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978-1-108-01827-2 - The Different Forms of Flowers on Plants of the Same Species

Charles Darwin

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THE
DIFFERENT FORMS OF FLOWERS
ON
PLANTS OF THE SAME SPECIES.



INTRODUCTION.

THE subject of the present volume, namely the differently formed flowers normally produced by certain kinds of plants, either on the same stock or on distinct stocks, ought to have been treated by a professed botanist, to which distinction I can lay no claim. As far as the sexual relations of flowers are concerned, Linnæus long ago divided them into hermaphrodite, monœcious, diœcious, and polygamous species. This fundamental distinction, with the aid of several subdivisions in each of the four classes, will serve my purpose; but the classification is artificial, and the groups often pass into one another.

The hermaphrodite class contains two interesting sub-groups, namely, heterostyled and cleistogamic plants; but there are several other less important subdivisions, presently to be given, in which flowers differing in various ways from one another are produced by the same species.

Some plants were described by me several years ago, in a series of papers read before the Linnean Society,*

* "On the Two Forms or Dimorphic Condition in the Species of *Primula*, and on their remarkable Sexual Relations." 'Journal

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the individuals of which exist under two or three forms, differing in the length of their pistils and stamens and in other respects. They were called by me dimorphic and trimorphic, but have since been better named by Hildebrand, heterostyled.* As I have many still unpublished observations with respect to these plants, it has seemed to me advisable to republish my former papers in a connected and corrected form, together with the new matter. It will be shown that these heterostyled plants are adapted for reciprocal fertilisation; so that the two or three forms, though all are hermaphrodites, are related to one another almost like the males and females of ordinary unisexual animals. I will also give a full abstract of such observations as have been published since the appearance of my papers; but only those cases will be noticed, with respect to which the evidence seems fairly satisfactory. Some plants have been supposed to be heterostyled merely from their pistils and stamens varying greatly in length, and I have been myself more than once thus deceived. With some species the

of the Proceedings of the Linnean Society,' vol. vi. 1862, p. 77.

"On the Existence of Two Forms, and on their Reciprocal Sexual Relation, in several Species of the Genus *Linum*." Ibid. vol. vii. 1863, p. 69.

"On the Sexual Relations of the Three Forms of *Lythrum salicaria*." Ibid. vol. viii. 1864, p. 169.

"On the Character and Hybrid-like Nature of the Offspring from the Illegitimate Unions of Dimorphic and Trimorphic Plants." Ibid. vol. x. 1868, p. 393.

"On the Specific Differences between *Primula veris*, Brit. Fl. (var. *offinialis*, Linn.), *P. vulgaris*, Brit. Fl. (var. *acaulis*, Linn.), and

P. elatior, Jacq.; and on the Hybrid Nature of the Common Oxlip. With Supplementary Remarks on Naturally Produced Hybrids in the Genus *Verbascum*." Ibid. vol. x. 1868, p. 437.

* The term "heterostyled" does not express all the differences between the forms; but this is a failure common in many cases. As the term has been adopted by writers in various countries, I am unwilling to change it for that of *heterogone* or *heterogonous*, though this has been proposed by so high an authority as Prof. Asa Gray; see the 'American Naturalist,' Jan. 1877, p. 42.

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pistil continues growing for a long time, so that if old and young flowers are compared they might be thought to be heterostyled. Again, a species tending to become dioecious, with the stamens reduced in some individuals and with the pistils in others, often presents a deceptive appearance. Unless it be proved that one form is fully fertile only when it is fertilised with pollen from another form, we have not complete evidence that the species is heterostyled. But when the pistils and stamens differ in length in two or three sets of individuals, and this is accompanied by a difference in the size of the pollen-grains or in the state of the stigma, we may infer with much safety that the species is heterostyled. I have, however, occasionally trusted to a difference between the two forms in the length of the pistil alone, or in the length of the stigma together with its more or less papillose condition; and in one instance differences of this kind have been proved by trials made on the fertility of the two forms, to be sufficient evidence.

The second sub-group above referred to consists of hermaphrodite plants, which bear two kinds of flowers—the one perfect and fully expanded—the other minute, completely closed, with the petals rudimentary, often with some of the anthers aborted, and the remaining ones together with the stigmas much reduced in size; yet these flowers are perfectly fertile. They have been called by Dr. Kuhn* cleistogamic, and they

* 'Botanische Zeitung,' 1867, p. 65. Several plants are known occasionally to produce flowers destitute of a corolla; but they belong to a different class of cases from cleistogamic flowers. This deficiency seems to result from the conditions to which the plants have been subjected, and

partakes of the nature of a monstrosity. All the flowers on the same plant are commonly affected in the same manner. Such cases, though they have sometimes been ranked as cleistogamic, do not come within our present scope: see Dr. Maxwell Masters, 'Vegetable Teratology,' 1869, p. 403.

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will be described in the last chapter of this volume. They are manifestly adapted for self-fertilisation, which is effected at the cost of a wonderfully small expenditure of pollen; whilst the perfect flowers produced by the same plant are capable of cross-fertilisation. Certain aquatic species, when they flower beneath the water, keep their corollas closed, apparently to protect their pollen; they might therefore be called cleistogamic, but for reasons assigned in the proper place are not included in the present sub-group. Several cleistogamic species, as we shall hereafter see, bury their ovaries or young capsules in the ground; but some few other plants behave in the same manner; and, as they do not bury all their flowers, they might have formed a small separate subdivision.

Another interesting subdivision consists of certain plants, discovered by H. Müller, some individuals of which bear conspicuous flowers adapted for cross-fertilisation by the aid of insects, and others much smaller and less conspicuous flowers, which have often been slightly modified so as to ensure self-fertilisation. *Lysimachia vulgaris*, *Euphrasia officinalis*, *Rhinanthus crista-galli*, and *Viola tricolor* come under this head.* The smaller and less conspicuous flowers are not closed, but as far as the purpose which they serve is concerned, namely, the assured propagation of the species, they approach in nature cleistogamic flowers; but they differ from them by the two kinds being produced on distinct plants.

With many plants, the flowers towards the outside of the inflorescence are much larger and more conspicuous than the central ones. As I shall not have occa-

* H. Müller, 'Nature,' Sept. 25, 1873 (vol. viii.), p. 433, and Nov. 20, 1873 (vol. ix.), p. 44. Also

'Die Befruchtung der Blumen,' &c., 1873, p. 294.

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sion to refer to plants of this kind in the following chapters, I will here give a few details respecting them. It is familiar to every one that the ray-florets of the Compositæ often differ remarkably from the others; and so it is with the outer flowers of many Umbelliferæ, some Cruciferæ and a few other families. Several species of Hydrangea and Viburnum offer striking instances of the same fact. The Rubiaceous genus *Mussaenda* presents a very curious appearance from some of the flowers having the tip of one of the sepals developed into a large petal-like expansion, coloured either white or purple. The outer flowers in several Acanthaceous genera are large and conspicuous but sterile; the next in order are smaller, open, moderately fertile and capable of cross-fertilisation; whilst the central ones are cleistogamic, being still smaller, closed and highly fertile; so that here the inflorescence consists of three kinds of flowers.* From what we know in other cases of the use of the corolla, coloured bractæ, &c., and from what H. Müller has observed† on the frequency of the visits of insects to the flower-heads of the Umbelliferæ and Compositæ being largely determined by their conspicuousness, there can be no doubt that the increased size of the corolla of the outer flowers, the inner ones being in all the above cases small, serves to attract insects. The result is that cross-fertilisation is thus favoured. Most flowers wither soon after being fertilised, but Hildebrand states‡ that the ray-florets of the Compositæ last for a long time, until all those on the disc are impregnated; and this clearly shows the use of the former. The ray-florets,

* J. Scott, 'Journal of Botany,' London, new series, vol. i. 1872, pp. 161-164.

† 'Die Befruchtung der Blu-

men,' pp. 108, 412.

‡ See his interesting memoir, 'Ueber die Geschlechtsverhältnisse bei den Compositen,' 1869, p. 92.

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however, are of service in another and very different manner, namely, by folding inwards at night and during cold rainy weather, so as to protect the florets of the disc.* Moreover they often contain matter which is excessively poisonous to insects, as may be seen in the use of flea-powder, and in the case of *Pyrethrum*, M. Belhomme has shown that the ray-florets are more poisonous than the disc-florets in the ratio of about three to two. We may therefore believe that the ray-florets are useful in protecting the flowers from being gnawed by insects.†

It is a well-known yet remarkable fact that the circumferential flowers of many of the foregoing plants have both their male and female reproductive organs aborted, as with the *Hydrangea*, *Viburnum* and certain *Compositæ*; or the male organs alone are aborted, as in many *Compositæ*. Between the sexless, female and hermaphrodite states of these latter flowers, the finest gradations may be traced, as Hildebrand has shown.‡ He also shows that there is a close relation between the size of the corolla in the ray-florets and the degree of abortion in their reproductive organs. As we have good reason to believe that these florets are highly serviceable to the plants which possess them, more especially by rendering the flower-heads conspicuous

* Kerner clearly shows that this is the case: 'Die Schutzmittel des Pollens,' 1873, p. 28.

† 'Gardener's Chronicle,' 1861, p. 1067. Lindley, 'Vegetable Kingdom,' on *Chrysanthemum*, 1853, p. 706. Kerner in his interesting essay ('Die Schutzmittel der Blüthen gegen unberufene Gäste,' 1873, p. 19) insists that the petals of most plants contain matter which is offensive to insects, so that they are seldom

gnawed, and thus the organs of fructification are protected. My grandfather in 1790 ('Loves of the Plants,' canto iii. note to lines 184, 188) remarks that "The flowers or petals of plants are perhaps in general more acrid than their leaves; hence they are much seldomer eaten by insects."

‡ 'Ueber die Geschlechtsverhältnisse bei den *Compositen*,' 1869, pp. 78-91.

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to insects, it is a natural inference that their corollas have been increased in size for this special purpose; and that their development has subsequently led, through the principle of compensation or balance-ment, to the more or less complete reduction of the reproductive organs. But an opposite view may be maintained, namely, that the reproductive organs first began to fail, as often happens under cultivation,* and, as a consequence, the corolla became, through compensation, more highly developed. This view, however, is not probable, for when hermaphrodite plants become dicecious or gyno-dicecious—that is, are converted into hermaphrodites and females—the corolla of the female seems to be almost invariably reduced in size in consequence of the abortion of the male organs. The difference in the result in these two classes of cases, may perhaps be accounted for by the matter saved through the abortion of the male organs in the females of gyno-dicecious and dicecious plants being directed (as we shall see in a future chapter) to the formation of an increased supply of seeds; whilst in the case of the exterior florets and flowers of the plants which we are here considering, such matter is expended in the development of a conspicuous corolla. Whether in the present class of cases the corolla was first affected, as seems to me the more probable view, or the reproductive organs first failed, their states of development are now firmly correlated. We see this well illustrated in *Hydrangea* and *Viburnum*; for when these plants are cultivated, the corollas of both the interior and exterior flowers become largely developed, and their reproductive organs are aborted.

* I have discussed this subject xviii. 2nd edit. vol. ii. pp. 152, in my 'Variation of Animals and 156. Plants under Domestication,' chap.

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There is a closely analogous subdivision of plants, including the genus *Muscari* (or Feather Hyacinth) and the allied *Bellevalia*, which bear both perfect flowers and closed bud-like bodies that never expand. The latter resemble in this respect cleistogamic flowers, but differ widely from them in being sterile and conspicuous. Not only the aborted flower-buds and their peduncles (which are elongated apparently through the principle of compensation) are brightly coloured, but so is the upper part of the spike—all, no doubt, for the sake of guiding insects to the inconspicuous perfect flowers. From such cases as these we may pass on to certain Labiatae, for instance, *Salvia Horminum*, in which (as I hear from Mr. Thiselton Dyer) the upper bracts are enlarged and brightly coloured, no doubt for the same purpose as before, with the flowers suppressed.

In the Carrot and some allied Umbelliferae, the central flower has its petals somewhat enlarged, and these are of a dark purplish-red tint; but it cannot be supposed that this one small flower makes the large white umbel at all more conspicuous to insects. The central flowers are said* to be neuter or sterile, but I obtained by artificial fertilisation a seed (fruit) apparently perfect from one such flower. Occasionally two or three of the flowers next to the central one are similarly characterised; and according to Vaucher† “cette singuliere dégénération s’étend quelquefois à l’ombelle entière.” That the modified central flower is of no functional importance to the plant is almost certain. It may perhaps be a remnant of a former and ancient condition of the species, when one flower alone, the

* ‘The English Flora,’ by Sir J. E. Smith, 1824, vol. ii. p. 39.

† ‘Hist. Phys. des Plantes

d’Europe,’ 1841, tom. ii. p. 614.
On the *Echinophora*, p. 627.

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central one, was female and yielded seeds, as in the umbelliferous genus *Echinophora*. There is nothing surprising in the central flower tending to retain its former condition longer than the others; for when irregular flowers become regular or peloric, they are apt to be central; and such peloric flowers apparently owe their origin either to arrested development—that is, to the preservation of an early stage of development—or to reversion. Central and perfectly developed flowers in not a few plants in their normal condition (for instance, the common Rue and *Adoxa*) differ slightly in structure, as in the number of the parts, from the other flowers on the same plant. All such cases seem connected with the fact of the bud which stands at the end of the shoot being better nourished than the others, as it receives the most sap.*

The cases hitherto mentioned relate to hermaphrodite species which bear differently constructed flowers; but there are some plants that produce differently formed seeds, of which Dr. Kuhn has given a list.† With the *Umbelliferæ* and *Compositæ*, the flowers that produce these seeds likewise differ, and the differences in the structure of the seeds are of a very important nature. The causes which have led to differences in the seeds on the same plant are not known; and it is very doubtful whether they subserve any special end.

We now come to our second Class, that of monœcious species, or those which have their sexes separated but borne on the same plant. The flowers necessarily differ, but when those of one sex include rudiments

* This whole subject, including pelorism, has been discussed, and references given, in my 'Variation of Animals and Plants under

Domestication,' chap. xxvi. 2nd edit. vol. ii. p. 338.

† 'Bot. Zeitung,' 1867, p. 67.

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of the other sex, the difference between the two kinds is usually not great. When the difference is great, as we see in catkin-bearing plants, this depends largely on many of the species in this, as well as in the next or diœcious class, being fertilised by the aid of the wind;* for the male flowers have in this case to produce a surprising amount of incoherent pollen. Some few monoœcious plants consist of two bodies of individuals, with their flowers differing in function, though not in structure; for certain individuals mature their pollen before the female flowers on the same plant are ready for fertilisation, and are called proterandrous; whilst conversely other individuals, called proterogynous, have their stigmas mature before their pollen is ready. The purpose of this curious functional difference obviously is to favour the cross-fertilisation of distinct plants. A case of this kind was first observed by Delpino in the Walnut (*Juglans regia*), and has since been observed with the common Nut (*Corylus avellana*). I may add that according to H. Müller the individuals of some few hermaphrodite plants differ in a like manner; some being proterandrous and others proterogynous.† On cultivated trees of the Walnut and Mulberry, the male flowers have been observed to abort on certain individuals‡, which have thus been converted into females; but whether there are any species in a state of nature which co-exist as monoœcious and female individuals, I do not know.

The third Class consists of diœcious species, and the

* Delpino, 'Studi sopra uno Lignaggio Anemofilo.' Firenze, 1871.

† Delpino, 'Ult. Osservazioni sulla Dioecia,' part ii. fasc. ii. p. 337. Mr. Wetterhan and H. Müller on *Corylus*, 'Nature,' vol.

xi. p. 507, and 1875, p. 26. On proterandrous and proterogynous hermaphrodite individuals of the same species, see H. Müller, 'Die Befruchtung,' &c., pp. 285, 339.
‡ 'Gardener's Chron.' 1847, pp. 541, 558.