Plate. XLVIII.

Fig. 1.

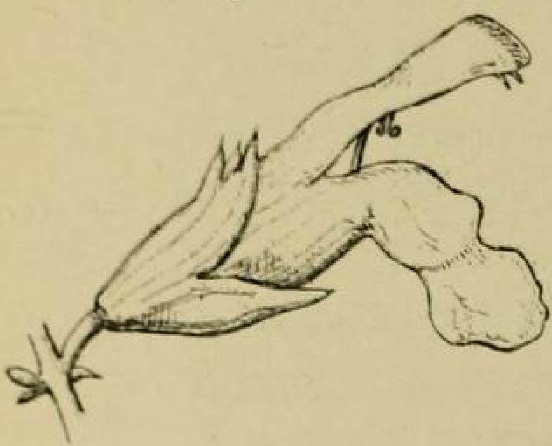


Fig. 2.

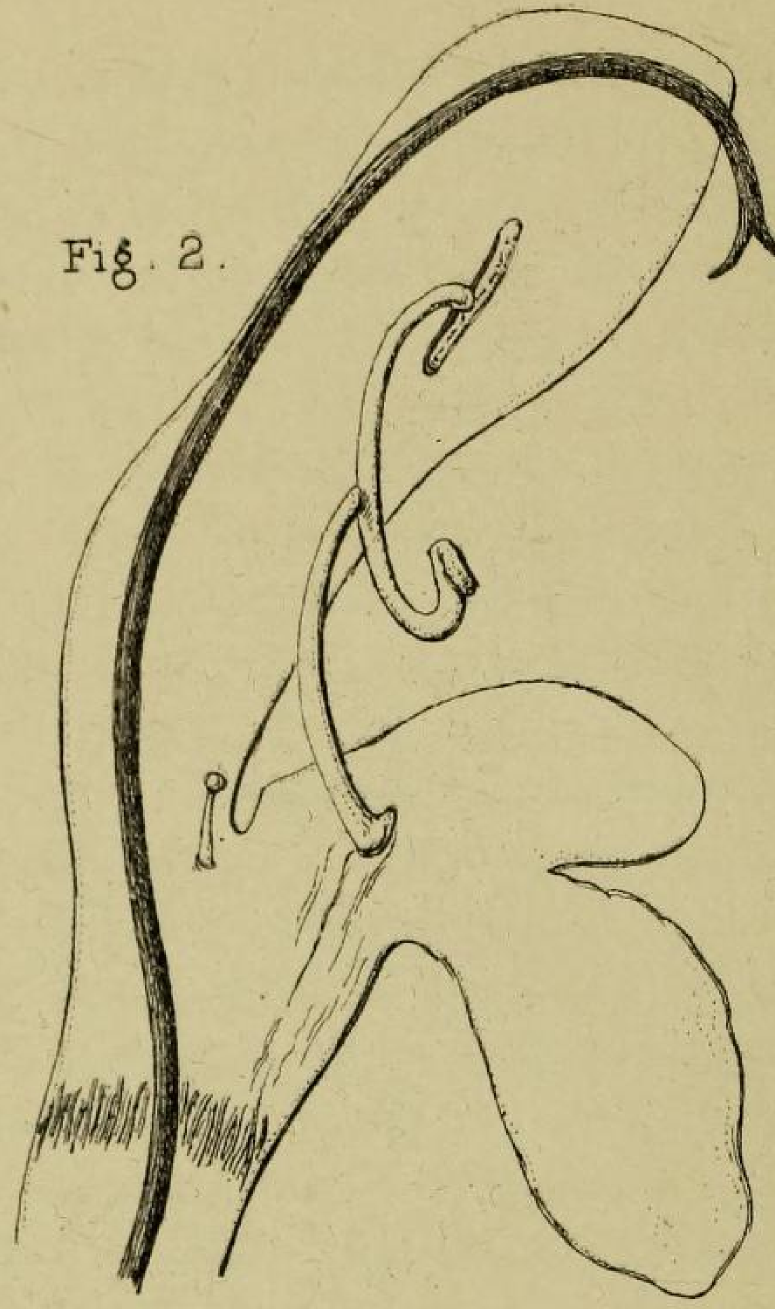


Fig. 6

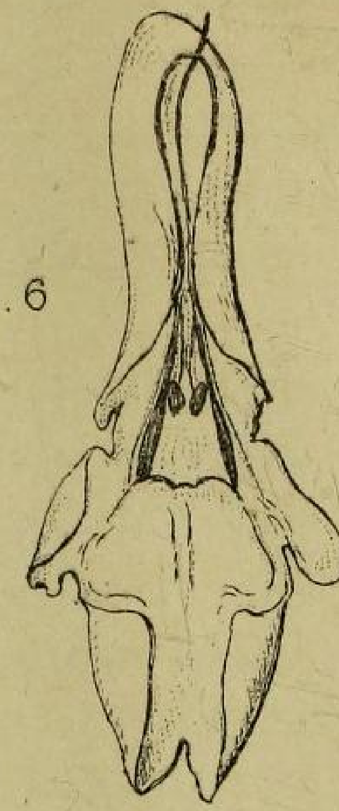


Fig. 4.

Fig. 5.

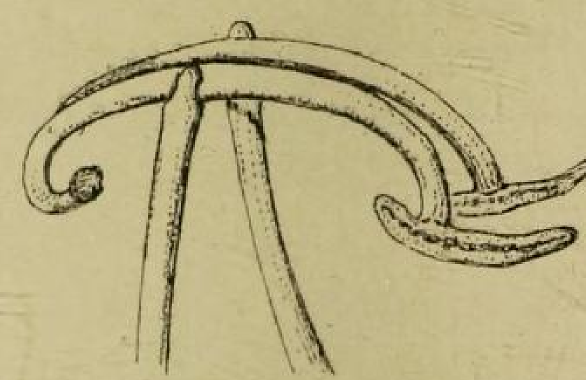


Fig. 3.

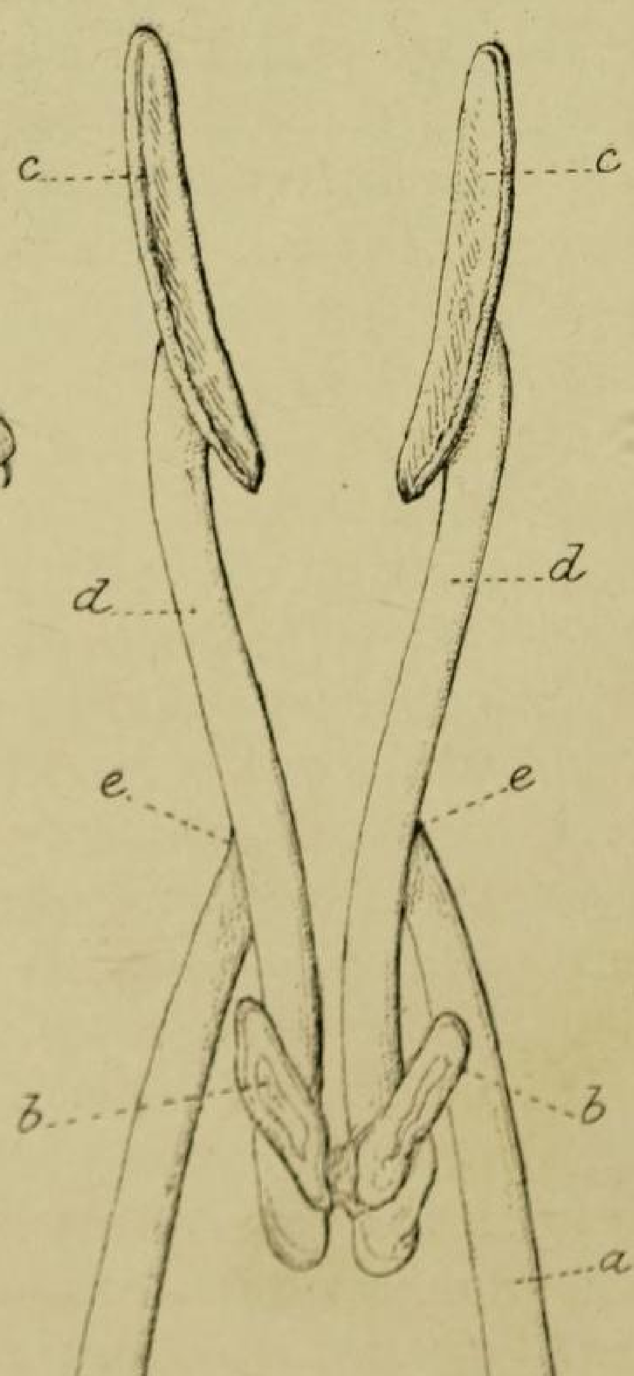


Fig. 7.

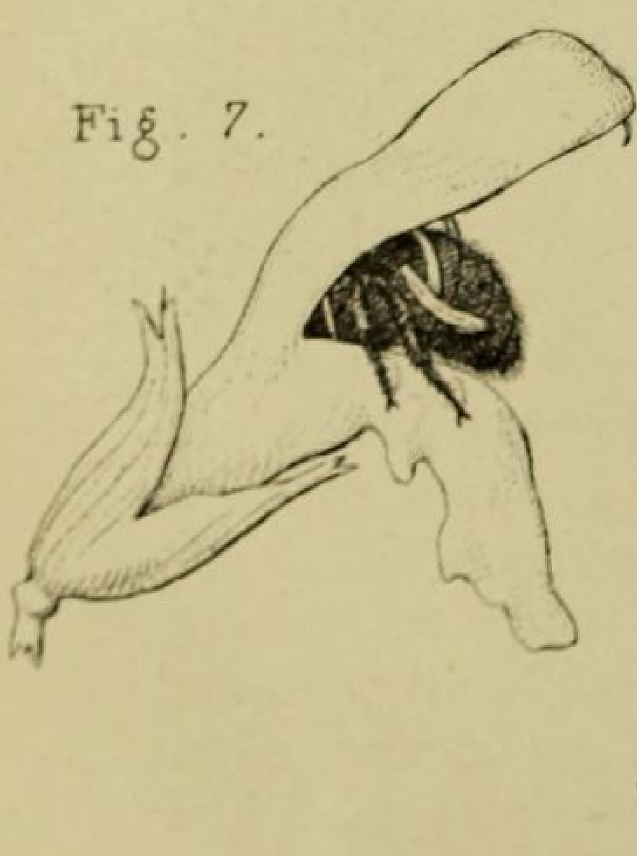


Fig. 8.

W. Ogle.

W. West imp.

The Structure of Salvia.

Plate XLIX.

Fig. 9.

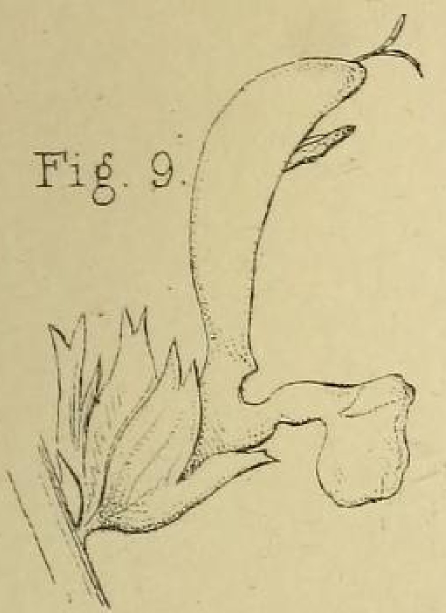


Fig. 12

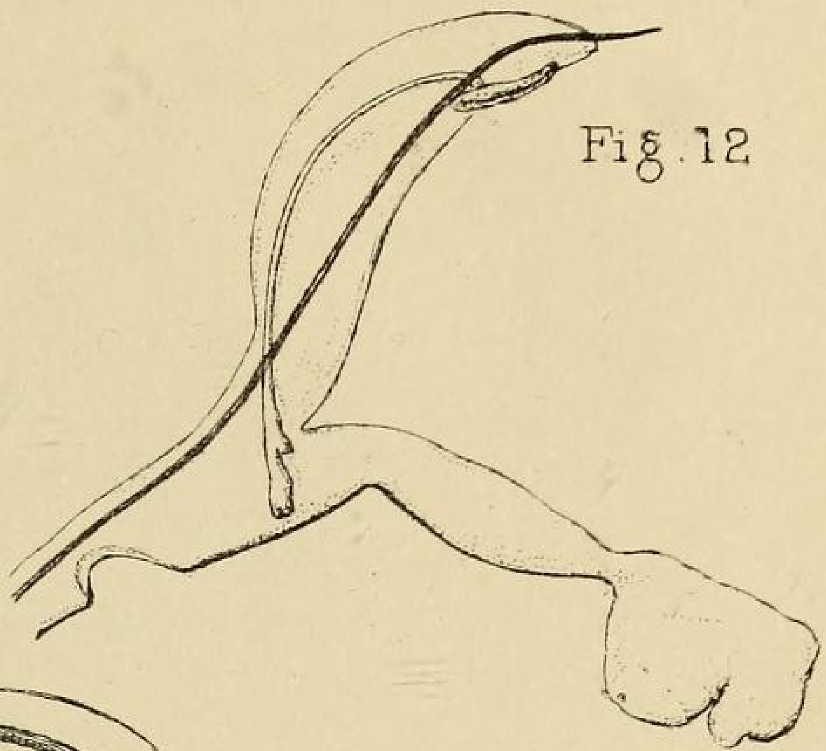


Fig. 10.

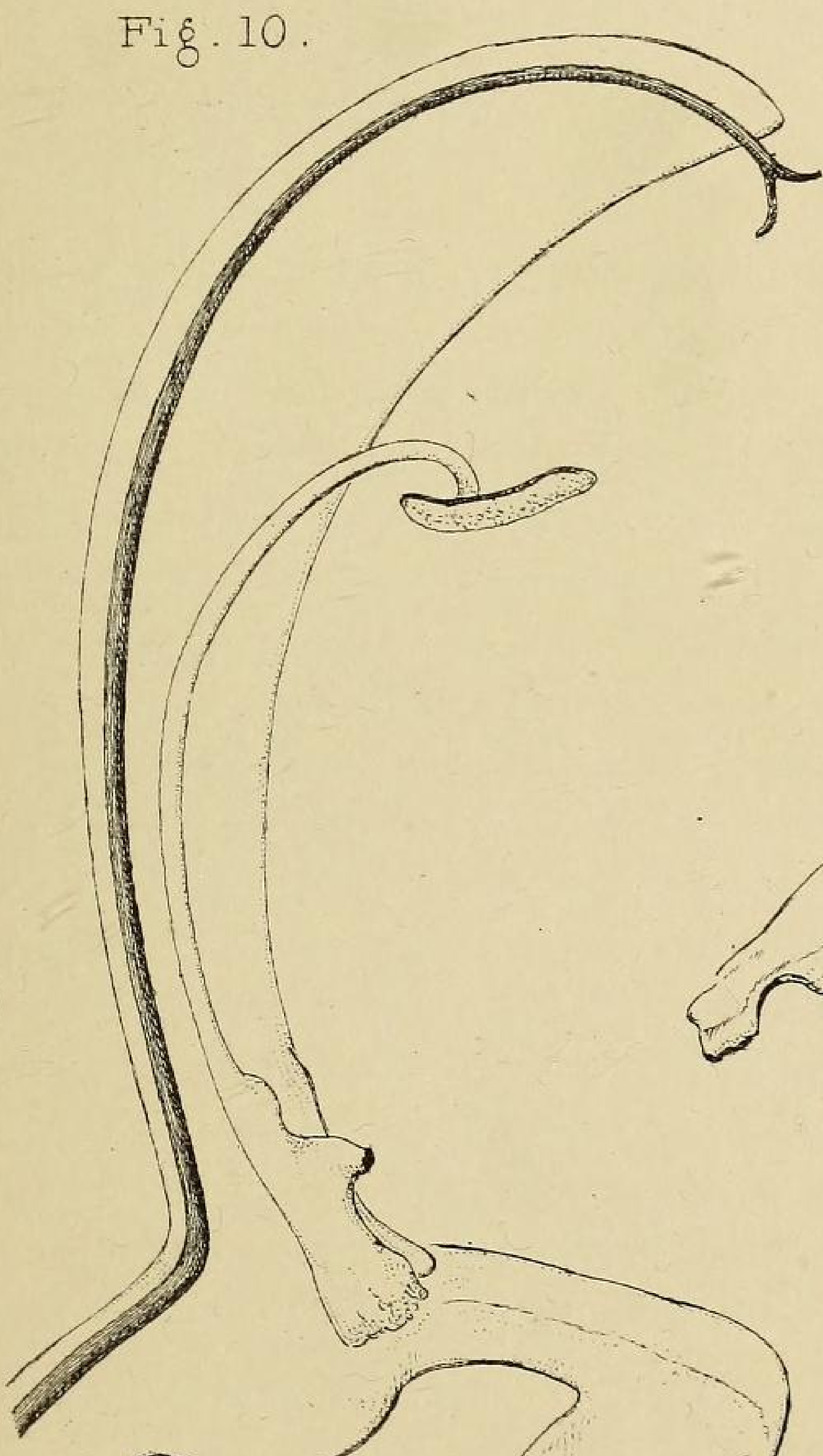


Fig. 11.

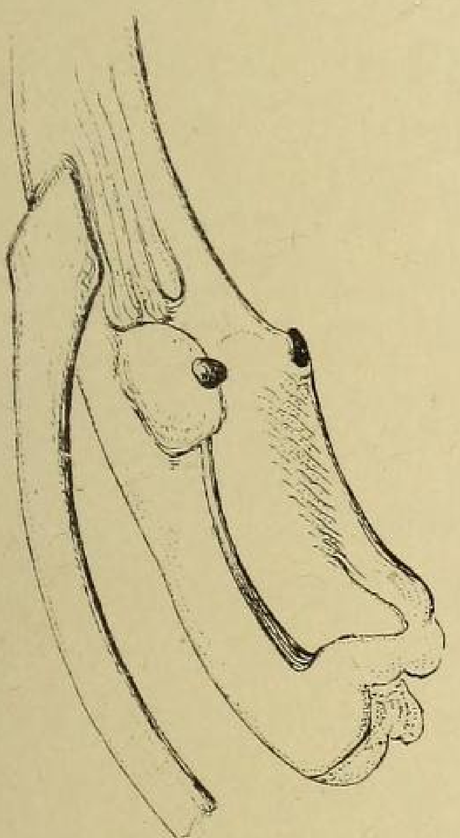


Fig. 13.

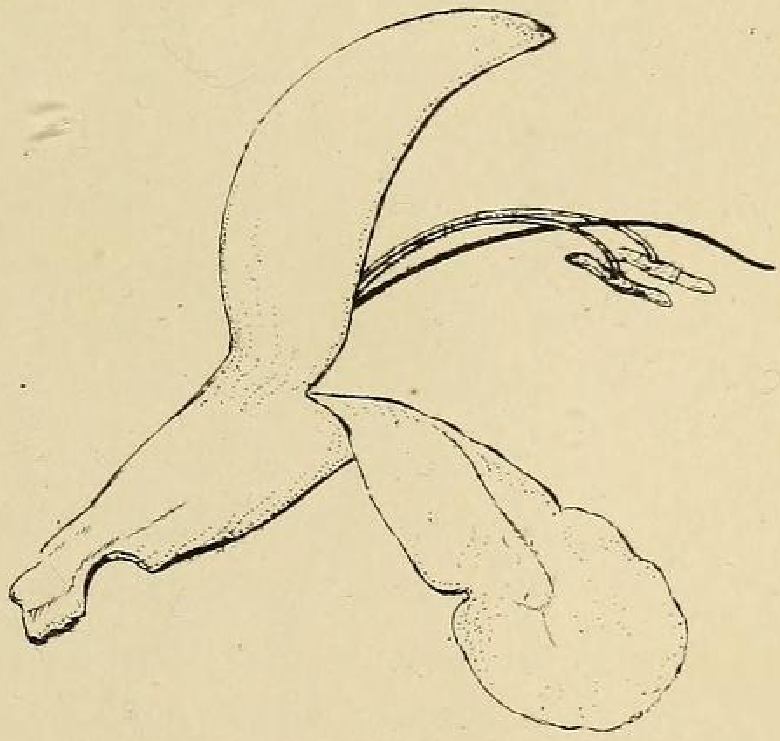
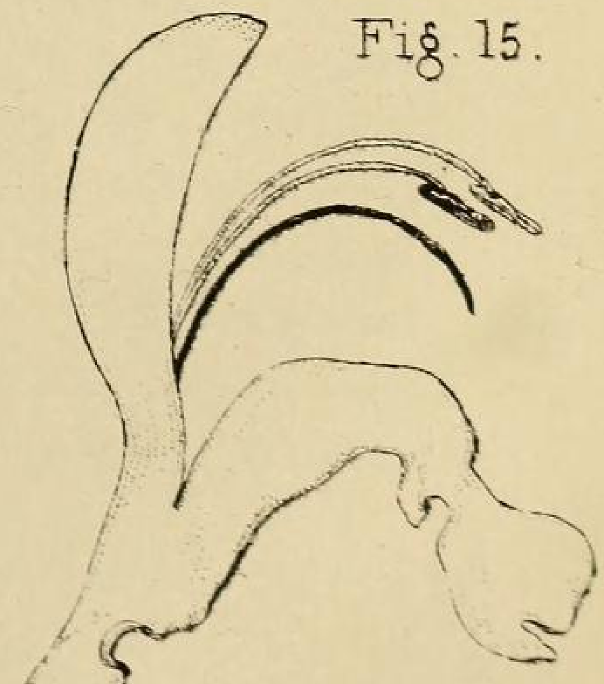


Fig. 14.

Fig. 15.



W. Ogle.

W. West imp.

The Structure of Salvia.

THE FERTILISATION OF SALVIA AND OF SOME OTHER FLOWERS.

BY WILLIAM OGLE, M.D.
Lecturer on Physiology at St. George's Hospital.

[PLATES XLVIII. AND XLIX.]

MR. DARWIN has, in many places, and notably in his book on orchids, insisted on the dictum, "Nature abhors perpetual self-fertilisation." Even in hermaphrodite organisms there exists, he believes, invariably some contrivance which either entirely prevents self-fertilisation, or at any rate ensures a more or less frequent intercross. In this paper I wish to add some more facts to the many which Mr. Darwin has adduced in support of this proposition. I think I shall be able to show, that in many species of salvia, and in some other plants, there are certain most ingenious contrivances, which hinder or impede self-fertilisation and ensure intercrosses between separate flowers.

The salvia in which I first noted the phenomena which I am going to describe, is a tall handsome plant, which I take to be a cultivated variety of *S. officinalis*. A single flower of the natural size is pictured in fig. 1. The corolla is two or three times as long as the calyx, with a widely open mouth and dilated tube, which admits of the entrance of humble bees. These seem to be especially attracted by this flower, and on my visits to a piece of ground where the plant grew in profusion, I invariably found a large number of them buzzing about the blossoms, settling on the tempting landing-place offered by the central lobe of the lower lip of the corolla, and diving into the recesses of the tube to enjoy the glandular secretion of the nectary at its base. There can, I imagine, be no doubt that the aromatic perfume of the whole plant and the glandular secretion of the fringe in the tube exist in order to promote the visits of bees to the flower.

There are in this salvia, as in others, four stamens, of which, however, the two upper ones are rudimentary. The remaining two have a very peculiar structure. Each consists of a short stout filament, which is inserted into the mouth of the tube, as represented in fig. 2, and which thence runs backwards, so as to have its upper end completely hidden from view in the hood formed by the upper lip of the corolla. The short filament terminates in a connective which is developed to such an extent as to be actually longer than the filament itself, and at the two opposite ends of the connective are the two anther cells. The portion of the connective uniting the upper anther cell with the filament, is much longer than that portion which unites the filament to the lower cell. The upper anther cell is also itself much larger than the lower one, this latter being, in fact, almost sterile, and furnishing little or sometimes no pollen. It is not, however, so completely transformed into a barren structure as is the case in many other species of salvia, to be spoken of presently. The upper cell, on the other hand, furnishes pollen in great abundance, and allows it to escape by dehiscing in the front longitudinally. The filament is attached to the connective externally by an excessively movable joint, so that a very slight pressure on either anther cell will cause the connective to turn on the filament with what the French would call a "mouvement de bascule." The joint is so strong that you may actually cause the connective to rotate four or five times in complete circles in the same direction on the filament before it is twisted off. The lower or sterile cells of the two anthers are adherent to each other, so that a slight pressure on *one* anther will produce rotation, not only in its own connective, but in both. This description will be more intelligible on looking at fig. 3. In fig. 3 the stamens are represented as seen when looked at in front; in fig. 4 they are seen from the side when at rest; in fig. 5, as seen from the side when the anthers are made to rotate on the filaments.

On looking at the front of the flower, the only parts of the anthers which are visible are the lower cells, with their portion of connective (fig. 6). These stick out into the gaping opening of the tube, projecting like an uvula into the throat. The rest of the anthers is hidden in the upper lip of the corolla, which forms a hood, closed more or less completely in front until the flower begins to wither. The lower anther cells project to such a distance in the mouth of the corolla as to render it quite impossible for a bee to get at the nectary without pushing directly upon their upper surface. No sooner does the bee exercise this pressure than the connective rotates. The upper anther cells emerge from the hooded receptacle in which they are hidden, and are seen to perform a circular movement forwards and downwards, until their dehiscent surfaces are brought into close contact with the back of the bee, one anther cell rubbing it on either side. This movement may be artificially produced by introducing a pencil into the mouth of the flower, but it is a far more interesting sight to watch it when brought about by the action of the bee. It can be seen with the greatest ease, and no one who has once seen it will doubt that the peculiar form and arrangement of the stamens is not an accidental and indifferent one, but stands in direct connection with the visits of the bee to the nectary; and that the curious modifications in the structure of the whole flower have occurred in order to ensure the adherence of the pollen to the back and sides of the bee (fig. 7).

It will be noticed that the lower anther cells, those against which the head of the bee strikes, are sterile or nearly so. This is an instance of the apparent occasional economy of nature. It would be, as will be seen presently, of little or no use that the bee should have pollen on its head. None, therefore, or little, is produced by the cells against which the head impinges; and the economy thus practised is very probably one of the conditions which favour the abundant production of pollen in the upper anther cells. In these it can be of use, and thus the material saved from the lower cells is expended here to greater advantage.*

It will also be noticed, as a further illustration of the accuracy of adaptation, that the upper portion of connective is very much longer than is the lower. In some other species of salvia this difference of length is much greater even than here. The result of this is, that the bee produces a very considerable rotation in the upper limb of the lever, notwithstanding that the direct motion produced by its own pressure on the lower limb is comparatively slight.

The shape of the corolla is also adapted to facilitate the motion in question or rather to increase its range. It will be noticed in fig. 2 that the tube bulges out just behind the barren anther cells. This allows of a greater displacement of the lower arm of the lever in a backward direction than would be possible were the bulging not present. It is easy to convince oneself, by inspection, that after the bee has struck the lower anther cells with its head, it penetrates still deeper, and that its back forces the cells into this retreat. It thus happens that, though the connective is not nearly so long in this species of salvia as in many others yet that the amount of motion produced in the

* I refer, of course, to the law of balancement of growth, which was thus expressed by Goethe:—"In order to spend on one side, Nature is forced to economise on the other side." The merit of having first propounded this law is claimed for Geoffroy St.-Hilaire, and also for Goethe. It had, however, been most distinctly enunciated by Aristotle. For instance, cf. his treatise "De Partibus Animalium," ii. 9: *ἅμα δὲ τὴν αὐτὴν ὑπεροχὴν εἰς πολλοὺς τόπους ἀδυνατεῖ διανέμειν ἡ φύσις, κ.τ.λ.*

fertile anther cells is as great as in any, and more than in most.

It will also be noticed that the fertile anther cells are guarded, by the closed hood in which they are concealed, from the wind and rain, so that their precious pollen is not vainly dispersed, but is carefully hoarded until it can be discharged with effect. In none of the many blossoms which I examined did I find the pollen loose in the hood of the corolla; and in no instance in which I was able to watch accurately the egress of a bee from a freshly opened flower did I fail to see the pollen adhering to its back and flanks. When the bee, smeared with pollen, leaves the blossom, the elasticity of the joint at the end of the filament causes the upper anther cells to retire again into their hiding-place, where they lie protected till a second bee visits the flower. This is, at any rate, the rule, but not unfrequently the retreat does not occur. The upper anther cells catch in the narrow opening of the hood, and remain outside exposed. It would thus appear than when the pollen has been shed in part, Nature is less careful in her provision for the protection of organs which are now comparatively useless.

Another point to be noticed in the stamens is the straddling position of the filaments. This is clearly explained by the necessity for a free entrance for the bee, whose passage would otherwise be obstructed. The shortness and firmness of the filaments is such as to give a fixed point for the motion of the connective with its terminal cells. In another salvia, a variety of *sylvestris*, the immobility of the filament, and consequently of the point on which the connective moves, is still further secured by a slight adhesion of the far end of the filament to the edges of the upper lip of the corolla.

The position of the joint which unites the connective to the filament also deserves a passing notice. The joint is lateral, the filament being united to the external surface of the connective, and not touching it behind, so as in no way to interfere with the swing of the latter backwards and forwards (fig. 5).

A more perfect arrangement than that which I have now described, for the transference of the pollen to the body of the bee, cannot, I think, be imagined. Every part of the stamens, even to the minutest details of structure, is so contrived as to ensure this result.

From the stamens I pass on to the consideration of the style. This, as in all labiates, is gynobasic, and from the ovary it runs at the very back of the corolla, being in contact with the posterior surface of the hood, and reaching to its very extremity; that is, to a point considerably beyond that where the upper anther cells lie concealed. As the style follows the curve of the hood, and this is not only closed behind but also slightly in front at the upper part, the style is necessarily so bent round as to point towards the opening of the corolla tube. When the flower first expands, and for some time afterwards, the tip of the style is seen just projecting from the highest point of the front opening of the hood (fig. 2). The extremity of the style is bifid, and the stigmas occupy the internal surface of the terminal divisions. When the flower is freshly opened these terminal divisions are not separated, but are in close adherence to each other by their inner or stigmatic surfaces; neither are the divisions, nor the style, as a whole, nearly so long as they afterwards become. In fact, the stigmas are not yet ripe, whereas the anthers are. This difference in the period of maturity of anther and stigma, in itself is a security against self-fertilisation, but there are additional safeguards. The style, as already said, is prolonged much beyond the upper anther cells, and thus it is impossible for these cells, when they move in and out of the hood, to strike upon the stigma. This is still further prevented by the anther cells being not only below but *in front* of the stigma, so that their motion occurs without passing by the style at all, and again by the dehiscence of the anther cells being on the side turned away from the style, namely, in front. The bee, in its exit from the flower, does not touch the stigma while it is in this state, as anyone will easily see if he watches a plant for a time; for the bee retires as he entered, along the lower lip, and the width of the opening is too wide for the back of the bee to come into contact with the end of the style. Even were this contact to occur by accident, it would probably be of no effect; for the stigma is at this period immature, and the viscid internal surfaces of the terminal divisions of the style are in contact with each other and not exposed.

The bee therefore flies off with its back smeared with pollen. Should it fly to another blossom in the same condition as that just described, its cargo of pollen will produce no effect; all that will happen will be that an addition will be made to the pollen on its back. But the bee will inevitably soon visit a blossom in a more advanced condition than was that from which its pollen was derived. Here it will find the stigma in a different position. After the blossom has expanded for a time, the style with its terminal divisions increases very considerably in length. These latter also separate from each other, and expose the mature stigmatic surfaces. The style, as it grows, is forced by the hood to lengthen in a curve, and thus the stigmas are brought into such a position that they block up the entrance into the mouth of the corolla, just as the lower anther cells block up its throat (fig. 8). A bee which visits the flower in this condition cannot possibly enter without rubbing its back against the projecting stigmatic surface, so that it cannot fail to leave some of its pollen adhering to the viscid organ. The stigma does not, as a rule, come so close to the lower lip as to be struck by the bee's head; this passes underneath it, and therefore it would be useless for the bee to carry pollen on its head. The sterility of the lower anther cells thus receives its explanation.

I think I have now shown that every portion of this flower, even to such trifling peculiarities as might have been supposed to be without import, is really so modified as to facilitate fertilisation by the aid of bees, and to ensure intercrossing. I will briefly recapitulate the chief points.

1. *The Corolla.* (*a.*) The lower lip affords a tempting landing-place on its middle lobe, while its side lobes regulate the direction in which the bee settles, and compel it to approach the tube in a direct manner. (β.) The deep tube of the corolla compels the bee to dive into it for a certain depth, to get at the nectary, and so ensures the necessary pressure on the projecting anther cells. (γ.) The secretion of nectar at the glandular base of the corolla attracts the bee by its taste and odour. (δ.) The upper lip forms a close hood, so as to shelter the fertile anther cells, and prevent waste of pollen. The same lip, owing to its being curved and closed behind, compels the style to grow in such a form as eventually to bring its stigma into contact with the pollen-smeared back of the bee. (ε.) The corolla bulges behind in such a way as to allow of free motion to the barren anther cells.

2. *The Stamens.* (*a.*) The filaments are short and firm, so as to afford a secure point on which the connective may revolve. This security is increased in one salvia, if not in more, by adherence of the filament to the upper lip of the corolla. (β.) The straddling position of the filaments leaves a free entrance for the bee. (γ.) The filament is articulated with the connective so as to allow of a larger range of motion. (δ.) The arm of the levers on which the bee directly acts is the shorter, so that the fertile cells are made to move considerably by a comparatively slight motion of the bee itself. (ε.) The lower anther cells are barren or nearly so, as pollen on the bee's head would be wasted. On the other hand, the upper cells are very fertile, and their dehiscence is on the side which is brought into contact with the bee's body, and which is turned away from the stigma. (ζ.) The lower cells project so that the bee must of necessity strike them.

3. *The Style.* (*a.*) The stigma ripens after the anthers. (β.) The stigma is so placed as to be protected from the pollen of the same plant. (γ.) The style grows in a curve, so as eventually to come in contact with the back of the bee.

I have described this variety of salvia at such length that it will be sufficient if I give a much shorter account of other forms. Neither will it be worth while to do more than select a few species from the very many I have examined.

Salvia glutinosa.—This salvia, in its general arrangements, has a close resemblance to that which I have just described at length. The most notable differences are these:—The lower anther cells are entirely unproductive of pollen, and, instead of projecting from the hood, lie inside the tube, the opening of which they block up. Neither in glutinosa nor in any of the other salvias to be hereafter described, is there the bulging recess in the hinder part of the corolla which I pointed out in the last species, and which allowed of a greater range of motion backwards in the lower anther cells. To compensate for this, these salvias have a more or less developed bulging out on the opposite side, that is, on the lower surface of the tube. This bulge gives a freer access to the nectary when the anther cells have been pushed back as far as they will go. This bulge is not nearly so marked in glutinosa as in many other species. The stigma in glutinosa, as in most species, matures later than the anthers; still the difference in time is not so great but that blossoms may be found in which there is a mature stigma, and anther cells containing pollen.

This species is fertilised by the large humble bees. The smaller humble bees and the hive bees visit it, but have not a proboscis long enough to reach the nectary. They have, however, learnt to overcome this difficulty. They make a hole in the tube of the corolla just above the nectary, and thus rob the flower of its secretion, without performing the duty which nature intended to attach to the enjoyment. How thoroughly the bees have acquired this treacherous habit, and how perfectly they have learned that their proboscis is too short to get at the nectary in any other way, anyone will see who spends half an hour in watching this plant. The bee makes straight for the hole in the tube, and never makes the slightest attempt to get in at the mouth. At any rate, though I have watched often, I have never seen it do so. Once or twice only I have seen the bee, instead of going to the hole, fix on the hood, and rifle the pollen. The hole in the tube is always made in exactly the same place, and nearly every blossom has one made into it sooner or later. On one occasion I examined a large number of flowers, and found the hole in 90 per cent. of them. This is an interesting example of the occasional imperfection of Nature's arrangements. One is reminded of a trap so faultily constructed that a cunning mouse can manage to carry off the bait, without setting the machinery in motion, by getting at it in some circuitous way. There are other plants, such as the common scarlet-runner, which are treated by bees in a similar way.

I come now to a number of species in which the lower anther cells are still further modified, being transformed into little hollow plates. The concavities of these plates are turned upwards, and by the union of the plates a little boat-shaped receptacle is formed, which more or less completely blocks the opening into the tube. (See figs. 9, 10, 11.) Under this heading come *S. sclarea, pratensis, sylvestris, grandiflora, patens, splendens,* and a vast number of others. The most interesting of them is *S. patens.* This one, therefore, I will describe.

S. patens. This large garden-flower can be easily obtained and examined. It will be found that there is a different mechanism for its fertilisation from that of any other species I have mentioned. The style, when it reaches the lower part of the hood, passes from behind forward between the two anthers, and higher up passes back again between them a second time, and then projects above them from the lip of the corolla. (Fig. 12.) At the points where it passes between the anthers, it is held firmly by them; and thus, when the anthers rotate the style moves with them, coming forwards and retiring back in company with the upper anther cells. These and the stigma retain their relative positions to each other while this motion goes on. (Fig. 13.) Should now a large insect visit the flower and push the lower petaloid anther cells in order to get at the nectary, its back will be struck not only by the polliniferous anther cells, but also a little farther back by the stigma. As the insect passes deeper into the tube, the anthers and stigma will be rubbed along its back in a direction from before backwards, the stigma being always in advance of the anther cells, and therefore not collecting any of the pollen. As the insect retires from the flower the anthers and stigma retreat into the hood. The insect flies off to another flower, and now the motion brings down the stigma on to the pollen-smeared place in its back. It will be noticed that, in this species, the upper division of the stigma is very much larger than the lower, which is in fact almost abortive, whereas in most other species the lower division is the lustier. The possible purport of this is to cause a greater interval between the pollen and the stigma, and thus to render the chances of self-fertilisation smaller. On examining the corolla tube, it will be noticed that there is a curious constriction in its lower part. By this the calibre of the tube is reduced at that point to a very small passage, and this passage is filled up completely by the style which runs through it; so that, in fact, at this point the tube is entirely blocked up. On now examining the inner surface of the tube with a microscope, it will be seen that the part above the constriction is thickly set with glandular hairs, while the part below is entirely devoid of them. It is by these glandular hairs that the fluid which attracts insects is secreted, and if a tube be opened carefully a drop of nectar will usually be seen just above the constriction. The use of the constriction seems, then, to be, to prevent the nectar from escaping below, and getting out of reach of the insect's proboscis. The glandular hairs are most abundant just above the constriction, and get scantier and smaller higher up. The purpose which is here served by the constriction is in many other species attained by the glandular hairs themselves, which are set so thickly as to form a dense fringe, which only just leaves room for the passage of the style, and with this completely blocks the tube. (See fig. 2.)

I come now to a matter which seems to me of considerable interest, but concerning which I would speak with diffidence. On examining a number of blossoms of *Salvia patens*, I found that there were two kinds. The great majority, in the arrangement of stamens and pistil, accorded with the description I have just given. In a certain number, however, the arrangement was different. In these the style was much shorter than in the others, and only passed once between the anthers, namely, at the lower part of the hood. (Fig. 14.) It thus projected from the hood *below* the fertile anther cells, and not above, as in the majority of blossoms. The consequence of course would be, that when the stigma and the anther cells are brought down on to an insect's back, the stigma would strike at a point nearer to the insect's head than would the anthers. (Fig. 15.) It is plain, that an insect visiting first one form of blossom and then the other would have the same points on its back in contact first with the anther cells of one blossom, and then with the stigma of another. This dimorphism would therefore be a second way of insuring crossing between different flowers. The blossoms with the long style I found very many times more numerous than the blossoms with the short style; and it may therefore be that these latter were only accidental, though tolerably frequent, deformities. It is plain, however, that if such dimorphism be of use to the plant by insuring intercrossing, the plant, when growing wild and subjected to a struggle for existence, might avail itself of this "accidental" occurrence, and that in time the short-styled flowers might come to be equally numerous with the long-styled ones.

The flower is not, as far as I can make out, fertilised in this country by any insect. Growing only in a cultivated condition, it is not subjected to any other struggle for existence than that entailed by the changing fashion and caprice of horticulturists. This, however, has been so severe, that I was unable to obtain last summer from Covent Garden shops any large number of specimens, and thus I am unable to say in what proportion the two forms of blossoms exist.

I will not weary the reader with descriptions of other species. I have examined some thirty, and in all have found some contrivance or other to interfere with self-fertilisation and favour intercrossing. The anthers are not always rotatory, but in such case their position and dehiscence are such as to render it impossible for a bee to get at the nectary from the mouth of the tube without carrying off some of the pollen on its body, which it will convey to another flower; while at the same time the position of the stigma, and its different periods of maturity, protect it from the pollen of its brother anthers.

I would now illustrate the facts I have described by the phenomena presented in the fertilisation of some other plants.

If a common mallow, or a hollyhock, be examined soon after it has expanded, the stamens will be seen rising up in the centre, and forming with their united filaments a tube, from the upper end of which the filaments again diverge, each to terminate in an anther cell, loaded with large grains of pollen. The ripe pollen drops in abundance from these anther cells, and may be seen lying at the bottom of the corolla. Here, at the points of junction of the separate petals, will be seen certain glandular bodies, one at each interval, which secrete a fluid which attracts bees and other insects. The fallen pollen will be seen adhering in quantities to this sticky secretion, so that an insect which comes to enjoy the nectar, can scarcely fail to carry off some grains attached to its head or body. At this time no stigma nor style is visible. This lies entirely out of sight in the tube of the filaments, and is, in fact, quite immature. It is only later on, when the pollen has been entirely, or almost* entirely, shed, that the stigmas make their appearance above the tube. When once they have emerged, their growth is rapid, and they soon assume, as they lengthen, such a position that an insect which visits the nectaries must in so doing impinge upon them, in which case it will leave upon them some of the pollen it has brought from a less mature flower.

Intercrossing, then, in these plants is secured by the stamens and stigmas reaching their maturity at different periods. But it is to be noticed, that this is not the case with all the *Malvaceæ*. There are some in which the stigmas are mature and protrude from the tube in the early period when the anthers are still charged with pollen, so that here self-fertilisation may occur with the greatest facility. Now, it is of great interest to note,

* Very frequently the stigmas make their appearance before all the pollen is shed; and in such cases they may get some grains from their brother stamens. But these will not be numerous; probably seldom enough to produce fecundation. For Gärtner has shown, that even thirty grains of mallow pollen are insufficient to fertilise a single seed; but that when forty grains are applied to the stigma, a few seeds of small size may be formed.—Cf. Darwin, "Animals and Plants," ii. 364.

that in these mallows there are no nectaries. The visits of insects are not required by the plant, and so Nature, who, as Aristotle says, *οὐδὲν ποιεῖ μάτην*, economises the bait by which they might be attracted. A more convincing proof of the ultimate end and purpose of nectaries, cannot, I think be adduced.*

Still more striking are the contrivances for ensuring an intercross in the curious *Lopezia racemosa.* If a flower of this plant be examined, it will be seen that the two anterior petals are bent at a right angle, so that their terminal limbs form a convenient landing-place for flies or other insects. These are, moreover, attracted thither by the secretion of two little glands, which are placed on the upper surface of the petals just at the bend. In the centre of the flower rises a strange-looking object, which, on investigation, is found to be formed of two stamens, and a small intervening style. The stamen which is placed towards the glandular petals, has a polliniferous anther, the dehiscence of which faces these petals. The other stamen is transformed into a petaloid organ, and its upper extremity is shaped into a little hood, into which the anther of the first stamen is fitted, so as to be entirely out of sight. Between the two stamens is a style, which is therefore also roofed over by the staminal hood. But when the flower first expands this style is very short, and its end does not nearly reach up into the hood, where the fertile anther is lodged. The style is indeed at this period quite immature, and the terminal stigma not developed, whereas the pollen is already ripe.

If now the front part of the staminal hood be touched ever so lightly, it will be seen to start back, liberating, in so doing, the polliniferous stamen which it had hitherto held prisoner. This, when let go, springs slightly forwards, and by the jerk the pollen is shot out in the direction of the glandular petals. Some of it will be found to lodge on the glands themselves, and to be retained there by the viscid secretion. None can possibly fall on the stigma, for this lies behind the stamen, that is, on the side turned away from the dehiscence of the anther. Even if any accident did convey a little of the pollen to it, it would be of no use, for, as already mentioned, the stigma is at this period quite immature.

Now, when a fly or other such insect lodges on the glandular petals, it can scarcely fail to touch the front part of the hood. The pollen will then be shot out—will strike the fly on some part of its head or body. Here it will lodge, and the fly will

* The fact that nectaries are absent from these *Malvaceæ,* in which the anthers and the stigmas ripen together, was observed by Vaucher, to whom, however, the fact was without significance, as he had no notion of the real use of nectaries.

carry it off to another flower. That the flies do thus act anyone may easily convince himself, if he watch a *Lopezia* for a short time. Sometimes the staminal hood appears to spring back, and to liberate the polliniferous anther without the aid of an insect, a mere current of air sufficing to produce the movement. But in this case the pollen is not necessarily wasted; when emitted, it adheres to the sticky surface of the glands, and an insect which afterwards comes to enjoy the glandular secretions will get many of the grains on its head and proboscis.

The insect then, smeared with pollen, flies off to another flower. If this be in a more advanced condition, the stamens will have withered up and disappeared; but the style, which was in the earlier flower short and immature, will have lengthened and developed at its termination a large viscid stigma, which occupies just that place which in the freshly opened blossom was occupied by the hood. It is plain that the insect which came into contact in the one flower with the hood, will now come in contact with the stigma, and will convey to its viscid surface the pollen grains with which it is smeared.

In *Lopezia*, then, the fecundation follows the same rule as in salvia and in mallows. The more advanced flowers are fertilised by the pollen of the less advanced ones. The same rule applies to the last plant of which I shall say anything, the blue larkspur of our gardens.

The strange irregularity of this flower is utterly unintelligible, excepting on the hypothesis that it is intended to promote intercrossing. On that hypothesis all is perfectly simple.

The two upper petals are transformed into glandular organs, and secrete a sweet fluid for the purpose of attracting bees or other insects. The posterior sepal is moulded into a spurlike cavity, into which this fluid is poured, and in which it is retained. The two lower petals are so shaped and placed as to form a convenient landing-place, on which a bee must light in order to get at the nectary. The same petals also serve as a protection to the stamens and pistil. These they roof over and guard from the rain and wind, and also from the direct contact of insects, which might otherwise disperse the pollen vaguely. It will at once be seen, on examining a flower, that when a bee lights on the landing place, the stamens and pistil lie underneath it out of harm's way. When the flower first expands, the stamens all hang downwards and forwards, and their anthers are not quite mature. Still more immature are the stigmas at this time. Soon after the flower has opened the stamens ripen, one by one, in succession, and each as it ripens turns upwards, changing its position, until the anther is brought to occupy the fissure which exists between the lower part of the two inferior petals; of those two petals, that is, which above form the landing-place. The anther is now just in the mouth of the opening into the nectary, and a bee cannot get at the sweet fluid without striking against it; in which case it will get smeared with the pollen grains. Some of the pollen will also fall into the glandular cavity, and this also will afterwards adhere to the proboscis of the insect as it sucks up the fluid.

As soon as all the pollen is shed the stamen falls back into its old position, and another stamen takes its place, and so on till all the stamens in succession have gone through the same order of changes. Then, and not till then, the pistil with its stigmas ripens, and as the carpels lengthen the stigmas come to occupy the same position in the interpetalous fissure, as was previously occupied by the successive anthers. A bee in getting at the nectary will now strike upon the stigmas, and if it have—as is probable—pollen grains on its proboscis, will leave these adherent to the viscid surface; and thus, as in the other plant I have described, the more mature blossoms are fertilised by the pollen of the younger ones.

The fertilisation once completed, all the paraphernalia constructed to bring this result about are thrown aside, as no longer of use. The glandular petals, the sepalous receptacle of the fluid, the landing-stage, all fall off, and the plant is spared the cost of their further maintenance.

The preceding paper was written in the summer of 1868. At that time I thought I was the first to have discovered the purport of the strange structure of the stamens in salvia. I learnt later from Mr. Darwin—naturally somewhat to my disappointment—that this was not the case; but that already two years earlier Hildebrand had published an extensive series of observations on salvia, in which the structure was fully explained. On reading Hildebrand's pamphlet, I found not only that this was as Mr. Darwin had told me, but that, even long ago, the main fact had been noted by Sprengel. I have, however, thought it well to publish my own observations for several reasons. In the first place, Hildebrand's paper is so little known apparently, that I can find no allusion to it in any English or French manual of botany. The curious anatomical structure of the stamen is described in all of them, and often is figured, but not a word is said of its physiological significance. A second reason is, that there are numerous minor points, which seem to me of much interest, which have been passed over by Hildebrand.

EXPLANATION OF PLATES.

Fig. 1. S. officinalis, var. grandifloras (?) (natural size).
Fig. 2. Flower in section. Magnified.
Fig. 3. Front view of stamens. Much magnified. *a.* filament. *b.* lower barren anther cell. *c.* upper polliniferous anther cell. *d.* connective; united by a joint to the filament at *e.*
Fig. 4. Stamens seen laterally, and at rest. Magnified.
Fig. 5. Stamens seen laterally when in rotation. Magnified.
Fig. 6. Front view of flower. Magnified.
Fig. 7. Bee visiting nectary and rotating the anthers.
Fig. 8. Flower some time after expansion. Pistil mature. Magnified.
Fig. 9. S. Sclarea. Natural size.
Fig. 10. S. Sclarea in section. Much magnified.
Fig. 11. Boat-shaped receptacle formed by union of lower anther cells in S. Sclarea. Much magnified.
Fig. 12. S. Patens in section. Natural size. Anthers at rest. Usua form.
Fig. 13. S. Patens, lateral view. Anthers rotated as would be the case were an insect to visit nectary. Usual form.
Fig. 14. S. Patens, occasional form in section. Anthers at rest.
Fig. 15. S. Patens, occasional form, lateral view. Anthers rotated.

Plate XLIX.

Fig. 9.

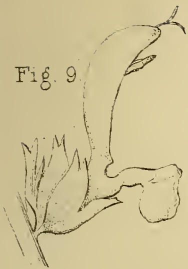


Fig. 12.

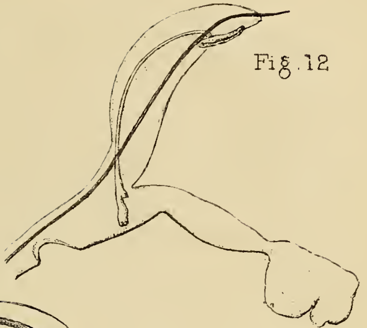


Fig. 10.

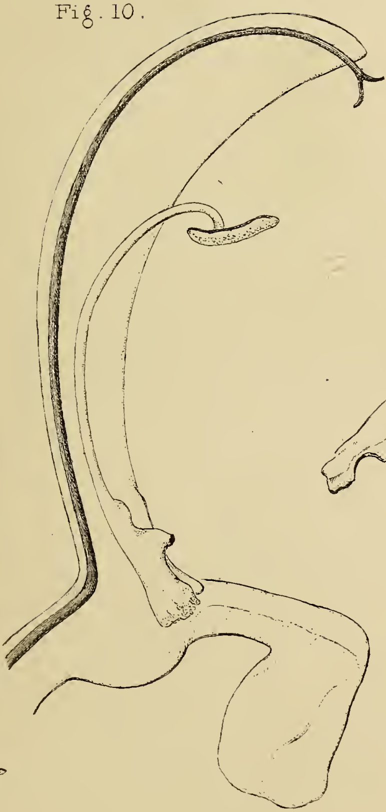


Fig. 11.

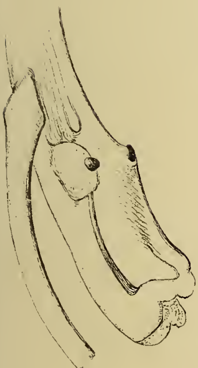


Fig. 13.

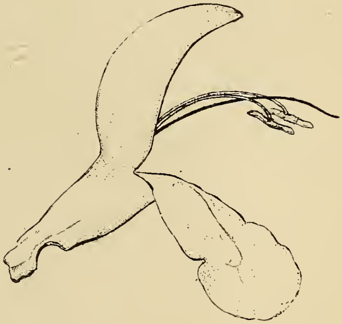


Fig. 14.

Fig. 15.

W. Ogle. W. West imp.

The Structure of Salvia.