On the Floral Structure of *Impatiens fulva*, Nuttall, with especial reference to the Imperfect Self-fertilized Flowers.

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(PLATE III.)

THE existence of inconspicuous self-fertilized flowers, extremely different from the large and conspicuously coloured ones, in at least three species of *Impatiens*, *I. noli-me-tangere*, Linn., *I. fulva*, Nutt., and *I. parviflora*, DC., is well known to Continental and American botanists, but appears to have received but little notice from most English observers; at least I find no detailed description of such flowers in the majority of works on English botany, or our ordinary text-books, though they are referred to in Dr. Boswell-Syme's edition of Sowerby's 'English Botany,' and in Dr. Hooker's 'Student's Flora,' and Bentham's 'Handbook of the British Flora.' The first observation of these inconspicuous flowers appears to be due to Weddell, in the case of *I. noli-me-tangere*, whose description of them is published in Jussieu's 'Monographie des Malpighiacées' and in Mohl's account of every thing that was known with respect to this phenomenon down to 1863 (contained in his paper, "Einige Beobachtungen über dimorphen Blüthen," in the 'Botanische Zeitung' for that year), and is referred to by Hildebrand in his 'Geschlechter-Vertheilung bei den Pflanzen,' and by Professor Oliver, in a paper on "Dimorphic Flowers," published in the 'Natural History Review' for 1862; Professor Asa Gray, also, in his 'Genera Floræ Americæ boreali-orientalis,' describes them in his diagnosis of that genus, and gives an admirable drawing of both kinds of flowers in the case of *I. fulva*. To Dr. Torrey, however, appears to belong the credit of having first observed them in the American species, he having already mentioned them in his 'Flora of the State of New York.'

Having had the opportunity during the past autumn of observing tolerably accurately the habit and development of these minute or "cleistogenous" flowers (as they have been termed by a German writer) of *Impatiens fulva*, I am able to add a few particulars to those already published, which may be interesting as a contribution to our knowledge of the phenomena of cross-fertilization and self-fertilization. That the existence of these flowers

should be unknown to those who have seen the plant only in the herbarium is not surprising, from a circumstance presently to be mentioned. The locality of the observations is one of its well-known habitats, the banks of the small but rapid stream the Tillingbourne, an affluent of the Wey, near the village of Shalford, in Surrey. Here it fringes the banks in great quantities every year, having apparently spread upwards from the Wey, a distance of from half a mile to a mile, notwithstanding the rapidity of the current, its seeds being doubtless carried by birds or other water-animals; for it appears to be strictly annual. My attention was first attracted to the subject by the great abundance of seed-vessels, notwithstanding the difficulty I had had in finding any of the flowers earlier in the summer, and the remark of a local naturalist that "it is one of those plants which bears seeds without producing any flowers."

Prof. Gray's description might be understood to imply that, in the earlier stages, the two kinds of flower-bud are identical, the difference in structure developing only after the premature fertilization of those which are not destined to produce conspicuous flowers. I believe, however, that the difference is original; at least, in the very earliest stage at which the buds are visible to the eye I could detect the external difference without difficulty. Figs. 1 & 2 represent the appearance of the flower-bud in both kinds of flowers at a very early stage, before the organs of reproduction are fully developed. The bud of the conspicuous flower (fig. 1) has the apex of the two exterior (lateral) sepals hooked, while in that of the inconspicuous flower (fig. 2) it is straight, the two buds at this stage being nearly equal in size. The removal of the two exterior sepals shows a still greater difference (figs. 3, 4), the spurred posterior sepal, or nectary, being very easily seen in the former case (fig. 3), while in the latter (fig. 4) the interior whorls of organs are, as described by Prof. Gray, nearly regular, but never developing beyond a very minute size.

The arrangement of the stamens in the conspicuous flowers, I find to differ slightly from Prof. Gray's generally very accurate description. The filaments, as shown in fig. 5, are coherent in their lower part, but free above, the anthers being again coherent. A single stamen, showing the mode of dehiscence and escape of the pollen, is shown in fig. 6. The pollen is disharged in dense white masses. The anterior stamen is decidedly longer than the

posterior, and is bent almost at right angles in its free portion, the point of the pistil being inserted into the bend. Springing from the posterior portion of the tube formed from the coherent lower portions of the filaments, is a membranous kind of wing, closely adpressed to the pistil—this wing, together with a slight projection from the anterior filament, completely closing in and covering the pistil. A section of the staminal tube, with the pistil, is shown at fig. 7, and, after the removal of the pistil, at fig. 8.

The development of the inconspicuous or "cleistogenous" flowers is entirely different. As already stated, the bud remains much much more minute, and the calycine and corolline whorls are much more regular. The buds never open, but are pushed off from the already fertilized ovary in the form of a cap, as shown in fig. 9. This takes place at so early a stage that it is very difficult to detect the process; indeed I examined hundreds of specimens without finding more than three or four instances of the half-expelled cap, which closely resembles the calyptra of a moss. The structure of the stamens is very different from that found in the conspicuous flowers. They are equal in length, the filaments free for their whole length, strap-shaped, and, although in the earliest stage straight (fig. 10), become afterwards remarkably contracted (fig. 11). The anther is scarcely broader than the filament; and the quantity of pollen is exceedingly small compared with that in the conspicuous flowers. Owing to the very obscure nature of the stigmatic surface, the exact period of impregnation is very difficult to determine; nor could I detect any dehiscence of the anthers for the discharge of the pollen. Prof. Oliver informs me that it is very commonly the case in closed self-fertilized flowers for the pollen-tubes to penetrate the substance of the anther itself. The mode in which the cap is thrown off presented a great difficulty to my mind. I find this to take place almost invariably at the very earliest stage with the first growth of the pistil (though this does not appear to be so much the case with the other species grown in this country, nor with *I. fulva* in America, to judge from Prof. Gray's description and drawing). Owing to the length of the petioles, the flowers are generally found beneath the leaves, so that the caps are lost. In a few cases, however, where there had been a distortion of the petiole, or some other cause of disturbance of the

ordinary arrangement, a careful search discovered cast-off caps in positions which suggested that they had been thrown off with some violence, from some cause comparable, possibly, to the elasticity of the valves of the ripe capsules. I am inclined to think, though further observation is necessary before this can be considered determined, that the filaments of these inconspicuous flowers are elastic, the different positions in which they are found at different stages of the bud being due to their efforts to throw off the cap.

With regard to the fertilization of *Impatiens fulva*, there can be no doubt that self-impregnation takes place in the "cleistogenous" flowers at a very early period, fruitful capsules appearing almost invariably to result from them. The conspicuous flowers are stated by all observers to be usually barren, though undoubtedly they sometimes produce seed-vessels; and, as far as I could observe, when this is the case the capsules contain the same average number of seeds as do those produced from the "cleistogenous" flowers. How the impregnation of these is effected I have been unable to determine. The arrangement of the stamens and the wing-like membrane before described appear to render self-fertilization absolutely impossible; and the singular part of these provisions is, that they do not seem to be constructed to favour cross-fertilization, but absolute sterility, as far as these flowers are concerned. The pendent position of the flowers causes the anthers to open with the opening directed downwards; and the inequality of the filaments already described occasions the line of the opened anthers to be horizontal. The whorl of stamens is very easily detached bodily, so as to expose the stigma; but I have failed to discover that this ever takes place spontaneously; the whole flower drops together, the pistil generally being detached at the same time; and were the pistil left behind, there would be nothing to cause insects to be attracted to it; and I can only suggest that the pollen is brought to it by the chance action of the wind. I have never seen any insect visit the *Impatiens*; but it would seem very strange if so handsome and complex a flower has been constructed without any benefit thereby resulting to the species. It would be interesting to know whether it is visited by insects in its native country. The only hint I can find on this subject is in a very old and scarce book, 'New England's Rarities discovered in Birds, Fishes, Ser-

pents, and Plants of that Country,' &c. By John Josselyn, Gent., London, 1675 *. "The Humming-bird Tree" (the drawing which accompanies it shows the plant described under this title to be *Impatiens fulva*). "This plant the Humming-bird feedeth upon, it groweth also in wet grounds, and is not at its full growth till July. It is garnished at the top with many dangling yellow flowers of a bright yellow colour." If this statement be correct, the manner in which the flower of the *Impatiens* is suspended appears admirably adapted for the Humming-bird to insert its head into the horizontal cornucopia-shaped "nectary" or posterior sepal, in doing which it would be almost certain to brush its head with sufficient force against the stamens to cause them to become detached, carrying with them the membrane which protects the stigma. But this can only be conjecture.

As to the relative abundance of the two kinds of flowers, and the time of the year at which they appear, I have never found the two kinds on the same branch, occasionally on different branches of the same plant, but more often on separate plants. This would account for the fact that the inconspicuous flowers are not to be found in herbaria. In the case of *I. noli-me-tangere*, Mr. Bentham and Dr. Boswell-Syme describe the two kinds of flowers as growing intermixed in the same raceme, although this is not borne out by Dr. Syme's own drawing. In the early part of September I found the inconspicuous-flowered plants to outnumber those with conspicuous flowers, certainly in the proportion of twenty to one. Walking for half a mile along both banks of the stream, in some places thickly fringed with the plant, I had some difficulty in finding thirty or forty specimens for the herbarium. The two kinds of plants grow, however, completely intermixed. Prof. Asa Gray states that "the minute fertile flower-buds begin to be produced earlier than the ordinary blossoms." Weddell, on the other hand, in the case of *I. noli-me-tangere*, asserted the inconspicuous flowers to be the latest, which assertion Mohl takes to be a *lapsus calami*, he having found in June abundance of these, while no trace of the more conspicuous flowers was to be found—whereas in September the latter were abundant, while the former had entirely disappeared. My own observation of *I. fulva* would lead me to suppose that the two kinds of flowers are absolutely synchronous.

* Quoted in the 'Proceedings of the Essex Institute' (Massachusetts) for 1857.

I have never noticed the least indication of any intermediate condition between the two kinds of flower, as is stated to occur in some species of *Oxalis* and *Campanula*.

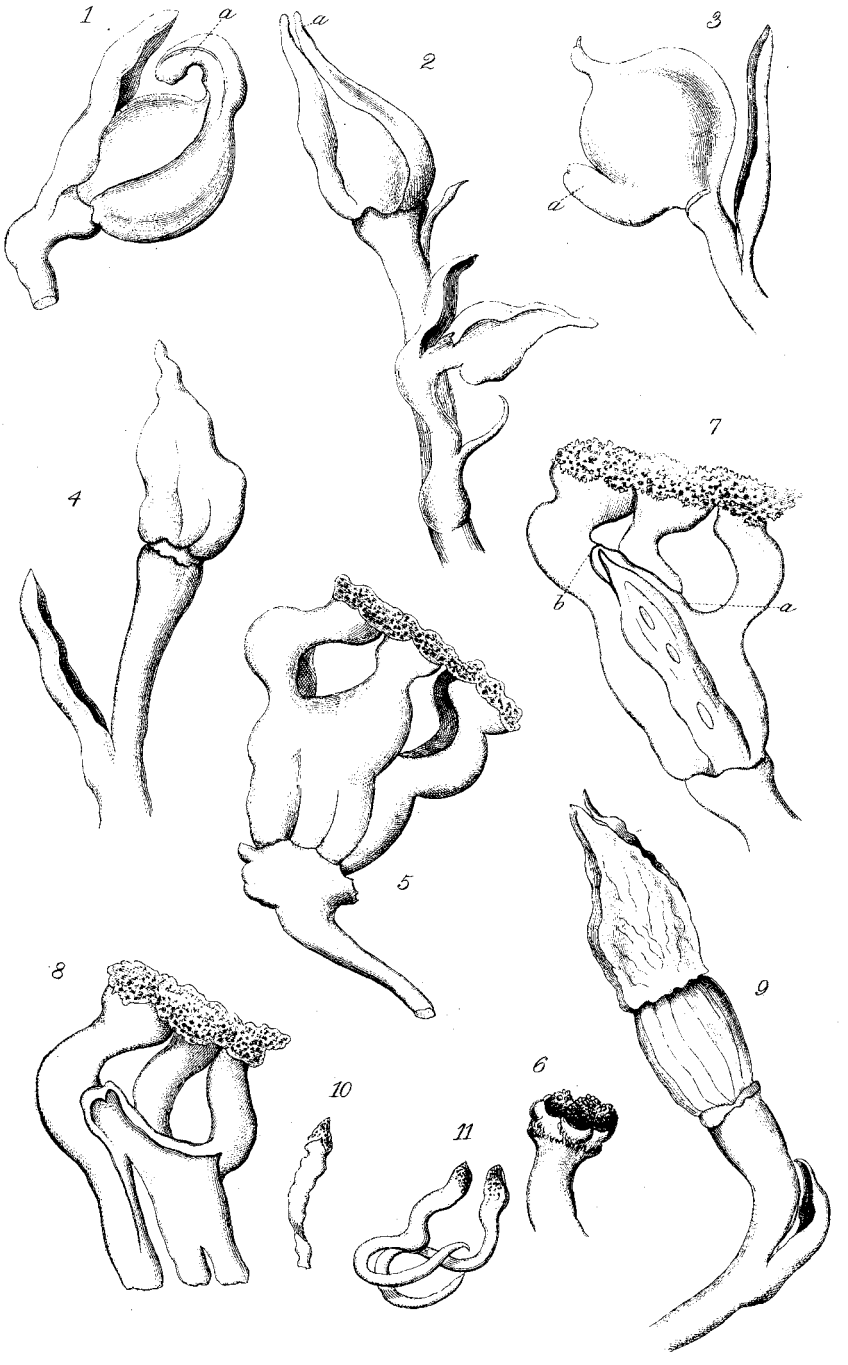
I have been unable this year to make similar observations on *Impatiens noli-me-tangere* and *I. parviflora*. Plants of the former, observed in the Botanic Gardens at Oxford on the last day of September, had abundance of the "cleistogenous" flowers with half-expelled corolla-cap, while scarcely any of the perfect flowers were to be met with, and those on different plants.

Mr. Darwin has kindly permitted me to append to this paper the following remarks with which he has favoured me:—"I am glad you have drawn attention to the difference in the bud-state of the perfect and imperfect flowers; for I remember, many years ago, objecting to Asa Gray that he considered the imperfect flowers (not, I think, in the case of *Impatiens*) arrested buds, and I maintained that their structure had been specially modified for their functions. From observations by myself in 1863, I find I was struck with the small size of the anthers, and the very small quantity of pollen. The grains are of the same diameter as in the perfect flowers, but they appeared to be more unequal in size. I distinctly saw pollen-grains protruding from the grains *whilst within the anthers*, and penetrating the stigma. I cannot believe that I could have overlooked the facts of the anthers not dehiscing. I do not mention in my notes that the pollen-grains are tied together by threads, as I do in the case of the pollen of the perfect flowers. I speak of the nectary in the cleistogenous flowers as a mere rudiment. From the fact of the nectary in the perfect flowers containing nectar, and from the pollen-grains being tied together by threads, I cannot doubt that they are crossed by insects, and I am almost certain that they are frequently visited by humble-bees. The structure of the flowers seems to me so well adapted for crossing, that I expected that the perfect flowers would be sterile without the aid of insects. In this I was quite wrong, as the perfect flowers, when protected, produced pods. Eleven such pods from perfect flowers, *spontaneously* self-fertilized, yielded on an average 3·45 seeds. I carefully brushed away the pollen from some of the perfect flowers, and fertilized them with pollen from a *distinct* plant, but got only three pods, containing, to my surprise, only 2, 2, and 1 seed. I attributed this poverty at the time to this plant probably requiring repeated doses of pollen, as is certainly sometimes the case."

To this I may append some remarks by Prof. Asa Gray in an article on "Dimorphism in the Genitalia of Flowers," in Dr. Seemann's 'Journal of Botany,' vol. i. p. 147, quoted from the 'American Journal of Science and Art,' vol. xxxiv., with corrections by the author:—"The second case, which belongs to structurally hermaphrodite flowers, is practically the reverse of the first. It is the case in which, besides the normal flowers of the species, which, for the most part, are rarely or sparingly fertile, other flowers are produced which never open, their development being, as it were, arrested in the bud, but which are very prolific of seed. Here the stigma is, and must needs be, fertilized by pollen from anthers of the same flower, the two being shut up together in the same closed bud. The acaulescent violets and the common wild species of *Impatiens* are good examples of this kind. In fact, impregnation is effected, as it were, in the early bud, wherefore we have indicated these as cases of precocious fertilization. Here the pollen is unusually active, sending out its tubes while still in the anther, and thereby, as in *Impatiens* &c., attaching the anthers to the stigma. We leave it to Mr. Darwin's sagacity to ascertain the end in the opposite case, noting that here the mostu ndoubted close fertilization for infinite generations shows no apparent tendency towards sterility, but rather the contrary."

EXPLANATION OF PLATE III.

Fig. 1. Bud of conspicuous flower, early stage.
a. Apex of lateral sepals.
2. Bud of inconspicuous flower, early stage.
a. Apex of lateral sepals.
3. Bud of conspicuous flower, lateral sepals removed.
a. Spur of posterior sepal.
4. Bud of inconspicuous flower, lateral sepals removed.
5. Androecium from conspicuous flower.
6. Single stamen from conspicuous flower.
7. Androecium from conspicuous flower, cut open to show position of pistil.
a. Membranous wing attached to posterior filaments.
b. Projection from anterior filament.
8. Androecium from conspicuous flower, pistil removed.
9. Calyx and corolla partially detached from pistil of inconspicuous flower.
10. Stamen from inconspicuous flower, early stage.
11. Stamens from inconspicuous flower, later stage.



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