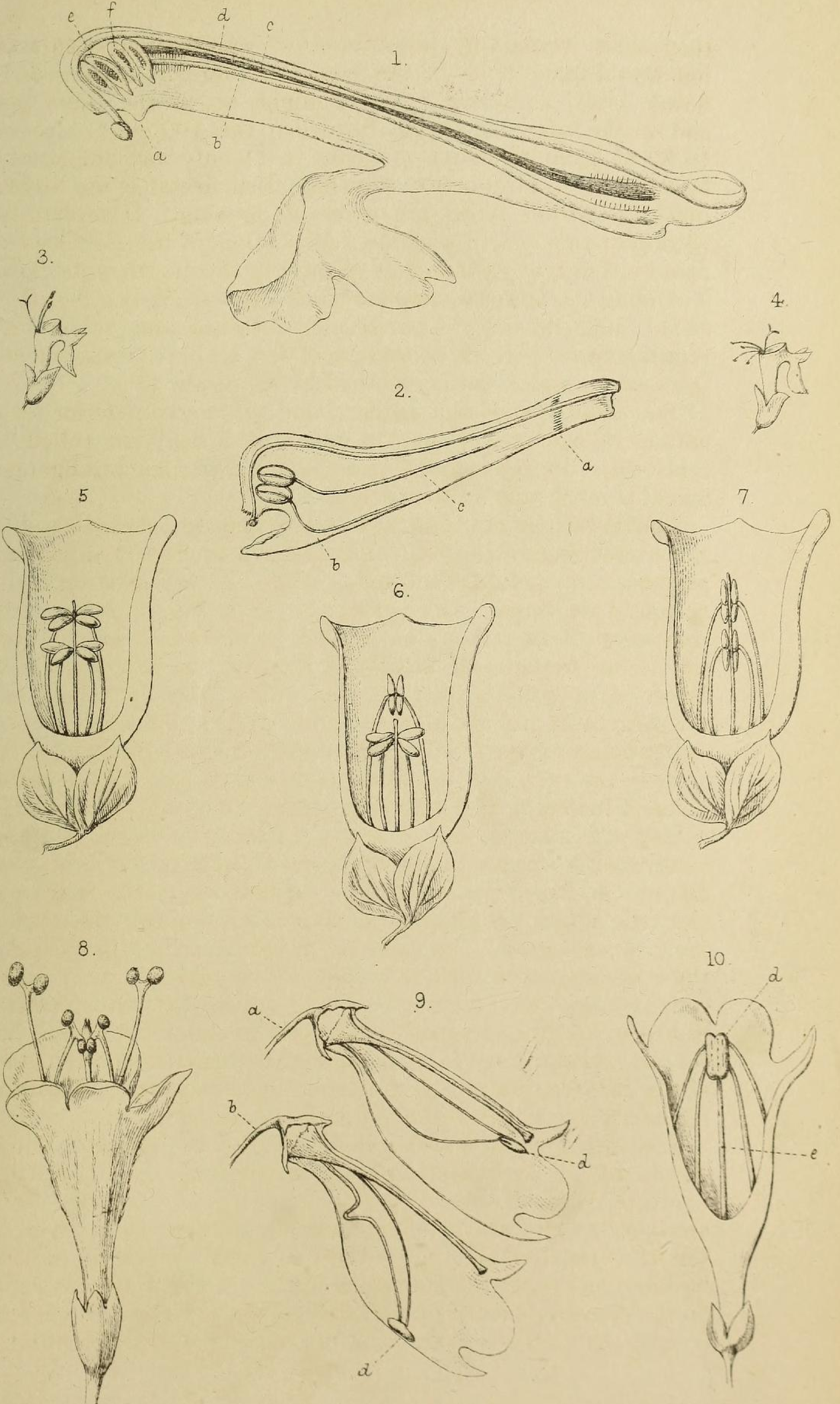


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The Fertilization of Plants.

# THE FERTILISATION OF CERTAIN PLANTS (DIDYNAMIA).

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[PLATE LVI.]

IN the July Number of this Review I described the fertilisation of Salvia and of some other flowers.* I showed how in each case arrangements existed either entirely to prevent self-fecundation, or, at any rate, to render it of rare occurrence. I wish now to show that the same fact is observable in all didynamia, and that the ordinary didynamous structure is indeed nothing more than a contrivance to facilitate intercrossing, and finds in its adaptation to this object its *raison d'être.*

I will begin with a flower abundant enough in our fields, the common red rattle (*Pedicularis sylv.*). This has a labiate corolla, and, as is the general rule in this form of irregularity, the tube furnishes a sweet secretion to attract insects, while the lower lip forms for them a convenient landing-place. The upper lip or hood is remarkably flattened, as though the flower had been pressed in a book. The upper end of this hood is closed for some little distance in front completely, and the stigma projects from it just at the point where the complete closure ceases. Below this again, from the stigma down to the projecting point, marked *a* in the illustration (fig. 1), the hood is practically closed by the close approximation of the two sides, so that the stigma is effectually shut off both above and below from the interior of the hood. Below the projecting point the hood is open in front, but the fissure is very narrow because of the flattening already mentioned. The style rising from the two-celled ovary runs at the back of the corolla in the closest contact with it, following its contour exactly, and thus the curved outline of the closed part of the hood causes the style to bend round, and brings the stigma into the position it occupies. The stamens are four in number, two rather longer

* viz. Mallow, Lopezia, Larkspur.

than the others. Their anthers are lodged in the closed part of the hood, filling completely all the vacant space. They are slightly attached by their external surface to the walls of the hood, while their dehiscence is on their internal surface; so that, if you split open a flower longitudinally, as in fig. 1, you expose the interior of the anther cells on one side to view. The dehiscing surface, therefore, of the anthers of the right side is face to face with the dehiscing surface of the anthers of the left. Now the edges of the open anther cells on one side exactly correspond with the edges of the open anther cells on the other, just as the edges of one valve of an oyster exactly correspond with the edges of the other. It will thus be seen that the pollen grains of the opposite anther cells lie in a common cavity, and so long as the opposing edges of the cells are held in close contact, the pollen is kept securely imprisoned. How is this holding together brought about? As to the upper anthers there is no difficulty, for the part of the hood in which they lie is so excessively flattened as necessarily to press them together. The two lower anthers are in rather a wider space, and might perhaps retreat from each other, and let the pollen escape, were it not for a number of stout hairs underneath them, which by their elastic pressure prevent the separation. These hairs spring from the filament of the upper anther on either side, which passes underneath the lower anther; and it is to be noted that no such hairs grow on the filaments of the lower anthers, where their presence would serve no useful end. The four anthers with the style so completely fill up the closed part of the hood that all is held tightly packed, and it is next to impossible for the parts to get disadjusted.

We have now to consider what is the use of this exquisite workmanship. It is very simple. The flower is visited by large humble bees, which are attracted by the nectar of the tube. As the bee approaches the mouth of the tube, it strikes the projecting stigma with its head, and then settles on the lower lip. It cannot now reach the nectary without inserting its head into the fissure of the hood; but this, owing to the flattening already described, is so narrow that the broad head dilates the hood, and forces the two sides more widely asunder. The necessary result of this can be foreseen. The anthers are attached, as I have said, externally to the inner surface of the hood; consequently, the widening of the hood draws the opposite anther cells apart. A little fissure is formed between the edges, which were before in close approximation, and through this the dusty pollen falls in a little shower on the back of the bee's head. With this adhering to it the bee flies off, and, striking the stigma of some other flower with its pollen-daubed head, fertilises it. I am unable to assert positively that the bee in its exit from the flower does not touch the stigma, and so fertilise the flower with its own pollen. The bee is so large comparatively, and so abrupt in its departure, that though I watched repeatedly, I was unable positively to assure myself on this point. But it appeared to me that it did not, and I fancy that the projecting point below the stigma serves as a safeguard against this (*a*, fig. 1). At any rate, it is easy to convince oneself by watching that not all the pollen is left on the stigma of the same flower, but that much is carried off to other blossoms. Moreover, when the bee leaves a flower, the stigma is already occupied with the foreign pollen which the insect left there in entering, and there is, consequently, little or no exposure of viscid surface to which the fresh pollen may adhere.

The structure of yellow cow wheat (*Melampyrum*) (fig. 2) so closely resembles that of red rattle that I need not describe it in detail. Here also the opposite anthers form one common receptacle, which is kept closed till a bee opens it by dilating the hood. There are some small differences to suit the arrangement to the somewhat different form and position of the flower, which is set horizontally, and not erect as in red rattle, but the main features are the same.* One little point is, however, worth noticing, and that is that the narrow hood fissure through which the insect must pass its head is made narrower still by the filaments of the front pair of stamens. The insect's head passes between these, pushing them asunder, and thus the dilating force acts still more directly on the opposing anthers than is the case with the other flower.

The cow wheat is fertilised by the small buff-bodied humble bee. The large humble bees also visit the flower, but apparently the fissure is too small for their heads, for they adopt the common treacherous habit of bees when they are unable to get in at the mouth, and make a hole in the tube just above the nectary, and so reach the secretion. The very small calyx admits of this robbery, whereas in red rattle the large leafy calyx acts as a safeguard.

What practised thieves these large bees are, is plain from the fact that, on gathering 100 open blossoms, I found the hole in 96, only 4 being intact. It occurred to me that I might use this habit of the bees to throw light on a point of some little interest, the period, namely, at which a flower begins to secrete its nectar. If there be nectar in the tube before the flower opens,

* In order that the pollen may escape and fall upon the bee, the fissure between the opposing anther cells must occur at their lowest part. This, in the erect *Pedicularis*, is on the side turned towards the tube; in the horizontal cow wheat, on the side turned towards the inferior lip. In each case the fissure occurs where it is required.

then these marauding bees would not wait for that occurrence, but would make holes in the buds. I therefore gathered 100 flower buds, as nearly open as might be, in the same place and on the same day as had furnished the 100 open blossoms. In 89 of them there was no hole, in 11 only was one present. It seems a fair inference from this, that nectar is not secreted until the flower is on the point of opening. It is plain how accordant this is with the view I have taken of the use of nectar; namely, that it attracts insects to enter by the mouth of the flower.

Among the figworts there are other species nearly allied to the two I have described—bartsia, for instance, and yellow rattle (*Rhinanthus*)—in which there is a very similar arrangement of the anthers and a similar method of fertilisation.

The coherence of the anthers, and the mechanism for fecundation in the species as yet mentioned, may be called exceptional. In most didynamia there is a simpler arrangement, and this must now be considered.

The flower which I shall take as an example—the woodsage, or *Teucrium Scorodonia*—though not very attractive in appearance, presents some points of interest. Figs. 3, 4 will give a sufficient notion of its shape. It will there be seen that the flower differs from most of its tribe in having no hood formed by the upper lip. The stamen and pistil are, however, protected while the flower is in bud by the lower lip, which is so bent back as to cover them in and shut out wind and rain, while it also prevents the premature visits of importunate insects. So soon as the anthers are ripe, this lip turns over and becomes the landing-place of insects. The stigma is at this time immature, and lies behind the stamens out of reach. The stamens, on the other hand, incline forwards (fig. 3), so that the ripe anthers, which dehisce in front, are in such a position that the bees, which visit the flower in abundance, cannot fail to rub the back of their heads against the pollen. So soon as the stigma is ripe, the stamens, which have now shed all or most of their pollen, retire backwards, bending over the upper lip; while the style comes forwards, and occupies the position which before was held by the anthers (fig. 4). It is plain that this arrangement brings about the fertilisation of the older by the younger flowers, an occurrence of which we have numerous examples.

Let me now notice another point. The stamens in this flower are of unequal length. Two are long, two short, or, in botanical language, the flower is didynamous. Can any use be ascribed to this arrangement? I think there can. Were all the stamens of equal length, the hinder pair would be impeded by the front pair, and the pollen of the former would be wasted on the posterior surface of the latter, and never come into contact at all with the bee. This evil is avoided by their longitudinal arrangement. It may indeed be objected that the evil would have been equally avoided by all four anthers being placed in one horizontal line. Of two perfectly equal arrangements, nature, however, can but select one. But, in fact, the horizontal position would not answer all the requirements. Let any one watch a bee visiting a woodsage. He will see that the anthers strike the top of its head just between the eyes, and smudge the whole intervening space with pollen. Had the two lower anthers been placed in a horizontal line with the upper ones, their pollen would have been shed on the eyes of the insect, and its visits discouraged. The pollen, moreover—and this is the point of chief importance—would have adhered to parts which are quite external to the range of a centrally placed stigma.

If the explanation I have just given be the true one, it should apply not merely to woodsage, but to all those numerous other flowers—labiates, figworts, and the rest—which have a similar arrangement of their stamens. Thus all such didynamous plants must be supposed to require the agency of insects for their due fertilisation. Now that this is really the case is, I think, highly probable. Why otherwise are they, as a rule, furnished with sweet secretions and aromatic odours which serve to attract insects? Why are their four stamens so arranged against the walls of the corolla as to leave a free and open access to the nectary? Why are all the four anthers and the style placed on the same side of the corolla, and in the median line? Why is the dehiscent surface turned towards the path which leads to the nectary and away from the stigma? Why does this latter so often become mature at a later period than the anthers? Why are there only four stamens, even when the corolla has five divisions, and why is the missing stamen invariably the posterior one? Why, lastly, do we so frequently find some or other arrangement in these didynamous flowers, which seems directly calculated to render self-fertilisation a matter, to say the least, of difficulty? All these questions admit of easy answers, on the hypothesis that didynamia are fertilised by insects, and are unanswerable on any other hypothesis.

Let any one, for instance, examine a spike of foxglove, beginning with the upper or less mature flowers, and going gradually downwards to the more mature. He will find, first, flowers in which neither anthers nor stigma are ripe. Then come flowers in which the upper pair of anthers are ripe, the lower pair and stigma still immature. Then all four anthers are found ripe, the stigma still remaining as before. Then, lastly, come flowers in which the bifid stigma is open and bent forwards, but in which the two upper anthers have discharged all their pollen, while the two lower ones have not yet exhausted their store. Now, why is it that the upper anthers are thus before the lower ones in their development? It cannot, I think, be for any other reason than that they are in closer proximity; in fact, close against the stigma, and that there would be great risk of self-fertilisation were they not to discharge their pollen before the viscid surface was mature; whereas the lower anthers lie at a distance, and are much less dangerous. Were this not the case, there is no reason why the upper should precede the lower. In fact, when a useful purpose can be served, we find the lower pair preceding the upper. This is the case with woundwort (*Stachys*). Here the lower pair ripen first, shed their pollen, and then retire laterally, one to the right, the other to the left. This they do in order to make room for the style to bend forwards, and come into proper position.

In examining the successive blossoms of a spike of foxglove, another fact will be noticed, which, as well as the general didynamous structure, testifies to the importance of a vertical arrangement of the anthers. Each of these has two large lobes, which in the immature blossoms are placed horizontally, so as to cover a considerable breadth of the corolla. Were they to ripen in this position, most of their pollen would be wasted, for it would adhere to the sides of the humble bee, in parts entirely out of reach of the centrally placed stigmas. To avoid this, the lobes, as they ripen, change their direction and become vertical, lying close to the median line. (These successive changes are shown in figs. 5, 6, 7.) Their range is thus made to coincide with that of the stigma; that is to say, a bee entering a freshly opened flower will have its back daubed with pollen in the same median line as will come into contact with the stigma when it visits a more mature blossom.

The imperative necessity of keeping the anthers in the same line with the stigma may perhaps explain the anomalous structure of the stamens in Prunella. In this flower, curious buttresses project from the outer side of the filaments against the inner surface of the wide hood. These serve, I imagine, to fix the anthers more securely in the median line and to prevent any lateral divergence.

There remains yet another point of interest. Why are there only four stamens in these didynamous flowers, even when calyx and corolla have five divisions? and why is the missing stamen invariably the posterior one? The reason is obvious. This stamen, were it present, would occupy the position which is wanted for the style. It is necessary that this shall lie against the wall of the corolla, so as to leave a free passage for insects. It is necessary that it shall lie against the *posterior* wall and in the median line, or its range will not coincide with that of the anthers, and the stigma will not strike the part of the bee on which the pollen is smeared. In fact, there is no other position but that of the missing stamen in which the style can be placed.

The best thing, therefore, that can happen is that this stamen shall not be developed at all; and this is what does occur in didynamous flowers. The next best thing is that, when developed, it shall get out of the way and make place for the style. This is what occurs in Pentstemon. Here four of the stamens and the style are arranged as in ordinary didynamous flowers. The fifth stamen, however, is present, but makes place for the style, by running from its insertion in the posterior median line right across the tube to the opposite side of the corolla. It is less in the way here than if it occupied its natural position. Still it is perfectly useless, and in some degree an obstruction. It is not therefore to be wondered at that, as a rule, it produces no pollen, and that not very rarely it is altogether absent. The Pentstemon would thus appear to be on its way to become didynamous.

Doubtless there are not a few didynamous flowers the structure of which may seem to be more or less in contradiction with the preceding remarks. The apparent contradictions are, however, I think, always capable of explanation. Some of these exceptions to the ordinary arrangement I will now consider.

*Scrofularia.*—In this genus the posterior stamen is still the missing one, although the style and other stamens are ranged against the anterior wall. The absence of the fifth stamen cannot therefore in this case be explained by its place being required for the style. It can, however, be accounted for on another ground. The stamen would be perfectly useless, for its anther would strike an insect on the back, while the stigma only comes into contact with the under surface. The anther is absent therefore on grounds of economy. But as its entire disappearance is not required to make room for the style, it is not surprising to find that it is not so completely absent as in other didynamia, but is represented by a scaly staminode of considerable size.

*Gesneria.*—Here we have a corolla in general form like that of a foxglove. The style also with its stigma occupies a like position as in that flower; that is, it runs in close contact with the posterior wall and in the median line, occupying the place of the absent stamen. The anthers of the four remaining stamens, instead of being arranged in pairs longitudinally, as in foxglove and most didynamia, lie in a horizontal line immediately in front of the stigma. In the case of Teucrium, I said that such an arrangement would not answer the requirements, because the two external anthers would smear their pollen on parts of the bee which would be quite out of range of the centrally set stigma. In Gesneria, however, this difficulty is overcome. In the first place, the stigma is very broad, so as to cover a large range. Then the anthers are individually very narrow, and, moreover, adhere to each other by their edges, so that the four together form a disk no broader than the stigma, immediately in front of which it lies (figs. 9, *a*, and 10). The dehiscence of these coherent anthers is, as usual, on the anterior face, that is, on the side turned away from the stigma. Thus, a bee entering the corolla soon after its expansion will get a smudge of pollen on the median line of its back. It will not touch the stigma, for this is shielded by the anther-disk. But when the flower has been some time open, a change occurs in the position of the parts. The filaments bend forwards, and carry the disk away from the stigma right across the corolla, until it comes into contact with the anterior lip, where it remains fixed (fig. 9, *b*). It is plain that when a bee visits a flower in this later condition, the same spot on its back, which in the earlier stage came in contact with the anther-disk, will now come in contact with the stigma: for this occupies the same position as did the disk, and is, moreover, of the same breadth. Thus in Gesneria—as in so many other cases—the more mature flowers are fertilised by the pollen of the less mature.

*Antirrhinum.*—The general arrangement of style and stamens in snapdragon is the same as in foxglove; but the persistent closure of the mouth of the corolla might seem a certain proof that the fertilisation is independent of insects. Any one, however, who watches the flowers with a little patience will soon see that the closure is not sufficient to exclude bees. Sometimes a bee will be seen trying in vain to force an entrance ; but in such case the flower is, I believe, invariably immature. So soon as the anthers are open, the tightness of the closure relaxes sufficiently to allow the bees to force their way in without any great exertion, and I have repeatedly seen them do so.

That such visits are required for due fertilisation I have, moreover, found on experiment. I covered a large Antirrhinum with a tent of gauze, so arranged as to exclude bees. The plant flowered abundantly ; but though in other Antirrhinums close by, which were not so protected, scarcely a single flower failed to be fertilised, only two small capsules were produced from all the numerous flowers of the protected plant ; and even of these two it was doubtful whether the fertilisation was not due to an accidental rent in the gauze that occurred towards the end of the experiment, and was not immediately mended ; so that possibly a bee may have got in at that period.

I was much struck in this and a few similar experiments by the long persistence of the corolla when fertilisation is prevented. I was informed, also, by a large horticulturist, that when the bees get at his flowers in the greenhouses the plants become almost worthless for sale, owing to the speedy fall of the blossom. The teleological significance of this is of course apparent. The corolla is of no further use when fertilisation has once occurred, and its maintenance is a useless burden. It is therefore cast off. But *how* this is brought about is not so obvious. I presume that the fertilisation causes a larger flow of nutriment to the stimulated ovary, and that this flow takes place at the expense of the corolla, which then perishes from starvation.

The last exceptions I shall consider are wild thyme (*T. serpyllum*) and marjoram (*Origanum*).

In each of these we have a didynamous flower, which certainly is fertilised by insects, for its anthers ripen and shed their pollen before the stigma is mature. The four anthers, however, are not placed longitudinally, one pair above the other, for the stamens diverge laterally and project beyond the corolla in a fan-shape. The breadth which the anthers thus cover is much greater than can come within the range of the centrally placed style. The difficulty, however, vanishes when, instead of examining a single flower, we consider the general mode of growth and the inflorescence. Thyme, as a rule, grows in patches. The small flowers are crowded together on the surface of the patch, forming a continuous carpet of bloom, from which project upwards the ripe anthers of the younger and the ripe stigmas of the older flowers. Over this carpet crawl the bees, their bodies so large in proportion to the individual blossoms as to be in contact with many at a time.

The crowded heads of marjoram form a similar carpet. Thus all parts of the under surface and sides of the bees get dusted with pollen, and similarly all parts come sooner or later into contact with stigmas. There is thus no occasion for that definite arrangement of the anthers which is profitable in the large-flowered didynamia. What is required is that the anthers should project beyond the corolla, and this they do.

It would clearly also be disadvantageous that the dehiscent surface of the anthers should be turned, as in most other didynamia, forwards. To ensure the readiest contact with the insect as it crawls over the flowers, this surface should face directly upwards. Now with the longer stamens, which are entirely free of the corolla, this is the case. The lower pair of anthers only, as a rule, half overtop the corolla's lip. The dehiscent side of their upper free lobe is turned upwards; that of the lower lobe faces forwards. Thus always the dehiscent surface assumes the most advantageous position. That of each free lobe is in the position which brings it into contact with the bee as it crawls over the surface; that of the protected lobe is such that it will strike the bee's head as it sucks the nectar (fig. 8).

In most thyme plants the flowers are hermaphrodite. The stamens project from the corolla when the flower first opens; but it is only at a later period, when the pollen is in great part shed, that the style lengthens, and the stigma in its turn projects. This would seem to afford a tolerable security against self-fertilisation. Nature, however, seems bent on erecting a still stronger barrier, by entirely separating the two sexes. For a considerable proportion of thyme plants have flowers in which the stamens are abortive, and reduced to mere rudimentary points inside the tube, while the stigma projects when the flower first opens.* There are thus thyme plants which bear only female flowers. Whether there are also others which bear only male flowers, I cannot say. I have, however, never found such an one. All that I have been able to make out is that very frequently in the hermaphrodite flowers the stigma fails to arrive at maturity. It seems hardly too rash to foretell that in the course of time these hermaphrodite flowers will cease altogether to possess stigmas, and that thyme will be purely diœcious.

Still more surely may it be foretold of another plant—the horsechestnut—that in time it will be purely monœcious. If one of its pyramidal flower spikes be examined, the greater number of the flowers will be found to have the following structure. A sweet fluid is secreted at the base of the corolla, and access is open to this just under the two upper petals, on each of which is a dab of bright colour, while the rest of the corolla is white. The stamens are so curved and the anthers so set that a bee cannot get at the nectary without smearing its under surface with pollen. In the midst of the stamens a small pistil will be seen, which never developes to maturity, so that these flowers are in fact male flowers. Some few flowers, on the other hand, will be found in the spike, and almost always in the lower part, in which the style and stigma are fully developed, and have just the same curved form and position as above belong to the stamens and anthers. In these pistillate flowers there are also stamens; but these are not turned towards the entrance to the nectary. Their anthers, moreover, as a rule, fall off without dehiscing, although there is pollen to be found on section within their lobes. These lower flowers, then, are practically female flowers, and their stigmas will strike

* The flowers in which the stamens are rudimentary have also a much shorter tube than have the ordinary ones, so short that the lower lip is in contact with and supported by the two anterior long teeth of the calyx.

the same part of a bee which above would be struck by the anthers.

Besides these male and these female flowers, others will be found—usually intermediate in position—which appear to be fairly hermaphrodite. In these not only do the anthers ripen their pollen, but the pistil, though it is not nearly so large as in the purely female flowers below, yet matures and is often fertilised. It is not without its use that the flowers which are becoming male should be at the apex, and those which are becoming female should be at the base of the spike; for thus any pollen which is shaken out by the wind will have a better chance of being utilised than were the positions reversed, as in poterium.

A word as to the dabs of bright colour on the upper petals. It is so excessively common to find such ornaments about the entrance into the nectary of flowers that one can hardly help suspecting that their position in that part serves some useful purpose. May it not be that the colour acts as a guide to the insect, attracting and directing it to the proper entrance? The marvellous ease and rapidity with which insects find their way to the nectary would thus in part be explained. A fact given by Mr. Darwin, as a striking case of correlation, seems to me strongly in favour of the explanation I have advanced. "I have recently observed," says Mr. Darwin, "in some garden pelargoniums that the central flower of the truss often loses the patches of darker colour in the two upper petals, and that when this occurs the adherent nectary is quite aborted; when the colour is absent from only one of the two upper petals, the nectary is only much shortened." *

I should say that in pelargonium, as in a host of other flowers, the anthers shed their pollen before the stigma is mature; and that anthers and stigmas turn when mature upwards, so that a bee, in getting to the nectary, rubs them with the under surface of its body, and thus carries the pollen of the younger flowers to the stigma of the more advanced ones.

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## EXPLANATION OF PLATE LVI.

FIG. 1. *Pedicularis sylv.* Longitudinal section, (*a*) point, which probably protects the stigma during egress of bee; (*b*) anterior filament, with hairs on its upper part where it passes under the lower anther (*f*) to terminate in the (*e*) upper one; (*c*) posterior filament, without hairs on the upper part; (*d*) style; (*e* and *f*) upper and lower anthers. The cells are open and face the spectator.

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* "Origin of Species," p. 145.

FIG. 2. *Melampyrum pratense.* Longitudinal section, (*a*) ring of glandular hairs; (*b*) filament of anterior stamen, on which the bee presses laterally; (*c*) posterior filament.

FIG. 3. *Teucrium scorodonia.* Just expanded. The anthers full of pollen, dehiscent in front, and anterior to the style.

FIG. 4. *Teuc. scor.* At a later period. The anthers empty, thrown back with the filaments; the style inclined forwards.

FIG. 5. *Digitalis purp.* All the anther lobes horizontal and not yet open.

FIG. 6. *Digitalis purp.* The upper anthers with their lobes vertical and dehiscent. The lower anthers still horizontal.

FIG. 7. *Digitalis purp.* The lower anthers also with vertical dehiscent lobes.

FIG. 8. *Origanum vulgare.* The style yet immature.

FIG. 9. *Gesneria sp.*? (*a*) Just open and with anther disk in front of the stigma; (*d*) anther disk. (*b*) Later stage — anther disk (*d*) against anterior wall.

FIG. 10. *Gesneria sp.*? Seen from front, a piece of the corolla having been removed; (*d*) anther disk in front of stigma; (*e*) style, the stigma hidden by the disk.