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§ 134. The Fertilization of Scrophularia.

By WILLIAM TRELEASE.

If one might judge from the number of published accounts, the process of pollination in all its details should be, in few genera, better known than in that which forms the subject of this note. Unfortunately, however, the student who compares these accounts finds that they differ greatly among themselves, while not a few fail to agree with what he observes for himself in studying the plants. For this reason it has been thought not unprofitable to combine an account of some observations made during the past three years by the writer, with a critical summary of the literature that he has had access to. Unless otherwise stated, what is said relates to *S. nodosa*, L.

The tube of the irregular gamopetalous corolla is inflated approximately to a sphere (Figs. 1 and 4), its limb projecting from the somewhat constricted mouth. The bilobed upper lip and the lateral lobes of the trilobed lower lip project straight forward, giving the flower some resemblance to the old-fashioned poke bonnets one occasionally encounters in country places; while the middle lobe of the lower lip is reflexed and closely applied to the outside of the tube. This structure, and the color, inconspicuous though it be, of the corolla, lead us to believe the flowers zoophilous, a belief strengthened by the fact that nectar is abundantly secreted from the expansion of the flower until some time after fertilization has been effected. The organ which secretes this fluid is an irregular annular disk which surrounds the base of the ovary (Figs. 2 and 3). Commonly, but not invariably, it is more prominent on the upper side; and unless the quantity of nectar is very great, it collects in one or more drops at the upper side of the ovary, though it has occasionally been found in sufficient quantity to fill the basal part of the corolla.

When a flower is about to open, its style will be found bent upward, the already mature stigma lying against or close to the top of the corolla, while the four immature stamens are crumpled down into its base, near the ovary. When the flower has opened, these organs retain essentially the same position, the style being so curved that the stigma lies just below the middle of the mouth of the corolla (Fig. 2). In this state the flower is functionally pistillate. After a varying period, depending largely upon the temperature prevailing at the time, the stamens begin to appear at the mouth of the corolla, successively taking their places close to the base of the reflexed lobe of the lower lip, and shedding their pollen. A considerable number of observations show that the inner (or lower) pair matures first, in some cases the one on the right appearing first; in others, that on the left. If, as is constantly the case in pleasant weather, when the insects which will be shown to visit the flowers are most active, the stigma has been fertilized before this, its style

will have bent downward and become closely appressed to the reflexed lobe of the corolla (Figs. 1 and 4); but in case no pollen has reached it, it will have moved little, and the relative position of the parts will be that shown in Fig. 3, where one pair of stamens is mature. In the former case the plant will be functionally staminate; in the latter, perfect. The species is, therefore, protogynous, as first noted by Sprengel (1, p. 323*). Ricca (1, p. 261) notices the reflexion of the style, supposing it merely a preventive of close-fertilization.

Theoretically, there should be five stamens in *Scrophularia*, but as a general thing only four are found, attached to the corolla near its base, the fifth being represented by a small truncate or notched scale adnate to the corolla just below the point of union of the lobes of the upper lip. That this body represents the missing stamens is shown by its position and occasional development into a poliniferous organ (Müller, 1, pp. 281–2). A natural question as to the reason for the common abortion of this stamen finds a ready answer in the mode of pollination. The stigma, and the anthers of the developed stamens lie at the bottom of the opening into the corolla, just where they are most efficient when the flower is visited for nectar by an insect; forthe latter, occupying the same relative position on all flowers visited, brings the same part of its body into contact with the mature organ, be it stigma or anther. Were the fifth stamen developed, it could be of no use while occupying its normal position, since its pollen would always be received by that part of the insect which never touches the stigma (Ogle 1, p. 51). The only alternatives are its suppression and its growth so as to lie with the others, at the lower side of the flower. The latter bringing the filament obliquely across the cavity of the flower, and obstructing it to a certain extent, even though the filament were closely applied to the side, is less practicable than the former, which, accordingly, Nature has adopted. Were it entirely useless we should expect it to be removed *in toto*; but the fact that a remnant constantly occurs, though differing greatly in size in the different species of the genus, leads us to look for some useful purpose that it serves. Sprengel (*l. c.* p. 322) saw in it a means of arresting any stray rain drops that might have crept under the rim of the bonnet, for he saw clearly that, for some reason, there is almost always a provision in nectariferous flowers for

Fig. 2.

Fig. 1.

Fig. 3.

Fig. 4.

* Where references are made as here, the first numeral indicates the book or article similarly numbered under the author's name, in the list at the end of this article.

protecting their honey from dilution by rain.* While, as he showed, the scale serves to a certain extent as a nectar-guard, its chief use appears to be that of guiding insects which visit the flowers so as to force them to enter all in precisely the same manner. This thought was first suggested by the longitudinal furrow on the lower side of the scale, the two sides projecting downward as far as their width permits. In this form it renders it far easier for insects to enter bodily or insert their heads immediately over the middle line than at either side. The position of the grooved scale, opposed to the sexual organs to which it serves as a guide, corresponds precisely to that of the guiding groove found in *Labiatae*, orchids, etc., and the very slight development of this body in some species is no stronger argument against this view of its function than the slight development of the guiding groove of some plants in the orders just mentioned is against its usual function when well developed. An interesting fact, first observed last spring, is that soon after fertilization has been effected and the stamens have shed their pollen, a slight jar causes the corolla to break loose from the receptacle ; immediately after which the calyx begins to close, forcing the corolla off much as in *Verbascum* and *Veronica*. Several times, I saw this brought about by the visit of wasps belonging to the genus *Eumenes*. Finding itself, and the corolla to which it clung, suddenly removed from the nectar it was after, appeared to be matter of much surprise to the wasp, which visited no more flowers on that plant. This phenomenon doubtless aids in securing the crossing of the different plants, in the genera in which it occurs. So far as made out, the process is quite similar in the three genera named ; though whether it is to be attributed to irritability or not is a matter about which opinions differ. In *Rhinathus major* and *R. minor* the corolla is also deciduous; here it does not fall from the receptacle, but tears across near the base, as stated by Rossmann (*Bot. Zeitung*, 1860, p. 217).

The inconspicuous lurid flowers, with but a faint variation of color pointing to the nectar, and their unpleasant odor, are less attractive to bees than to wasps, and it is upon these insects that the flowers chiefly depend for their cross-fertilization. Sprengel states that he has seen a large and a small wasp collect nectar from *S. nodosa* (*l. c.* p. 324). H. Müller found the most frequent visitors for nectar to be *Vespa vulgaris*, *V. rufa*, *V. Germanica*, *V. media*, and *V. holsatica*. In smaller numbers he found the following bees : *Bombus agrorum* (once), *Halictus sexnotatus*, *H. zonulus*, *H. flavipes*, (1, p. 283). The same observer records *Bombus senilis* as also visiting the flowers for nectar (2, p. 267). Darwin speaks of the flowers of *S. aquatica* as being fertilized by wasps (1, p. 176 ; 2, p. 147)

* The notion formerly was that nectar, being less attractive to insects after dilution, was protected from the rain by these devices. Since, however, the osmotic nature of the secreting process seems probable, it is likely that the necessity for maintaining a dense syrup on the surface of the gland is the principal reason for the existence of these nectar-guards, though the reason first mentioned is undoubtedly of considerable importance. Some remarks on this subject may be found in the *Botanical Gazette* for Nov., 1881, p. 287.

Prof. Farlow saw only hive-bees collect nectar on *S. nodosa* (Gray, 1, p. 151). Meehan finds *S. canina* visited by "small sandwasps and other winged insects" (1, 108). Dr. Gray states that *S. nodosa* is visited by hive-bees (2, p. 111; 3, p. 36; 4, p. 220); and Darwin quotes this statement (3, p. 424). Wilson observed a wasp while collecting nectar from *S. nodosa*, and quotes Müller and Darwin on the visits of wasps to this species and to *S. aquatica* (1, pp. 565–6). Delpino finds wasps on the flowers in Italy (1, p. 212), and Lubbock also speaks of their visits (1, p. 137). Finally I have observed *Eumenes fraterna* and *Odynerus albophaleratus* collecting nectar from the flowers several times in New York, New Jersey and Wisconsin, and small bees belonging to two or more species of *Halictus* were occasionally noticed similarly employed. The former cling to the flower, inserting only their heads, as Sprengel and Müller have shown to be the case with the larger wasps; the latter creep bodily into the corolla. Both are forced by the shape of the corolla and the presence of the arched fifth stamen to enter in the median line. The nectar is also attractive to certain large ants, which, were they more active, would give efficient aid in the transfer of pollen from flower to flower; their sluggishness, however, renders their services of little value and, as they seldom travel from plant to plant, the crossing they do effect is merely between flowers of the same stock. The flowers are also sometimes visited for their pollen; Sprengel found "ein Insekt welches eine Aehnlichkeit mit einer Biene, und auch einen Stachel im After hat, aber viel kleiner ist, als eine Biene" (probably a *Halictus*) engaged in collecting pollen from *S. nodosa* (*l. c.* p. 324); Müller saw *Halictus sexnotatus* employed in the same manner; and near Madison I had an opportunity to watch a species of the same genus as it collected pollen. From the above statements it appears that the nectar of *Scrophularia* is attractive to wasps, bees, and ants, principally the first-mentioned; and there is every reason for believing that the entire genus is adapted to profit especially by the visits of these insects, which appear to find the nectar more palatable than do bees. As in *Symphoricarpus racemosus* and *Ribes Cynosbati*,* which are also largely visited by wasps, and also have corolla tubes of comparatively little depth, *Scrophularia nodosa* is occasionally perforated (Sprengel, l. c., p. 324), and here, as there, the depredator is, no doubt, one of the larger species of *Vespa*, though direct observation has failed to discover its identity, as yet.

Sprengel saw that insects must transfer pollen from older to younger flowers while gathering nectar, and that the result was crossing, and not close-fertilization; and most later observers agree with him. Mr. Wilson is, however, the first who has tried to show how the inconspicuousness of the flowers and the *proterogyny* are of value to the plant (1, p. 565), both being correlated with the adaptation of the flowers to *wasps*, these partly predaceous insects being enabled by their acute senses to discover inconspicuous objects with little difficulty. Mr. Wilson believes, and rightly, that a flower adapted to fertilization through their agency can reach its highest

* Bulletin Torrey Club, June, 1881, pp. 68–9.

perfection only when, being easily discernible by them, it is as little attractive as possible to other insects. The color and odor of the flowers of *Scrophularia*, and the quality of their nectar evidently tend to this end. The same observer, watching a wasp on *S. nodosa*, found that the first flower on the stem which it visited was the top one; from this it passed to the others in a somewhat irregular manner going downwards, and finally left the plant from the lowest flower (*l. c.*, p. 565). This procedure was said to bring the insect first to the younger, pistillate flowers; then to the older, staminate ones. My own studies show a very great irregularity in the visits of wasps, but this irregularity is largely conducive to cross-fertilization in its widest sense. So far as I know, the insects which visit the flowers for pollen go only to those whose anthers are dehiscent, and can have little influence in effecting pollination, except in cases where the stigma is still unfertilized when the stamens begin to mature.

So far as may be judged from reliable statements, and from personal observation, *Scrophularia* is therefore perfectly adapted to cross-fertilization by the aid of insects, and the favored visitors are wasps. Sprengel could not believe that if, as Kölreuter and Medicus insisted, fertilization was intended to be effected by the successive rising of the stamens and their bursting beside the stigma, the flowers would remain merely pistillate for some two days before the stamens came up to fertilize them. He went, however, to the other extreme, believing that fertilization has always occurred, and the style becomes reflexed before the anthers dehisce, self-fertilization or close-fertilization by any means being thus excluded. Henschel, though far from a believer in Sprengel's views, found that before the anthers of *S. Scorodonia* and *S. glandulosa* had come to maturity the style was reflexed (1, p. 103). Dr. Müller was the first to show that *Scrophularia* is far better fitted to maintain existence than its adaptation for cross-fertilization alone implies; for he found that, as has been stated in describing the order of maturity of the organs, if unfertilized—and this frequently occurs in damp, cold weather, when insects are least active in their visits—the stigma remains in its position until the stamens mature, and so, in a sense, the belief of Kölreuter and Medicus is realized. This fact is of easy observation, and no doubt accounts for the similar belief of Mr. Meehan whose keen eyes detected insects upon the flowers of *S. canina*, but could find no pollen upon the stigma of a flower until after the dehiscence of its own anthers. Henslow (1, p. 371), with a strong predisposition to see adaptations for regular self-fertilization, comes to the same conclusion from a study of dried specimens of this species, and finds his belief confirmed by what Mr. Meehan saw. Dr. Gray, like Sprengel, looking at the matter from another standpoint, seems to have overlooked the provision for regular self-fertilization in case crossing has not occurred, though it is to him that we owe the interpretation of Nature's golden rule to flowers: "get fertilized, cross-fertilized if you can, self-fertilized if you must, but at all events get fertilized." Speaking of *S. nodosa* he says: "self-fertilization here can hardly ever take place, and only through some disturbance of the natural course" (4, p. 220); a similar statement is also made in

2, p. 111. From flowers which, if not crossed, are self-fertile, it is but a step to such as are regularly self-fertilized, but with a possibility for occasional crossing; and a step further leads to cleistogamous flowers, incapable of crossing, and constantly self-fertilized. It is a significant fact that the latter are never produced to the exclusion of others capable of being crossed, their occurrence under any circumstances being merely a sure means of securing some offspring with as little drain as possible upon the system of the plant.

Through the kindness of Mr. Watson, I have been able to examine the specimens of *Scrophularia* in the Gray herbarium, with the following results. So far as could be judged from dry s ecimens, protogyny with the characteristic relations of stamens and pistil found in *S. nodosa*, occur in *S. aquatica*, *S. bicolor*, *S. calliantha*, *S. canina*, *S. chrysantha*, *S. floribunda*, *S. glabrata*, *S. grandidentata* (?), *S. hirta*, *S. Hispanica*, *S. incisa*, *S. laciniata*, *S. mellifera*, *S. multicaulis*, *S. Oliveriana*, *S. peregrina*, *S. racemosa*, *S. sambucifolia*, *S. Scopolii*, *S. Smithii*, *S. sylvatica*, *S. tricopoda*, *S. trifoliata*, and *S. variegata*. In all of these, crossing appears well provided for, while the position of the parts in some flowers of several species render it probable that self-fertilization is possible, later, if this has not occurred. No species were found in which there was reason to believe that synacmy and regular self-fertilization occur; but in a considerable number the specimens did not allow an opinion to be formed. Cleistogene flowers were found only in *S. arguta*, where they were first detected by Durieu de Maisonneuve in 1856 (1, p. 569), and later mentioned by Kuhn (1, p. 67); and it is needless to say that open entomophilous flowers occur on the same plants, although the specimens do not allow me to state whether dichogamy is present or not.

Before closing, reference must be made to several conflicting statements about the sort of dichogamy found in this genus. As stated before, Sprengel found that the pistil matures before the stamens; this and *Euphorbia* being the only genera known to him as possessing what he called "weiblich-männliche Dichogamie." Axell (1, p. 39) doubts this without having studied the plant; but Hildebrand (1, p. 21), Müller and others have no difficulty in finding this state of things which we call to-day protogyny, and I know of no statement implying the reverse, saving that by Prof. Beal (1, p. 202), which is a slip as shown by the context. Mr. Pryor makes the following statement about *S. aquatica* which at first seems unintelligible: "The anthers may be seen (*a*) projecting some distance above the lower lip of the flower, while the style is still undeveloped, and concealed some way down in the tube. In other cases (*b*) the stamens and styles alike have risen, but not to the same extent as in *a*, above the level of the surface; while in a third instance (*c*) the anthers are barely visible, but the greatly lengthened style is closely reflexed over the lower lip of the corolla, and indeed almost reaches the upper border of the sepals. Are these several changes only the result of growth, or is there anything like trimorphism in these plants? More probably, perhaps, as in case of some of their nearest allies, they are regularly protandrous, and these appearances would thus find a ready explanation" (1, p. 259). Stages *b* and *c* are readily under-

stood, being nearly what we show in figures 3 and 4, their order of succession being reversed. Mr. Pryor appears to have entirely overlooked the first stage, shown in figure 2, and his *a* is an abnormal state of things which the writer has seen a number of times, the style being dwarfed and the stigma usually incapable of fertilization. When such cases are seen on the living plant it is very easy to convince oneself that such styles never elongate so as to give rise to *b* and *c*.

As to the organ which secretes the floral nectar, mention is made of it in many of the essays and theses on "nectaries" which were the fashion fifty to seventy-five years ago, the usual statement being that the glandular organ is the disk described above. This view is also held by Sprengel, Müller and Delpino; the latter, however, considering it a part of the ovary rather than of the receptacle (1, p. 93). Dr. Gray (1, p. 151) states that "the nectar sought by insects is here secreted abundantly by the corolla, at its base at the posterior side, and to some extent by the disk which girts the base of the ovary; the posterior face of the scale which represents the anther of the fifth stamen is apparently glandular, but hardly if at all nectariferous." That the corolla takes any part in the secretion appears to require further demonstration.

If, as we hope is the case, the conflicting statements concerning *Scrophularia* have been reconciled, it remains only to state in summary: 1, that the flowers (taking *S. nodosa* as the type) are adapted by their coloring, odor, nectar, form and protogyny to cross-fertilization by wasps; 2, that in case the insects fail to do their part, self-fertilization is fairly well assured, though we have known it to fail occasionally; 3, that the existence of species which are adapted to close-fertilization without a previous chance for crossing remains to be proved; 4, that cleistogene flowers are produced, so far as we know, by only one species, *S. arguta*.

DESCRIPTION OF THE FIGURES.—Fig. 1, old flower in the staminate stage, x 2. Fig. 2, newly-opened flower in the pistillate stage, the nearest side of the calyx and corolla being removed, x 2. Fig. 3, unfertilized flower in which the inner stamens are maturing, the nearer side of the calyx and corolla being removed, x 2. Fig. 4, old flower in the staminate stage, seen obliquely from in front, x 1½.

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§ 135. A New North American Lichen.

By H. Willey.

Mr. C. G. Pringle, who in the past two years has added to our knowledge of the Lichen Flora of Northern New England and Lower Canada, last spring collected in Arizona, some lichens, among which there is one that is new and particularly interesting.

This lichen, for an inspection of the specimen of which I am indebted to Charles J. Sprague, Esq., of Boston, was collected in the Santa Rita Mountains, Arizona. It belongs to the genus *Omphalodium*, and is considered by Prof. Tuckerman to be a subspecies of *O. Hottentottum*, (Thunb.), and is to be distinguished as

O. Hottentottum, var. Arizonicum, Tuck., ined. The genus belongs to the family Umbilicariae, and is distinguished from *Umbilicaria* by the thalline margin of the apothecia, on which account *O. Hottentottum* and the only other species, *O. Pisacomense*, May. & Fl., a South American lichen, are referred by Nylander to *Parmelia*. *O. Hottentottum* is a rather rare Cape of Good Hope lichen marked by the ciliate margins of the thallus and of the apothecia ; though this character is not constant.

In var. *Arizonicum* the lobes are more rounded and crenate than in *Hottentottum* ; the upper side is smooth and greenish-glaucescent, the under side fuscous-black, naked, smooth at the centre, and becoming lacerate in anastomosing ridges towards the circumference. The apothecia are numerous, scattered, at first concave, then plane, with an inflexed, entire or more slightly crenulate thalline margin, reaching 9mm. in diameter ; the disk dark chestnut ; the hymenium, which rests in the gonidial stratum, is pale ; thekes inflated ; spores in 8s, ovoid or elliptical, colorless, measuring from 11– to 15–thousandths of a millimetre in length and from 6 to 9 in breadth. The spermogones are numerous near the margin of the lobes, black, more