On the Pollination Mechanism of *Incarvillea Delavayi*, Franch.

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With three Figures in the Text.

THE genus *Incarvillea* belongs to the Natural Order Bignoniaceae. The trumpet-shaped flowers are borne on a racemose inflorescence whose axis is about $1\frac{1}{2}$ to 2 feet high. Most of the flowers are placed near the top of the inflorescence: the few scattered lower down are arrested: they develop up to a certain stage, but grow no longer than about a third of an inch. The corolla tube of the ordinary flower is about two inches long, and directed slightly downwards (Fig. 1).

My attention was first drawn to these flowers because they possess a large sensitive stigma of the *Mimulus* type (Fig. 2, C, D, and E). A closer examination showed that there was a further point of interest in that the anthers had attached to them curious stiff, downwardly directed

FIG. 1. Side view of flower of *Incarvillea Delavayi* (slightly reduced).

(as the flower is naturally placed) prongs, and the opening of the anther-lobes and the consequent setting free of the loose pollen follows the manipulation of these. Each anther has two of these prolongations, one to each lobe (Fig. 2, E and F), and they are arranged so that one lobe of each anther must open and discharge some of its contents when the insect goes into the flower, and the other lobe is emptied of some of its contents on the insect coming out of the flower. The latter seems devoid of smell, at least in so far as it can be noticed by human senses, and the attractions that the flower has to offer are colour, conspicuous size, herding together at the top of the inflorescence axis, and a quantity of honey secreted by a large nectary situated round the base of the ovary. When the flower is quite open, the free portions widen

out so that the whole structure is about two and three-quarter inches long: the calyx tube is about three-quarters of an inch long. The width of the tube, at the place where the anthers are placed, is half an inch, and the width at the open end of the tube is about three-quarters of an inch (see Fig. 1). The tube is mostly yellow in colour, with purple spots, and the free portions are rose-purplish with purple spots.

FIG. 2. A. Anther-lobes of longer stamen: 1, side view; 2, back view; 3, front view. $\times 2$. B. Back view of shorter stamen. $\times 2$. C. Young stigma: 1, front view; 2, side view. D. Diagrammatic view of flower from below (with a slit in the side). E. Diagrammatic longitudinal section of flower. F. Diagram of anther showing the pad touching the style. $\times 1\frac{1}{2}$. *p.* process; *p.o.* outer process; *p.i.* inner process; *b.* 'buffer' or pad; *a.i.* inner anther; *a.o.* outer anther; *f.* filament; *s.* style; *s.l.* stigmatic lobe; *d.* slit in anther lobe.

ment (Fig. 2, A). As the flower grows older the anther-lobes on the shorter stamens become of dissimilar size (Fig. 2, B), and the lobes on all four stamens diverge until the axis of the two lobes of each stamen are in line and at right angles with the filament at the point of origin. This is comparable with the state of affairs in *Digitalis*. The stamens also change their positions relatively to the other parts of the flower. As the flowers grow older the filaments of the anthers twist round,

The earlier opening flowers are lighter than those that mature later. A number of lines run down the corolla tube; these may be interpreted as being honey guides, and two marked ridges run down the tube anteriorly. The lower petals are slightly larger than the upper ones, so that the corolla is asymmetrical. The flower does not completely open in dull and cold weather. (This condition probably does not occur in its native habitat in Yunnan.) The position of the flowers seems to be determined partly by gravity and partly by light, as in the *Narcissus*. No experiments were tried to test this statement, but most of the flowers were discovered to have so twisted their stalks (their origins are symmetrically placed on the axis) as to be facing away from the wall in the garden in which they were growing, and towards the south-west. Gravity probably has even more effect than this upon the development of the flower. In the young buds the stamens are similar and symmetrically arranged, and the axes of the anther-lobes of each anther are parallel with each other and with the fila-

as has been described by Dr. Ogle in the case of the Foxglove (13), and as a result of this twisting the anthers take up their characteristic position, two on each side of the style (Fig. 2, D). Not only is this the case in *Incarvillea*, but the anthers are pressed closely against the style, a protuberant pad from the connective forming the actual point of contact and preventing the anther-lobes from touching (Fig. 2, F). We have, therefore, two pairs of opposed pads, touching the style, which act as buffers when the pollinating insect presses against the downwardly protruding anther-prongs. A few belated flowers opened at the top of the axis; they had but short stalks, and other, unopened buds were placed just above them. In these circumstances they were unable to twist round and take up their usual position, and it was found that the stamens did not change from the juvenile position. These latter changes are therefore probably under gravitational influence. Although these flowers never completely opened, both stigma and pollen matured, as both organs were capable of functioning; and the ovary, after fertilization, gave rise to a fruit.

The first prong of an anther that an insect would touch on coming into the flower is so arranged that a slit in the anther-lobe is placed above it and runs to the end of the lobe. The other thorny projection has the slit situated just below it (Fig. 2, E and F). In each case the surface of the lobe on either side of the slit is not a gently curved one, but is raised up in places and depressed in others. The significance of this configuration I hope soon to make clear. On the insect's back touching the first pair of prongs, one on each side of the style, the pressure is communicated to the pads and the two stamens and the style are kept rigidly in position. The sides of the slit or anther-cleft are pressed closely together and are therefore kept shut. When the insect touches the next pair of prongs, which will of course be on the same two stamens (and I imagine that a large insect like a humble-bee would touch both pair of prongs at the same time), not only are the pads brought into play, to cause the whole apparatus to remain in position, but as they are of some size and would not suffer much compression, in spite of their spongy nature, the sides of the anther-lobes are kept away from the style and do not touch it. This allows of considerable deformation taking place in the second pair of anther-lobes, and in consequence of this the slit opens and a certain amount of dry pollen is shed, passively, on the creature's back. The prongs, however, are very elastic and are attached each to a massive base composed, in great part, of thick-walled cells that resist a change of shape; therefore, on the insect passing, the projections are set free with a reverberation, which, if sufficient, causes a further and wider shedding of pollen, and, in any case, would redistribute the pollen-grains in the sac. It is seen, therefore, that the inequalities on the surface of the sac serve a double function. They prevent the pollen in the sac from being all shed at once, so allowing of several visits to the flower, and they also bring

about a wider shedding of the grains on to the insect's back than would be the case if the surface were smooth. It is possible that the creature makes several contacts with any one prong: this would result in several separate sheddings. On the insect passing to the next pair of stamens the same procedure takes place, so that on an insect entering the flower only the inner lobes of the anthers shed pollen on to it, and these probably do so on about the same spot. I am, of course, quite unable to be sure of this; the movement in or out of a flower can be imitated on the anthers by passing a finger along the points of the prong-like projections, but the exact details of pollination can be made out only in the natural habitat of the plant, and by an examination of the pollinating insect itself. When the insect makes its exit from the flower the reverse process takes place; only the outer lobes of the anthers open and pollen is shed from them. The figure of the anther given in Engler (14) shows a quite similar set of prongs, arranged as in *Incarvillea Delavayi* and *Incarvillea grandiflora* (a few flowers of this species were examined by me), and the connectival pad is also present, but the figure given of the flower of *Incarvillea Sinensis* shows the stamens emerging from the mouth of the corolla tube; if this is a normal flower of the plant, the pollination mechanism cannot be the same as in the two species here described. The flower, however, is drawn almost in a vertical position, and in two flowers of *I. Delavayi* that developed in a similar manner, owing to the flower-stalk being short and the other buds being crowded around it, the anthers were not able to take up their normal, adult form. This may have been the case in the specimens figured in Engler. It would seem probable that neighbouring genera have similar mechanisms and would repay any observation of them. Schumann (14) describes and figures the lobes of *Amphicome* as having thorns and a leaf-like broadened connective. Unfortunately I have been unable, so far, to obtain specimens of this genus.

The possibility that some stimulus mechanism might be connected with pollen discharge in *Incarvillea* was not left untested. It was found that anthers which had been placed in alcohol for a period of at least a year were able to behave in a similar manner to the live ones. Sections of the anthers showed that they are provided with the usual fibrous cells; these, most probably, are concerned with the preliminary opening of the slit, and may also function in other ways: for example, in assisting in maintaining the necessary slight resistance to change of shape on the part of the anther. A microscopic examination of the stigmatic lobes of *Incarvillea* did not show the presence of any *Incarvillea* pollen, but there was plenty of foreign pollen, and an examination of this indicated that it was mostly that of the *Rhododendron*—some few plants of which grew in the garden near the experimental plants. As these are humble-bee flowers, and as I have seen these insects visiting the *Incarvilleas*, I have

but little doubt that they are responsible for the presence of the foreign pollen on the stigmas. That they do not seem to have pollinated the *Incarvillea* plants with their own pollen is no proof, however, that they are unable to set the mechanism in motion for the discharge of the pollen-grains, nor does it show that the grains are unable to adhere to their bodies. There were only three *Incarvillea* plants growing in my garden, and although I placed these close together, the chances of a bee's visiting two of these flowers, one after the other, were exceedingly small, because there were but a few flowers out at a time, probably never more than four. The stigmas are covered with papillate hairs that are doubtless used in pollen fixation. The flower is sufficiently preserved from self-pollination by the closure of the stigmatic lobes on stimulation. In the flower of *Thunbergia alata* (8, 11), which in mechanism comes closer to *Incarvillea* than any other plant known to me, it is curious to find that Darwin reports (3, 4) 'spontaneously self-fertilized fruits'. The stigmas of *Thunbergia* are not, as far as I am aware, sensitive; their position, however, and the method of shedding pollen in this plant suggest either that Darwin's plants were parthenogenetic or that insects did visit them and cause pollination, although they may not have been the insects that usually bring about the transference of pollen in this genus. The figure of the flower of *Thunbergia alata* copied from Hildebrand's paper and figured in Loew's 'Blüthenbiologie' suggests that the anther-lobes are smooth and all the spines backwardly directed from the anthers. Lindau's figures (9) bear this out for *Thunbergia reticulata*, and it will be found that here the anther-lobes remain parallel, and the spines are so arranged that an insect only causes pollen to be shed on its emerging from the flower.

The flowers of *Incarvillea* had been found, in previous years, to be visited commonly by earwigs, and though it is not suggested that these creatures brought about the pollination in these cases, the plants undoubtedly bore fruits containing what looked like quite well-developed seeds. These seeds have not, however, germinated. This year, besides the earwigs, other visitors have been noticed, mostly a large garden ant—attracted by the honey—aphides, and an occasional humble-bee. I see no reason why the last named should not be able to bring about the pollination of these flowers, and, indeed, I should think that the setting of seed in the cases mentioned above was probably due to their agency. The humble-bee has about the right-sized body for the corolla tube, and also (I should imagine) the strength necessary to move the anther spines. I cannot, however, think how the pollen adheres to his body except one postulates that, as happens in other cases, a sticky secretion from the stigma is deposited on it as the bee passes into the flower. The stigmas I examined, however, were not sticky. The flowers, which grew in my garden and gave rise to fruit, had all been hand-pollinated; and all the flowers that had not been so treated

withered. The first few flowers to be pollinated by hand were not covered afterwards, but the last few were more carefully treated. They were unopened, but adult, flowers, and they were bagged after the pollination had been effected. Self-pollination and cross-pollination both gave rise to young fruits: these did not mature; this was not due to any deficiency on their part, but to a withering away of the inflorescence axis. I hope, in time, to overcome what is probably only a cultural difficulty and to get the seeds to ripen and to germinate.

POLLEN OF *INCARVILLEA*.

The pollen-grains (Fig. 3) resembled those of *Thunbergia alata* as figured by Goebel (6) in the 'Outlines of Classification and Special Mor-

FIG. 3. Pollen-grains of *Incarvillea Delavayi*, A-F, and of *I. grandiflora*, G-L. All $\times 330$. A and B, same grains at upper and lower focus respectively, B with the slits seen in A dotted in. C and D, upper and lower views of the same grain. E, an air-dried grain. F, size of grain in 25 % sugar solution. G and H, same grain at upper and lower focus. K, a similar grain. L, a small grain. (A, B, C, D after treatment with sulphuric acid.)

phology'. They were dry, and on placing them in water they were immediately ruptured; even in a mixture of equal portions of water and glycerine the majority of the grains were destroyed after a few minutes. The exine was cutinized and was resistant to the action of sulphuric acid; while the intine was dissolved in this reagent and gave the usual tests for cellulose. After such treatment, and occasionally before treatment, when mounted in strong sugar solutions, it could be seen that the outer wall was covered with

very minute papillations. The exine had long slits very much like those of *Thunbergia* (Fig. 3, A, B, C, D), but while in this genus the slits form one or two continuous lines, in *Incarvillea* the grooves only occasionally join together, so that we never get the appearance seen in Fig. 295—V, VII, and IV—of the 'Outlines' (Goebel) (6), the closest approximation being shown in my Fig. 3, C, where a few slits will be found to join, with the result that a portion of the outer wall opens out after the inner wall has been dissolved by sulphuric acid. An opportunity presented itself of examining a few withered flowers of *Incarvillea grandiflora*, in which plant the floral mechanism is quite similar to our species, the difference being in details, such as the longer flower stalk and the slightly different colour and marking. The pollen of *I. grandiflora* proved to be similar to that of *I. Delavayi*, but there were fewer slits and a very few small adult grains were to be observed amongst them (Fig. 3, G, H, K, L); the meaning of this heterospory is not clear to me. As there were two lengths of filament, pollen-grains from the anthers at different levels were examined in both species and closely compared as regards size and markings, especially as some such differences might have been expected, and in *Torenia*, for example, one pair of anther-lobes bears dry, the other pair moist, pollen; no differences, however, of any kind could be noticed in the case of *I. Delavayi*. Whether the different sized grains are commonly found in *D. grandiflora* or whether they are confined to the longer or shorter stamens, I am unable to state. In *Torenia* (2, 10), it will be remembered, only the dry pollen is immediately effective in pollination; the moist pollen having to be dried before it will bring about fertilization. In *Lagerstroemia indica* (4, 7) there are also two kinds of stamens—conspicuous ones, with moist pollen, visited by the insects and used as food, and inconspicuous ones containing dry pollen, used in pollination. Seemingly both kinds of pollen can in this case cause fertilization without any preliminary treatment. In *Incarvillea* the moist pollen need not be dried before it is effective. On exposure to air the pollen-grains immediately begin to lose water, get slightly smaller, and change shape from the spherical; the portions of exine between adjoining slits heaping themselves up (Fig. 3, E) (cf. figures of *Thunbergia* (5)), the water loss probably taking place mostly through the intine and the lips of the slit then approximating, and further loss causes a hinge-like movement along the crack. This approximation of the sides must considerably reduce the further loss by evaporation. Such drying would probably take place on the back of the insect carrying the pollen from one flower to another, though it is questionable whether the slight irregularity of surface so brought about is of any great importance for further fixation to the creature. The presence of slits and the high osmotic pressure of the contents, the evidence for the existence of which will be described below, I regard as adaptations to prevent drying.

Strasburger has (in his paper 'Ueber den Bau und das Wachsthum der Zellhäute' (15)) described shortly the development of the walls of the pollen-grains of *Thunbergia alata* and *T. reticulata*. I hope to study the development of the peculiar exine of the *Incarvilleas* at some future date.

All efforts to bring about the germination of the pollen-grains failed; 25 per cent. and 30 per cent. sugar solutions were tried, ordinary room temperatures and above room temperatures, up to 35° C., in the light and in the dark, and in some cases peptone was added to the sugar solution. Only the very first beginnings of a tube were noticed, and these were commoner at the higher temperatures, but did not persist in growing. At quite low temperatures, however, they were evidently able to germinate, in the open air, on the stigma of the plant, as when they were placed there the ovaries began to swell in a few days' time and the fruit to ripen. I had but few fresh flowers to experiment with, and these had to be carefully conserved, so I could only make one preparation in sugar solution including a stigma, but even in these conditions the grains did not germinate properly. The moist-air method advocated recently by Anthony and Harlan (1) in the 'Journal of Agricultural Research' was also used, but with no favourable result. When placed in the sugar solution the grains at once increase in size (Fig. 3, F) markedly, and some few (when the 25 per cent. solution was used) burst open. The slits widen, and by next day those grains that show the beginnings of germination have an irregular bulge coming from the portion of the intine lying between the openings of the exine. The walls of these bulges soon thicken considerably and growth stops. The intine, both of grains showing signs of germination and those that show no such indications, are very much swollen, and I am of the opinion that it is this increase in size that stops the growth of the contents.

SUMMARY.

A mechanical method of pollen-discharge is described in *Incarvillea Delavayi*, a plant possessed of a sensitive stigma. The pollen of the plant is dry, and is similar in structure to that of *Thunbergia alata*. The high osmotic pressure of the contents and the approximation of the walls of the surface slits, after drying, are regarded as adaptations to prevent too great a loss of water in pollen transmission.

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