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## Reviews.

XXV.—On the Two Forms, or Dimorphic Conditions, in the Species of *Primula*, and on their remarkable Sexual Relations. By Charles Darwin. Linnean Society's Journal, VI. (Botany), pp. 77-96.

We do not wish to attach an undue importance to the observations which have been here recorded by Mr. Darwin upon the remarkable sexual relations which he has proved to exist between individuals of that very commonest and most familiar of our spring favourites, the Primrose; yet we may say, with all sincerity, that Botanical Science has, of late years, been enriched with few of equal value. And this impresses us as especially the case if we regard the impulse and direction which these observations must necessarily give to future investigation. The simple fact that, in one set of primroses or cowslips, the stigma reaches to the mouth of the corolla-tube, the anthers being externally invisible, while in the other set the anthers surround and close its mouth while the stigma is far down the tube, is not, of course, advanced by Mr. Darwin as novel. As he says, gardeners speak of the two forms as the "pin-eyed" (with stigma at the mouth of tube) and "thumb-eyed" (with anthers at mouth of tube). Children too, he tells us, select the former for their necklaces; the upper part of the corolla-tube being wider, and not closed by sessile anthers, they more easily slip them over each other. It is the satisfactory explanation which, with characteristic sagacity, this distinguished zoologist offers of the (botanical) fact that primarily concerns us, and it is this that we so greatly admire.

We feel that we are yet far from being in a position to enter upon a discussion of the general question of sexuality in plants: it is a very large subject, and the basis upon which we can rest an argument is much too slender for useful application. We shall be content,

therefore, to devote the short space at our disposal to a review of the facts and conclusions established by Mr. Darwin, directing attention to other instances of dimorphism in other and very different species of flowering plants.

We may, after a certain fashion, rudely group the kinds of dimorphism exhibited in the flower under two heads. First, a dimorphism, apparently favourable to variation, marked primarily by a partial or complete separation of the sexes, which may be accompanied or not by alteration in the form or arrangement of the parts of the perianth surrounding them; and, second, a dimorphism, conservative, and unfavourable to variation, marked primarily by an alteration in the form or arrangement (frequently a reduction) of the outer whorls of the flower, which more or less completely enclose and seal up the sexual organs, which are never wholly separated.*

Such grouping we may well designate as rude, but there do certainly appear to be two classes or kinds of dimorphism, which even in the present state of our knowledge—feeling as it were our uncertain way—it may be well to distinguish, and we do not see how better to define them than as above.

It is to the first group that we may refer the primroses, and with them a very numerous company indeed of trees, and shrubs, and herbs. There are comparatively few natural orders of flowering plants out of the 200 or 300 which are generally recognized, in which we do not find more or less of a diclinous condition—a condition which necessarily involves "dimorphism" in respect of the sexual organs. There are numerous Orders invariably, or almost invariably, characterized by unisexual flowers. There are others again in which a tendency to this condition is more or less conspicuously manifest in many of their members. A large proportion of the trees of temperate Europe bear only flowers thus dimorphic. In the oak, beech, chestnut, and pine, for example, this dimorphism is extreme. In the stamen-bearing flowers, we find no rudiment of a pistil—in the pistil-bearing, no rudiment of stamens. But between plants which we may regard as wholly homomorphic, and consequently with flowers completely hermaphrodite, and the extremes just cited, we have an infinity of intermediate conditions.

Parting from the hypothetical truly homomorphic hermaphrodite, we find in the case of Mr. Darwin's *Primulas* one of the first grades of incipient dimorphism of which cognizance can be taken.

Hence one peculiar interest of his observations, to which we recur. Besides the differences already mentioned in the relative length of the style and height of the anthers in the corolla-tube of these plants, Mr. Darwin points out that in the long-styled form the stigma is globular and rough with minute papillæ, and the pollen-grains about

* This second group we have not framed to include a dimorphic condition of the male flower, or of the female flower, of a unisexual plant. We are not aware, however, that such exist. If there be none, the circumstance is worth noticing.

7/7000ths of an inch in diameter, while in the short-styled form the stigma is depressed and nearly smooth, the pollen-grains ranging from 10/-to-11/-7000ths of an inch in diameter. Our own observations entirely confirm the minute accuracy of these statements, though of the relative sizes of the pollen-grains we have only judged by comparison of them by the eye, on the same slip of glass under the microscope.

To these differences between the two forms, we may add another, noticed while dissecting the flowers. The ovules of the long-styled *Primula*, which Mr. Darwin states to produce a smaller number of seeds, are considerably larger (and probably less numerous) even before the flower expands, than in the short-styled form, which he finds to produce the larger number of seeds. These two forms—the long-styled and short-styled—occur in nature in about equal proportions. It is not yet satisfactorily shown that the same plant can produce both forms, though this is a point to which we think further attention might be directed, especially in those species which have occasionally a second or autumn flowering.

Now the carefully conducted experiments of Mr. Darwin, which are described in detail in his paper, show a remarkable difference in the influence exercised by the pollen upon the stigma of its own flower and upon the stigma of a flower of the other form. Fertilisation of a flower by pollen of its own form he terms 'homomorphic,' by the pollen of the other form 'heteromorphic.' And it is the heteromorphic unions which he shows to be pre-eminently fertile. If, therefore, the abundant production of good seed be advantageous to the species, so must be heteromorphic fertilisation, a process dependent however upon circumstances, which we may call accidental, though they are nevertheless certain and ever-acting. The agency of insects is absolutely necessary for the crossing of the different forms, and there can be no question but that the part they play in this economy is of the very highest importance. Having explained the provision which nature has made to favour the crossing of distinct individuals, Mr. Darwin suggests the possibility that the species of *Primula* may possibly be tending to a dioicous condition. In their present condition they are, as he observes, 'subdioicous hermaphrodites.' We are not in possession of corresponding facts relative to any other species in either of the groups which are distinguishable of dimorphic flowers; so that, unable to institute a single comparison, we are reduced to the necessity of speculating upon very meagre materials. We have referred the case of the *Primulas* to one category with unisexual or diclinous flowers, whether of monoicous or dioicous plants does not immediately affect the question. We have done so simply because between the comparatively trivial amount of diclinism in *Primula* and the more extreme instances which are at hand on every side in overwhelming number, we are utterly unable to draw the line.

Before we proceed to give a few instances from our second

category we would just recall a difficulty which constantly presents itself when we contemplate this subject from—so far as we can apprehend it—Mr. Darwin's point of view. If these plants be tending to a diclinous condition, if such a condition advantage the species, how and why did they ever become hermaphrodite? We cannot help conjecturing that there may be in plants two counter-agencies at work, the one acting as a constant check upon the other; the one conservative, favouring the persistence of unaltered forms, indicated in the general barrenness of hybrids and the difficulty of crossing many nearly allied species as well as in other and special arrangements which we shall afterwards advert to, the other favouring, it may be ever so slightly, a tendency to vary, indicated by the various grades of diclinism, as also by special obstacles contrived absolutely to prevent self-fertilisation in hermaphrodite flowers.* While we may, with perhaps the greater shew of reason suggest that certain species are tending to a separation of the sexes, we must not forget that arguments may be advanced to shew that it is not impossible but that they may be striving towards more perfect hermaphroditism, especially if we bring to mind the evidence (to which indeed we are scarcely hardy enough to attach a particle of weight) furnished by the 'Geological Record.' This evidence does certainly appear in favour of a greater predominance of unisexual forms at an early period than obtains at the present day. A consideration of instances referred to our second kind of dimorphism may perhaps enable us to appreciate better the phenomenon, and further illustrate the remark that there may possibly be two counter agencies at work manifesting themselves in various dimorphic conditions.

Linnaeus in the 'Praelectiones Botanicae'† remarks of *Viola mirabilis* that the early flowers provided with a corolla are often barren, while others appearing subsequently and destitute of a corolla are fertile. This observation was extended by Gingins who published a Memoir on the Violaceae in 1823. He shewed that violets presented the singular peculiarity of producing imperfect flowers, more or less destitute of petals, but with perfect fruits, which fruits he adds are "quelquefois même plus parfaits que ceux qui succédent aux fleurs complètes." M. Monnier of Nancy, yet further extended our knowledge of this dimorphic condition in the violets.‡ He says of *Viola hirta* that none of the early spring flowers yield fruit, "they all abort and wither up;" after the first flowering the leaves assume a fuller development, they become more hairy and bear in their axils flowers destitute of corolla and with the five stamens almost always free and shorter than the ovary. The peduncles bearing these flowers curve downward and bury the ovaries under the surface of the soil where the seeds are ripened. M. Monnier found the sweet-scented

* Conf. Hooker Introd. Essay to Tasmanian Flora, x.
† Ed. 1792, p. 401.
‡ Guillemin's Archives de Botanique, 1833, i. 412.

flowers of *V. odorata* to be quite infertile. In this species, as in *V. hirta* (which some botanists unite with it) it is the later flowers, without corolla and with stamens of variable length, which give the fertile capsules. Plants of the double violet he showed also bore apetalous flowers. *V. ericetorum* was found to exhibit the same phenomenon. This botanist concluded from his observations that the species of the section *Nominium** of the genus *Viola* have two flowerings, the first vernal with well-developed petaloid flowers not maturing seeds, the second aestival, with abortive corollas but always fertile. The dimorphism in *Viola* has been more recently examined by M. Michalet† and M. Müller.‡ The former says that the earlier of the 'apetalous' flowers offer transitional forms between the two states, which, however, he did not sufficiently follow. The second flowering lasts from the close of the first through part of the summer even until autumn; the May and June flowers being scarcely one-fourth the size of the earlier ones. In these he finds the calyx to be hermetically closed over the flower, leaving a large and empty space above the ovary, which he considers may favour fecondation. The sepals are afterwards burst open by the enlargement of the capsule. The petals are not entirely absent but fall considerably short of the sepals; they are membranous and hyaline, occasionally they are reduced to one or two, hence the summer flowers are not correctly described as truly apetalous. M. Michalet observes that he never found the anthers open, even in flowers the ovary of which was certainly fertilized. The style is much shorter than in the 'petaloid' flowers, the stigma truncate and funnel-shaped at top, the cavity opening into the ovary. The stigmatic surface seems smooth and not papillose. How fecondation is effected in these flowers he is unable to say.

A case parallel to the above is described by M. Michalet in the Wood-sorrel (*Oxalis Acetosella*), with the difference that the early and beautiful petaloid flowers are regularly fertilized, and produce perfect seeds. In the second or summer flowers, the sepals are closely applied and hermetically closed over the essential organs as in the violet. The petals, usually of the normal number, are much shorter than the sepals; they are rarely all wanting. There are ten stamens, of which five are smaller and appear quite barren; the five larger ones are fertile, and incline over the stigmas, with which they are described as being apparently united by delicate filaments. The part which these play, M. Michalet is unable to explain. The anthers appear to remain closed, and the pollen seems as it were deliquescent. The seeds of the smaller flowers, which are ripened under the surrounding moss and detritus, offer no apparent difference from those of the normal ones. The same observer finds

* Messrs. Hooker and Bentham in their "Genera Plantarum" attribute dimorphous flowers to all the sections excepting *Melanium*.

† Bull. Soc. Bot. France, vii. 465.

‡ Bot. Zeit. 1857, 729.

hypogean flowers of *Linaria spuria* which ripen seed, but these flowers offer no notable difference from the rest.

We have ourselves examined the dimorphic flowers both of *Viola* and *Oxalis*, but have nothing to add to M. Michalet's detailed account. Another case of similar character, however, in a far removed natural order, has recently been closely under our notice; and as it is one which we believe is not widely known, although it has been carefully investigated by M. Brongniart, and is described by M. Ad. de Jussieu in his "Monographie des Malpighiacées," and by Torrey in his 'Flora of New York' (i. 428), we may be permitted to give some account of it here. Our observations have been made solely upon dried specimens, so that we can only speak to structural facts. The most important problems which these phenomena suggest, it is needless to say, can only be solved by study and carefully watching of the living plant, and this we have not yet had the opportunity of doing. Linnæus long ago* wrote of *Campanula perfoliata*— "flores laterales raro corollo instructos producit, sed tantum calycem semen continentem; flores vero terminales perfecti sunt." This species we have not examined, though, from M. Jussieu's account,† it would appear to have been the same that M. Brongniart observed. This excellent botanist found, in the smaller flowers, a 'tympanum' covering the base of the calyx-tube. This is the rudiment of the corolla. On removing it he found the stigma and stamens with well-formed pollen. Our attention has been devoted to two Indian species (*C. canescens*) alluded to by Messrs. Hooker and Thomson in their Præcursores ad Floram Indicam,‡ and *C. colorata*. We find the smaller and apparently apetalous flowers to be usually lateral, often borne on short racemes springing from the lower leaves of the stem, though sometimes they abound along the branches of the principal inflorescence. They are various in size, from that of a coriander seed to a pea. The ovary is inferior, as in the normal flowers, though occasionally only two-celled. The limb of the calyx is not always regularly five-lobed, but often, and especially in the smallest flowers, three-lobed or irregularly divided. The disc of the flower is covered by a *completely closed* hairy membrane, with a slight mammilliform elevation in the centre. This membrane is the rudimentary corolla, and the number of petals composing it is indicated by converging lines. On dissection, this elevation is found to cover a pentagonal or five-lobed body which at first sight resembles a stigma, but examination shows that each lobe is opposite to a corresponding lobe of the calyx-limb, and that each lobe of the pentagonal process is united to the base of the opposed calyx-lobe by a delicate cord, the filament in fact of the stamen, of which the lobe of the central body to which it is united is the anther. The stamens are extended horizontally between the upper mem-

* Prælectiones Botanicæ, 399. † *Op. cit.* 84.
‡ Journ. Linn. Soc. ii. 7.

brane and the lower, which separates them from the ovary, and the anthers, closely applied, are apparently quite connate and together adnate to the stigma. We have observed in soaked specimens what we have every reason to believe are true pollen granules, with their tubes penetrating the tissue of the stigma.

The contents of the ovary do not appear to differ in the normal and abnormal flowers. In *Campanula colorata* we have seen flowers intermediate in character between those above described, and normal ones, in which the corolla, instead of being imperforate, opened by teeth in the centre, though falling short of the calyx-lobes in length, —the style considerably lengthened and the anthers free. In connection with the occurrence of dimorphous flowers in Campanulaceæ, it may be well to bear in mind that the method of fertilization of the normal flowers was long a puzzle to botanists. For a detailed notice of the various hypotheses suggested to explain it we must refer to M. A. de Candolle's Monographie des Campanulées (1830) and especially to M.M. Brongniart* and Tulasne's† Papers in "Annales des Sciences Naturelles." In these flowers the anthers open and discharge their pollen before the expansion of the corolla. M. Du Petit-Thouars conjectured that the stigmas were fertilized before it opened. He found that the stigmatic lobes were slightly divergent in the bud at a time when the anthers might be supposed to open and that they again close shortly before the corolla expands: after its expansion they are once more divergent. This view was considered to be supported by the case of the allied Goodenieæ and Scaevolae in which the pollen is received into a capsule or indusium terminating the style before the flower opens. When the corolla expands the indusium in these plants is closed. Again, much attention has been directed to what have been termed the 'collecting-hairs' with which the style in the Bell-flowers is so frequently clothed. A function has been attributed to them in the fertilisation of the flower, but this, as Brongniart showed was due to imperfect observation. These hairs, which brush off the remaining pollen from the anthers as the style shoots up through them, frequently become invaginated, like the finger of a glove drawn back half way up: the sheathing portion entangles a few of the grains so that they appear actually drawn into the tissue of the style: hence the mistake. M. Tulasne, whose observations are of the highest authenticity, finds that pollen received upon the stigma produces the tubes which fertilize the ovules. How the pollen reaches the stigma must be more fully settled by careful observation. It is highly probable that insects play an important part in its conveyance, as various observers have suggested. There are other plants belonging to different Natural Orders to those above noticed, which offer like dimorphism. In Caryophyllaceae, Maximowicz,‡ describes a *Stellaria* (dis-

* 2e Sér. xii. 244. † 3e Sér. xii. 71.
‡ Primitiae Fl. Amurensis. 57.

tinguished generically under the name of *Kraschenikowia*), "floribus superioribus sterilibus, infimis (radicalibus) anantheris fertilibus carnosulis." The flowers from the axils of the lower leaves become buried in the soil and are described as "floribus * * clausis * * * petalis staminibus stylisque nullis, capsulae rotundatae parietibus carnosis, seminibus fuscis * * * embryone peripherico arcuato albumineque normali! donatis." The normal flowers are petaloid with the stamens nearly equalling the sepals. He says, "verosimillime capsulae intra paniculam steriles." M. Weddell* and Asa Gray,† describe dimorphism in the genus *Impatiens:* M. Weddell in the common *I. Noli-me-tangere.* In this plant some of the fruits ripen without the previous expansion of the flowers to which they belong. All the whorls of the flower exist, but excepting the ovary, they are extremely small and rudimentary, uniting into a little hood, which the fruit, in elongating, bears up with it and wears as a cap. These abnormal flowers arise near the normal ones, but usually in lateral peduncles. Dr. Gray gives some interesting particulars respecting the structure of the normal flowers of the American species, in which certain membranaceous appendages of the filaments are connivent and more or less coherent over the summit of the pistil, entirely preventing the access of pollen in the greater proportion of even fully developed flowers, which, consequently, fall away unfertilized. In some, however, the growing ovary pushes the stigma through the cap, thus securing its fertilization.

M. Jussieu records dimorphous flowers in the section *Meiostemones* of the Natural order Malpighiaceae. In Acanthaceae (*Ruellia*) it was long ago observed by Dillenius. And we might adduce other instances, but these must suffice, for we possess no instance of this kind of dimorphism, referred to our second category, which has been fully and satisfactorily described, much less explained; indeed the examples which we have given are amongst the most marked and the best observed.

The main feature and that to which we would wish to direct attention in, at least some, of these cases, is the occurrence of a second kind of flower in which it would seem that nature has especially contrived to exclude the possibility of fertilization by other than own-flower stamens. It is true that the anthers in the closed flowers of *Viola* and *Oxalis* are stated never to have been found open, but in the *Campanula* observed by us the pollen evidently had access to the stigma; and indeed, M. Michalet points out, as we have said, the existence of fine threads connecting the anthers with the stigmas in the "hermetically closed" flowers of *Oxalis.* These fine threads, there can be no doubt, are the pollen-tubes. It is impossible that we should here enter upon the *rôle* of these remarkable flowers in the economy of the species to which they belong. We do not possess, as we have already said, a sufficient basis of

* Jussieu, Malpighiacées, 85. † Gen. United States, ii. 131.

facts to work upon. It must suffice to suggest conjecturally that a conservative agency, if we may so term it, is at work in the vegetable kingdom, over and above the inherent check of a like tendency possessed in a high degree by the great majority of species, which absolutely prevents miscellaneous or wide hybridization or crossing. We do not forget that the question of hybridization of distinct species may be entered upon, to a certain extent, apart from that of the crossing of different individuals of the same species, and that a most important distinction may be drawn between them, but facts fail to show how far the check which prevents a crossing of species operates in preventing too wide a crossing of individuals of any one species, if indeed it operate in the latter case at all. We have alluded to what have seemed to be special contrivances in certain flowers to *prevent* self-fertilization. Several familiar cases might be quoted but we have already exceeded a reasonable limit, and until some more careful observers, with a measure of that earnest diligence in an unprejudiced search after truth, which so pre-eminently characterizes Mr. Darwin, shall have described to us the true character and end of some of these anomalous structures it would be useless to offer any blind speculations with regard to them. Finally, let us beg those who have opportunity,—and but a short time each day, if perseveringly devoted to the purpose, will suffice for important results,—let us beg that they will select for careful watching and study either one of the common cases of dimorphism mentioned above, or some of the plants which we have adverted to as offering obstacles to self-fertilization. Either class promises well to be resultful. Let us just observe that it is by no means essential that the observer should be a "botanist." Mr. Darwin is not a botanist, nor did he ever pretend to be such, yet his observations prove of the very highest value to botanical science.

[In the above paper we have not referred to the phenomenon of dimorphism exhibited by various Orchidaceae. We hope to return to the subject, in connection with Mr. Darwin's new work on the 'Fertilisation of Orchidaceae' in a future number.]