

ON THE FERTILISATION OF A FEW COMMON PAPILIONACEOUS FLOWERS

[NOTE TO EDITOR.—THE enclosed paper was written in the autumn of 1869, and then submitted to Mr. Darwin. With his usual kindness he encouraged me to proceed with it; and with his usual thoroughness he advised me to make it more complete than it is before giving it to the public. At the same time, he lent me various publications, containing articles on the subject of fertilisation, and, amongst others, some by the Italian botanist, Delpino, who has done so much in this field. I found that he had in two or three publications in the years 1867 and 1868, anticipated most of the observations contained in the accompanying paper; and I proposed to myself to attempt a *résumé* of what had been done of late years in the matter of fertilisation of flowers by Delpino, Hildebrand, and others. But this, though a labour of love, is a greater labour than I can manage, and other calls have grown upon me. I therefore send the paper to you as it stands, begging that this note may be prefixed in order that I may not be thought to be appropriating Delpino's observations.—T. H. F., October 1872.]

AFTER reading Mr. Darwin's book on Orchids and his papers on *Lythrum* and *Primula*, I made some notes on the fertilisation of *Phaseolus* and some of the *Campanulaceæ*, which had the good fortune to meet with his approval, and which he had the kindness to send for publication to the *Annals and Magazine of Natural History*, where they appeared in October 1868. The comparison of *Phaseolus* with other *Papilionaceæ* flowers led me to think that Mr. Darwin's fertile ideas might receive many illustrations from the structure and functions of this beautiful and interesting tribe; and the following are observations made during the summer of 1869 upon

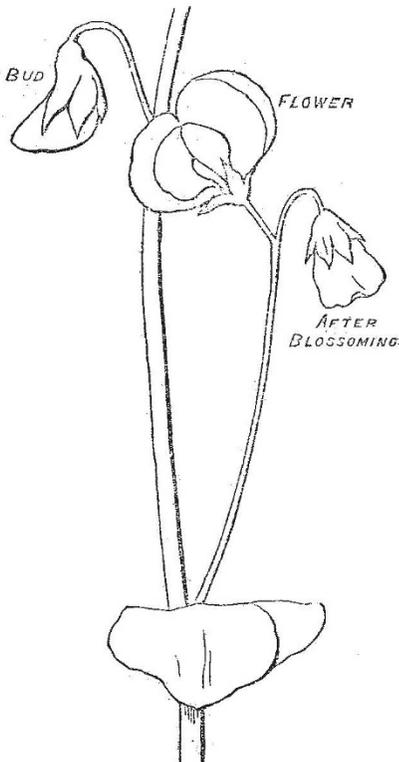


FIG. 1.—*Pisum sativum* (Common Pea) (peduncle and pedicels).

a few of the commonest of them. I am painfully conscious how imperfect want of time, of opportunity, and of knowledge has left them; and how many points there are, even in these few flowers, which require a much

more careful inquiry. Indeed, every new flower has its own peculiarity; and almost every new peculiarity suggests the observation of facts in other flowers not previously noticed; so that the task is endless. Again it is difficult to feel sure of a conclusion unless the whole process of fertilisation by insects can be watched, and to a dweller in towns, ignorant of insects and their habits, it is impossible. If, however, these observations should lead to further inquiry and discussion, they may not be useless. The flowers in question are *Pisum sativum*, several species of *Lathyrus*, *Vicia*, and *Phaseolus*, *Robinia pseud-acacia*, *Wistaria*, *Onobrychis sativa*, *Trifolium repens* and *T. pratense*, *Lotus corniculatus*, *Lupinus*, *Ononis*, *Anthyllis*, *Ulex*, *Genista*, *Sarothamnus*, and *Cytisus*.

Pisum sativum, or Common Pea.—The blossoms are generally two upon a common peduncle, and each flower has a separate short pedicel (see Fig. 1). The peduncle generally approaches the perpendicular and

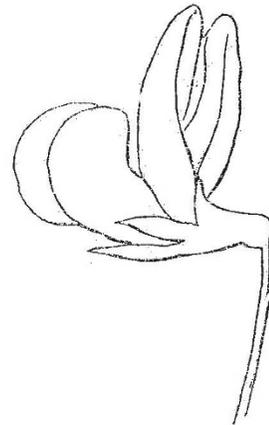


FIG. 2.—*Pisum sativum* (mature flower).

maintains its position through the stages of bud, blossom, and pod, except that it gets stiffer. The short pedicels, however, change their position twice. In the bud they are bent down so that the base of the calyx is uppermost, and the upper edge of the folded vexillum lowest. In this stage the large calyx covers with a weather-proof awning the tender blossom. As the flower opens the pedicel straightens itself; and when the blossom is fully open it is quite straight, and at an angle of 45° to the peduncle. The effect of this is to raise the flower so that the keel and wings become almost horizontal, whilst the showy limb of the vexillum, bent upwards from the claw, displays a perpendicular face (see Fig. 2).

The wings are slightly attached to the keel at the base of their limbs; and the limbs project outwards and a

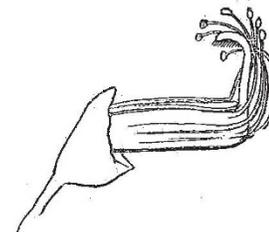


FIG. 3.—*Pisum sativum* (lateral view of pistil and staminal tube, with calyx and corolla removed, and tenth stamen separated).

little upwards in front of and above the keel, so as to make an excellent lighting place for insects. The keel is boat-shaped, recurved at the apex, and the lower edges

are joined together from the base to the apex. The stamens are diadelphous, the filament of the tenth stamen being separate at the summit and base, and separable in the middle (see Fig. 3). They are of nearly equal length, the pollen is abundant and rather moist, and is shed at the time the blossom expands. The upper parts of the filaments are stiff enough to keep their place, but not so stiff as the style. The lower parts of the filaments form a stiff tube, expanded towards the base, so as to leave a large cavity round the base of the ovary. This cavity is abundantly supplied with nectar. On each side of the tenth stamen at its base, there is a wide aperture, through which apertures, on removing the vexillum, this cavity with its nectar is easily seen (see Fig. 4).

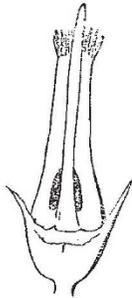


FIG. 4.—*Pisum sativum* (front view of staminal tube, with tenth stamen, front showing apertures into nectary on each side the tube).

The style is at right angles to the horizontal ovary, and curves towards the vexillum at the top. The stigma is at the extremity, and faces outwards and upwards towards the vexillum. On the inside for some distance below the stigma it is clothed with stiff hairs, which are set so as to point upwards towards the stigma (see Fig. 5). The style appears to be formed by two folds of the carpellary leaf, which bend outwards from the point where the style joins the ovary, so that the outer side or back of the style which lies towards the suture of the keel, and which has no hairs on it, is formed, not of the outer suture of the carpel, but of the edges of these folds.

At the time the flower opens the stamens have shed, or are shedding, their pollen, which lies in an abundant mass at the apex of the keel around and above the stigma.

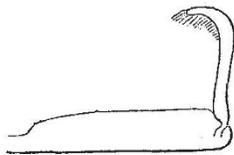


FIG. 5.—*Pisum sativum* (pistil).

The back of the stiff elastic style almost touches the keel; and on pressing down the wings, which, as above noticed, are attached to the keel, the back of the style, which has no hairs, is pressed against the keel, whilst the brush on the front and sides of the style sweeps the moist pollen upwards and pushes it out of the apex of the keel and against any object which is entering the flower, and to which the pollen, being moist, will adhere. On removing the pressure the parts take their place again, whilst on repeating the pressure the same process may be repeated, until the whole of the pollen in the upper part of the keel is brushed out.

As soon as the flower closes and before it withers, the pedicel again droops, the flower becomes pendent, and the calyx again acts as a pent-house to the young pod (see Fig. 1).

Now, undoubtedly, the stigma of one of these flowers is always covered with its own pollen; but if self-ferti-

lisation were the rule, the elaborate structure I have described is meaningless, whilst if the purpose is that insects shall carry the pollen from flower to flower, it becomes a curiously elaborate and complete piece of mechanism having a special object. The change of position of the flower by the bending, straightening, and second bending of the pedicel, so that the tender opening bud and the young fertilised ovary are protected from rain and cold; whilst the open blos-

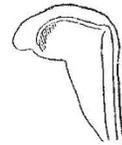


FIG. 6.—*Lathyrus* (keel and pistil).

som displays itself in the most attractive and convenient form and position for insects; the conspicuous vexillum; the wings, forming an alighting place; the attachment of the wings to the keel, by which any body pressing on the former must press down the latter; the staminal tube inclosing nectar, and affording by means of its partially free stamen with apertures on each side of its base, an open passage to an insect seeking the nectar; the moist and sticky pollen placed just where it will be swept out of the apex of the keel against the entering insect; the stiff elastic style so placed that on a pressure being applied to the keel, it will be pushed upwards out of the keel; the hairs on the style placed on that side of the style only on which there is space for the pollen, and in such a direction as to sweep it out; and the stigma so placed as to meet an entering insect,—all these become correlated parts of one elaborate mechan-

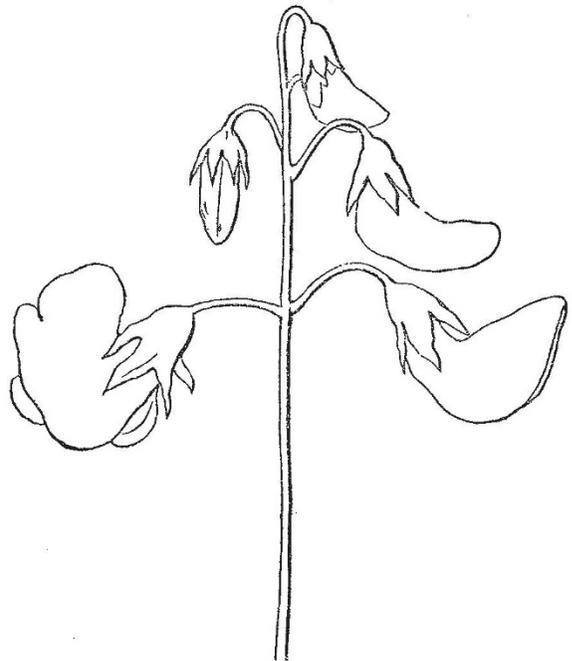


FIG. 7.—*Lathyrus latifolius* (Everlasting Pea).

ism; if we suppose that the fertilisation of these flowers is effected by the carriage of pollen from one to the other.

I have, however, not observed the bees or other insects at work on these flowers, whilst they are to be found in abundance on the neighbouring broad beans and scarlet

runners. Do the white pea-blossoms attract night-flying insects?

Lathyrus odoratus.—This is, so far as the above functions are concerned, so like *Pisum*, that it is scarcely worth while to dwell on the differences. In colour and smell, of course the difference is great, and consequently in the attractions for different insects. The changing position of the pedicels; the brush to the style; the free or partially free stamen, and the nectar inside the case of the staminal tube, and the openings into that tube, are the same (see Fig. 6).

Lathyrus macrorrhizus, is, so far as I have observed it, similar.

Lathyrus pisiiformis is like the other Lathyri in the above points, except that in the long raceme of flowers, the whole peduncle, and not only the pedicels of the separate flowers, is pendent in the bud. It stiffens and becomes upright as the blossoms open, and the pedicels also stiffen and become horizontal. After flowering the peduncle remains stiff and upright, but the pedicels droop.

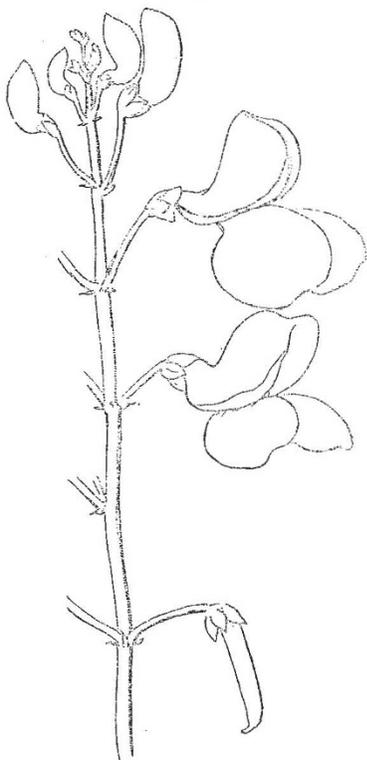


FIG. 8.—*Phaseolus multiflorus* (Scarlet Runner).

Lathyrus pratensis.—The fertilising apparatus is the same as in the above Lathyri.

Lathyrus sylvestris, or *latifolius*, or Everlasting Pea.—Here the many-flowered raceme is itself upright, whilst the pedicels bend, straighten themselves, and again bend, as in *Pisum* (see Fig. 7). In the fertilising apparatus the mechanism is the same as above described, with the exception that there is a very decided obliquity in the keel and in the style, though not so decided as in the following.

Lathyrus grandiflorus.—In this flower the peculiarities, as distinguished from the above-mentioned Lathyri, are as follows:—The pedicels bend, straighten, and bend themselves again, as above mentioned; but the effect generally, if not universally, is to make the large showy vexillum, and not the keel, horizontal. The vexillum, consequently, and not the keel, would be the natural alighting place for an insect. The wings are at right angles to the vexillum, and the recurved point of the keel projects between them and over-

hangs the vexillum. An insect alighting on the vexillum, and thrusting itself towards the nectary, must push the wings, and with them the keel, upwards, and make the style and the pollen come out; but they will come out downwards on to the back of the insect, and not on to his thorax or belly.

Another peculiarity is that the keel, and with it the style, is very oblique, and the upper part is flattened, and is twisted so that the back of the style does not press against the keel. Correlatively both sides of the style are well furnished with hairs, and both sides equally operate in sweeping the pollen out of the keel. In this respect *Lathyrus grandiflorus* seems to show a gradation towards *Phaseolus*.

Phaseolus multiflorus, or Scarlet Runner.—In the position of the blossom whilst flowering, in the nectar-holding cavity of the staminal tube, and in having an entrance to the cavity by the separation of the tenth stamen, this flower resembles *Lathyrus* and *Pisum*, but it offers the following peculiarities (see Fig. 8):—

The pedicel of the bud before flowering is perpendicular and stiff, and the bud consequently upright; the pedicel becomes rather more horizontal as the flower opens, and in blossom the wings are horizontal, whilst after flowering the pedicel becomes quite horizontal, and the pod gradually sinks, and ultimately becomes pendent. Correlatively, there is no large pent-house of a calyx, as in *Pisum*, to protect the young blossom; but the same object seems to be effected by the smooth, strong, thick vexillum, the edges of which are in the bud closed valvately over the tender folded interior petals; whilst in the bud of *Pisum* the whole of the petals, whilst sheltered by the calyx, are tender and unclosed. The young pod of *Phaseolus*, also unlike the thin glabrous pod of *Pisum*, is thick and covered with short hairs.

The keel, which in some Lathyri is very oblique, is in *Phaseolus* so twisted, and has its edges so joined, as to form an imperfect tube containing the stamens and style; it makes with them nearly two complete spiral turns, and its mouth points obliquely downwards. The stiff, elastic style is clothed with stiff hairs or bristles, forming a circular brush at the point in the tube where it is surrounded by, and in contact with, the moist, sticky pollen of the mature anthers. The stigma is on the lower side of the style, just appearing at the mouth of the tube, is sticky, and is clothed with fine hairs.

The filament of the tenth stamen is entirely separate from the others, and is furnished with a sort of tooth or appendage on the outside, upon pressing which the stamen is drawn back, and free access is given to the nectar-holding cavity. On the other hand, there is no such aperture on each side of the base of the tenth stamen as there is on each side of the base of the semi-adherent filament in *Pisum* and *Lathyrus*.

A bee lighting on the wings, or rather on the outer wing, opens for himself a way to the base of the flower. At the same time, the wing being attached to the spiral tube of the keel, he pulls it outwards, the consequence of which is that the stiff style is thrust outwards and at first downwards, so that the sticky stigma first touches the entering insect and sweeps from his proboscis any pollen he may have brought from other flowers. As he passes further, the stigma protrudes further, turns upwards, and the brush of the style, loaded with the sticky pollen of its own anthers, sweeps against, and leaves its load on, his proboscis, with which he departs for other flowers.

The mechanism of this flower is truly wonderful. For further details I could refer to papers by Mr. Darwin in the *Gardener's Chronicle* of October 24, 1857, and November 14, 1858, and to the notes of my own in the *Annals and Magazine of Natural History*, October 1868.

Phaseolus vulgaris is similar to *P. multiflorus*.

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(To be continued.)