious to notice what modifications this further step entails. The pistils of the ray, as before, are without unnecessary tufts of hair and bear their stigmas on a bifid extremity. The disk-flowers have their anthers as usual united into a tube: now, were the pistil altogether absent, there would be no means of bringing the pollen to the surface. The style, therefore, remains with its terminal brush; but as there are no stigmas this tufted extremity no longer requires to be divided. It is therefore simple and not bifid.

The two capitals I have described are from one group of composites (*Senecioids*). In the other groups the main facts are the same: that is to say, the anthers in all form a tube from which the growing style brushes out the pollen; in all the pollen is spread on the surface before the stigma of the same flower is mature, and in all there are collected in one head flowers in different stages, so that in all intercrossing by aid of insects must be the rule. But the position and arrangement of the hairs on the style which sweep out the pollen differ in each group; and it is this difference which furnishes the characteristic mark of each subdivision.

I pass on to one of the most attractive of irregular forms—the Papilionaceous. The whole purport of this is to ensure the transfer of the pollen to an insect, which is the same thing as to ensure repeated intercrossing. I will take as an example the common furze (*Ulex*). The upper petal—standard—requires little notice. It serves, by its size and brilliancy, to add to the attractiveness of the flower, and also as a protection to the more important parts below. The two lower petals are united together to form a kind of boat—carina—in which are lodged the pistil and stamens. The comparison to a boat is rather far-fetched, for not only is the casina closed below in the part which would represent the keel, but also above; so that the organs within are close prisoners. Were the upper edge of

the carina not thus united, the style and stamens would not remain in the cavity; for their elasticity tends to make them spring upwards, so that they are always pressing from within against the upper side of the carina. Consequently, if a flower be gathered and the carina be gently opened above with a needle, the pistil and stamens will be seen to spring from their prison. The same result will ensue if simply downward pressure be made on the carina, for this is so united to the axis as to admit easily of depression. Should, then, a bee settle on the upper surface of the carina, the weight will tend to depress this. This will assist the upward pressure of the organs within, and if the weight be sufficient they will break through the cohesion of the petals which opposes them and spring upwards, while the carina will sink downwards. In the mature flower the weight of a bee is often insufficient to effect this; either the cohesion of the petals being stronger or the upward pressure of the style stamens being weaker than at a later period. So that one may frequently see a bee visit a just opened flower without liberating the reproductive organs. Probably these are not then in that state of maturity which would render their liberation advantageous. But if a flower be mature, the first time a bee visits it the carina is depressed, the stamens and pistil fly upwards and strike the under surface of the insect with some force. A little cloud of pollen is seen to be thrown off by the shock, some of which will adhere to the insect, and cannot fail to be frequently carried to another flower, while the rest is scattered over the neighbouring flowers, in many of which the stigmas are already exposed by previous visits of bees.

I have spoken as though the bee settled directly on the carina. In reality it settles not on this, but upon the side petals—*alæ*—the legs of the one side of its body upon the one, those of the other side upon the other. These *alæ* afford a better landing-place than would the narrow edge of the carina. The weight, however, still acts upon the carina as much as if the bee had settled directly upon it. For there are, on the outer surfaces of the carina and on the inner surface of each *alæ*, certain projections and recesses which fit into each other, so that *alæ* and carina are locked together, and depression of the former implies necessarily depression of the latter.

In many species of *Leguminosæ* this jointing together of *alæ* and carina is replaced by actual coherence. Such, for instance, is the case with the Sweet-pea, Scarlet Runner, &c. In some species the upward spring of the stamens and pistil when set free from the carina is even more marked than in *Ulex*—as in Broom, or still more conspicuously in *Medicago*. In most, however, no such motion can be observed. In these cases the contact of pollen and stigma with the bee's body is brought

about simply by the descent of the carina, the reproductive organs themselves being entirely passive. As these have no tendency to spring upwards, there is no occasion for the upper edges of the carina to be united together. Such an arrangement would indeed interfere with easy depression. The edges, therefore, are either left ununited in their whole length, in which case the descent of the carina leaves the stamens and pistil fully exposed; or they are united for some distance, but a fissure is left between them at the distal end, through which pollen and stigma protrude during the depression. What the special objects of these variations may be I do not profess to know. The same general purposes are, however, plainly discernible in each case. These are—the protection of the reproductive organs at ordinary times from wind, rain, cold, and other noxious influences, and their exposure, at the moment of a bee's visit, in such a way as to ensure their contact with its body.

In the generality of Papilionaceous flowers it is the under side of the bee which is struck by the anthers. A striking exception is furnished by the French Bean (*Phaseolus comm.*) and the Scarlet Runner (*Phas. coccineus*) (fig. 4). The carina in these flowers is closed, excepting at the very end where the stigma projects very slightly from a round opening. It is adherent to the alæ, not merely jointed with them. Instead of lying between them in a more or less horizontal position, it rises up vertically, and is coiled into a spiral form. This spiral is such that the opening at its end lies just above the only passage by which access can be had to the nectary. On looking at a flower in front (fig. 4), one sees this passage on one's left; and one sees that there is no open passage on the right, the carina being so placed as to block it up. A bee, then, in order to get at the nectar, must push its head and thorax directly underneath the opening from which the tip of the stigma is protruding (fig. 5). While doing this its weight acts through the alæ, on which it stands, upon the adherent carina, which it depresses. The terminal opening is thus brought close to the bee, while the carina is stripped from the style—on which the weight does not act—and leaves a considerable length of this with the stigma uncovered, and in contact with the back of the bee. Judging merely by the length of the stamens, one would expect that the same movement which exposes the style would also expose the anthers, for these lie round the style only just behind the stigma, that is, round a part which the movement does lay bare. But the style is stout and resisting, whereas the filaments are slender and limp, and not firm enough to resist the friction of the retiring carina, with which they are therefore drawn back. The anthers, as they retreat, are of course rubbed against the stationary style. This is set with dense hairs, point-

ing towards the terminal opening (fig. 6). These hairs answer to the so-called *poils collecteurs* in the composites: they sweep off the pollen, so that when the style is protruded its exposed portion—which alone is hairy—is seen thickly covered with the grains. None, however, are seen on the stigma; for, the style being longer than the stamens, this lies beyond the anthers, and the movement only separates them still more. The viscid surface of the stigma is moreover turned away from the anthers, so that any grains which may drop from them accidentally will not light upon it.

The weight of the bee, then, causes a viscid terminal stigma, succeeded by a pollen-smear style, to protrude from the carina, and both come into contact with the upper surface of the insect. The stigma strikes it first, and as the bee pushes deeper into the corolla the viscid surface is rung along its body from before backwards, and will inevitably carry off any pollen which may be there. For not only is the stigma viscid, but it is set round with a brush of fine hairs, which assist in collecting the grains. These are truly *poils collecteurs*, and must be carefully distinguished from the longer hairs on the style, which, as I have already said in speaking of the composites, would more fitly be called *poils expulseurs*. The surface which has been swept by the stigma immediately receives a fresh supply of pollen from the style which follows closely behind, and thus the bee leaves the flower in a condition suitable for the fecundation of the next which it visits.

Both humble and hive bees fertilise this Bean. Most of them have, however, learnt to get at the nectary feloniously by making a hole in the tube. In other similar instances it has always seemed to me that there was an evident reason why the bee should not go in at the natural opening. Either its proboscis was too short, or its head too large. But in this instance no such explanation is possible; for while some bees visit the flower in the natural way, others of the very same species and of the same size avail themselves of the shorter cut, which involves less effort on their part. Whenever I have watched an individual bee visiting a succession of Bean flowers, I have always seen it visit them all in the same way. If it entered the first by the mouth, it continued to do so throughout; if by the artificial opening, it kept persistently to the same plan. It would thus appear that the habit is not an instinct, belonging by inheritance to the whole species, but is in each case the result of individual experience. As with the same experience some bees have acquired the habit and others have not, we must admit not only that these insects are intelligent, but that they differ from each other in their degrees of intelligence, some being slow in acquiring knowledge, others quicker.

The Scarlet Runner is one of the very few plants on which I have found time and opportunity to experiment. Having covered a large portion of a plant with gauze so as to exclude the visits of bees, I found that out of a vast number of blossoms thus protected not a single one produced a pod, while the unprotected blossoms were for the most part fruitful.* Even of unprotected blossoms a very considerable proportion failed to produce pods—a much larger proportion, I think, than is the case with most flowers. This is probably due to the fact already mentioned, viz. that most bees have learnt to get at the nectary by nipping the tube. I have more than once watched for a considerable time without seeing a single bee visit the flowers in any other way. Were all bees equally clever, there would be an end of Scarlet Runners; unless indeed either nature or artifice were to induce some modification of structure—such as the large calyx of *Pedicularis*—by which the tube might be protected, and the bees again driven to the mouth.

Very similar to the Papilionaceous flowers are the Fumitories, as regards the mechanism for their fertilisation. Here again, two of the petals are partly united so as to form a receptacle, in which are lodged the reproductive organs (fig. 7). The arrangement of the other two petals is such that an insect, in order to get at the nectary, is forced to light on this receptacle, which is expanded laterally so as to form a convenient landing-place. When the insect is so placed, its weight causes the receptacle to sink, and the reproductive organs issue from their hiding-place and strike the insect on its under surface. Here also the emergence of the organs is due sometimes simply to the descent of the receptacle, and sometimes is assisted by a tendency of the elastic style and stamens to spring upwards.

The next and last flowers I shall deal with are some in which the anthers alone are irregular. Everyone knows the cross-leaved Heath (*Ericatetralix*), so common on boggy mountains. This has a corolla (fig. 8) which may be roughly described as bell-shaped, and which hangs when expanded, as a bell should, with its mouth more or less downwards. The style will stand for its clapper, but with this difference, that it reaches to the very mouth of the bell, or even projects slightly, when it terminates in a semiglobular stigma. The viscid surface of this

* A similar experiment, however, which I made on the Kitchen-garden Pea (*Pisum sativum*) gave a very different result. The protected flowers formed pods as well as the unprotected. The Pea, then, is capable of self-fertilisation, without the aid of insects. This, however, does not exclude the probability of more or less frequent intercrossing; and it seems to me impossible to suppose that the Pea should possess, without any purpose, a mechanism which in other Papilionaceous flowers, as *Phaseolus*, &c., has a distinct use.

faces downwards, that is, away from the cavity of the bell. The style rises from a superior ovary, under which is a disk that secretes a fluid highly attractive to all kinds of bees. From beneath this spring eight stamens, which soon converge and end in a circlet of anthers set closely round the style (fig. 8). Each anther consists of two cells, adherent in their lower and middle-parts, slightly divergent at their apices. From the base of each cell a curious flat process is thrown out almost horizontally, towards the inner wall of the corolla, which it nearly touches. Thus when one looks into the mouth of the bell one sees sixteen processes radiating from the centre like the spokes of a wheel, and forming an imperfect barrier between the upper and lower halves of the bell. The other ends of the two cells of each anther, as already said, diverge slightly, and near the apex of each, on the external lateral aspect, is an oval opening or pore (fig. 9), which gives issue to the pollen. As the whole corolla hangs upside down, the pollen grains would at once fall out from these pores as soon as dehiscence occurred, were there nothing to prevent it. But even then it is clear that the grains would not light on the viscid surface, for this faces in the wrong direction. The pollen, however, is prevented from so falling; for each anther cell adheres just in the part where its opening is situated to the corresponding part of the adjoining cell of the next placed anther in the circlet. Thus the pore of a cell, say the light cell of an anther, is, so to speak, closed by the pore of the left cell of the next adjoining anther; and so on all the way round. Thus the pollen is kept imprisoned in the cells by their mutual adherence. A very little force, however, is enough to dislocate this chain of anther cells. If a slight pressure be made down upon one of the radiating processes, which form the long arm of a lever of which the filament is the fulcrum, the upper ends of the corresponding anther cells, which form the other arm, are lifted up, and break from their union with their neighbours. The pores are then disclosed, and the pollen grains fall out in obedience to gravity. When a bee visits a flower it pushes its head against the mouth, which is too small to admit it, but which it obstructs completely. In so doing the head necessarily strikes against the viscid stigma, and will leave on this any pollen grains that it may have. The bee then extends its proboscis down to the disk to suck the nectar. The proboscis can scarcely get there without striking one or other of the processes, and as soon as it does this the jointed chain of anther cells, as before explained, is dislocated, and a shower of pollen falls from the exposed pores on the insect's head. This the bee carries off, and will, of course, give up to the stigma of the next flower it visits.

In our botany manuals the structure of the individual anther-

is always minutely described, but no mention is made of the all-important fact of the adherence of the contiguous cells of neighbouring anthers in their dehiscing portions. This, however, is easily seen if one selects a young flower which has not yet been visited, and removes the corolla with due care. Actually to see the bee strike the processes is of course impossible; but I have often seen one come to a flower with a clean head, and leave it with a head dusted with pollen grains.

In the fine-leaved Heath (*Erica cinerea*) there is a mechanism for fertilisation precisely similar to that of *Tetralix*. Probably the same is the case with all those Heaths in which the anthers are provided with processes.

In the closely allied *Vaccinium* there is a somewhat different though very similar arrangement. Here also the anthers are furnished with processes, which act as in the Heaths. But the pores at the farther end of the cells are not placed on the sides, as in the Heath, but are actually terminal (fig. 10). They cannot therefore be closed as before by lateral adherence of contiguous cells. The closure, however, is effected in another way. The apex of the cell where the pore is placed presses against the style, so that the style itself serves the office of a cork, and prevents the escape of the pollen. The filament is so bent as to act like a spring, and keep the anther firmly pressed against the style (figs. 10 and 11). It is only when pressure is made upon some of the processes that the corresponding anther is tilted up, its terminal pores exposed, and the pollen allowed to escape. This pressure is applied, as in the Heath, by the proboscis of the bee. The result, as before, is a shower of pollen upon the insect's head, which it carries off and leaves upon the slightly projecting stigma of the next flower it may visit.

In the common *Arbutus* the mechanism of the anthers is similar to that in *Vaccinium*—that is to say, the pores are blocked up, while the flower is undisturbed, by the style itself. The arrangement is shown in fig. 12, which represents the position of the parts in a mature flower. In fig. 13 the same parts are shown in a yet unopened flower-bud. It will be noticed that the position of the anthers is exactly reversed in the two figures. In the bud the processes of the anthers and the parts in which the pores will afterwards appear are turned away from the mouth of the flower. In the mature blossom they are turned towards it. The anther, therefore, has undergone a revolution, has been turned upside down during the ripening of the blossom; and it is plain that if it had not done so, but had retained the position it held in the bud, the pollen could not have fallen out of the cells, seeing that the mature flower hangs with its mouth downwards.

The way in which this revolution of the anther is brought

about appears to me to be as follows. In the bud the sharp-pointed end of the anther (fig. 13) adheres to the style, with which it is in contact, by means of a sticky, gum-like fluid. Sometimes the anther-point does not seem to be in actual contact with the style, but to be united to it by a slender white thread (fig. 13). This thread, however, I take to be some of the same gum-like fluid, which has been accidentally pulled out and then has dried. Be this as it may, in some way or other the point of the anther is at this period attached to the style, and therefore fixed. The other end of the anther is jointed movably to the filament. Consequently, as the growing filament increases in length, a bend necessarily occurs at this joint, the lower end of the anther being tilted up, and the anther made to rotate round its fixed end. This motion continues till the anther reaches the position it holds in the mature flower (fig. 12), when the opposing style hinders any further rotation. Such lengthening of the filament as may occur after this can only take place by the filament itself curving outwards; and the more it is thus curved, the more firmly will it press the anther against the style, and the more securely, therefore, will the pollen be retained. No pollen escapes during the rotation, for the pore remains closed until it comes into contact with the style.

It may seem strange that Nature should have adopted so apparently roundabout a plan for bringing the anthers into their necessary position. Why should they not have been developed from the first inverted, and with their pores in contact with the style, in which case no rotation would have been requisite? In answer to this, it may be said that Nature by no means invariably selects the most direct path to reach her end, but, as the student of development well knows, frequently proceeds in a zigzag in the production of an organism; and not rarely, after following some definite path for a certain distance, may even retrace her steps, obliterating as she does so her footprints, and start afresh in a new direction.

The flowers with which I have now dealt in this and two former articles are numerous, and belong to many different orders. In all we have seen that there are special arrangements to ensure the transfer of pollen to the body of an insect, which is the same thing as saying that there are special arrangements to ensure at least occasional intercrossing.* If to these be added the Orchises, *Tynnums*, *Tythrums*, *Primulas*, &c., &c., which Mr. Darwin has long since shown to be dependent upon insects for their due fertilisation, and to these again such other instances as have been described by other observers, we have

* See "Popular Science Review," July 1869.

a vast array of facts telling all the same tale, that it becomes impossible to refuse assent to the Darwinian generalisation, "Nature abhors perpetual self-fertilisation."*

EXPLANATION OF PLATE LIX.

- FIG. 1. *Feverfew*. A central flower just expanded: (a) anther-tube closed.
- FIG. 2. *Feverfew*. A flower somewhat less central: (a) anther-tube broken open, and the pollen escaping.
- FIG. 3. *Feverfew*. A still more peripheral flower. The style projecting from (a) the anther-tube; (c) the stigmas exposed; (b) tufts on extremities of style.
- FIG. 4. *Phaseolus coccineus*. Front view, (a) standard; (b) right ala, pulled somewhat aside; (c) left ala, cut off at point where it adheres to carina; (e) vertical carina; (d) terminal opening of carina, with tip of stigma protruding.
- FIG. 5. *Phas. cocc.* Lateral view. Letters as in fig. 4.
- FIG. 6. *Phas. cocc.* End of style and stigma, highly magnified: (a) stigma with hairs round it; (b) long hairs of style; (c) opening at end of carina.
- FIG. 7. *Fumitory*. The two outer petals cut off. A and B the two inner petals, united at c and expanded laterally at E into a landing-place; F the fissure through which the reproductive organs issue; D the diadelphous stamens and the style.
- FIG. 8. *Erica tetralix*. The filaments not represented excepting cut ends of two at d; (c) ovary; (e) hypogynous disk; (b) style surrounded by circlet of anthers; (a and a₁) these letters point to the processes of one and the same anther. So also do (b) and (b₁). The cell to which a belongs coheres with the cell to which b belongs externally, in the part removed farthest from the processes.
- FIG. 9. *Erica tetr.* Single stamen: lateral view; (a) processes; (b) filament, cut short, (c) pore.
- FIG. 10. *Vaccinium myrt.* Two stamens *in situ*, showing how the terminal pores are set against the style.
- FIG. 11. *Vacc. myrt.* A single stamen: (a) terminal pores; (b) filament; (c) processes.
- FIG. 12. *Arbutus*. Two stamens *in situ* in mature flower; their pores against the style.
- FIG. 13. *Arbutus*. Two stamens *in situ* in bud: (a) the closed pores. The stamen on the left is attached by its sharp end to the style by a thread.

* The various mechanical contrivances described in the preceding paper have never, so far as I know, been described before. But my acquaintance with botanical literature is next to nothing, so that it is quite possible that such descriptions may have been given repeatedly without my knowing it. Should such be the case, my ignorance must be my apology for passing over any previous observations without notice.