

ART. XVI.—*Notice of Darwin on the Effects of Cross- and Self-Fertilization in the Vegetable Kingdom*;* by ASA GRAY.

MR. DARWIN, in the title of his new work, refers only incidentally to adaptations for cross-fertilization,—a subject which has given origin to a copious literature since he opened it anew in his book on the Fertilization of Orchids, in 1862. A new edition of this latter book is on the eve of publication in England, and we believe that this author's scattered papers on cross-fertilization, as secured by various contrivances, are about to be collected, revised, and issued in a book form. In the volume now before us, Mr. Darwin deals with the effects of cross- and self-fertilization, recounts at length the experiments he has devised and carried on, collects and criticises the results, glances at the means of fertilization, and the habits of insects in relation to it, and ends with some theoretical considerations or inferences suggested by or deduced from the facts which have been brought to light.

If writing for the popular press, we should be bound to say that this book is not light reading. Three-fourths of its pages and of the chapters are devoted to the details of the experiments and the sifting and various presentation of the results; and the remainder, although abounding in curious facts and acute suggestions, is yet of a solid character. The bearings of various points upon what is called "Darwinism" are merely touched or suggested, here and there, in a manner more likely to engage the attention of the thoughtful scientific than of the general reader.

That cross-fertilization is largely but not exclusively aimed at in the vegetable kingdom, is abundantly evident. As Mr. Darwin declares, "it is as unmistakably plain that innumerable flowers are adapted for cross-fertilization, as that the teeth and talons of a carnivorous animal are adapted for catching prey, or that the plumes, wings, and hooks of a seed are adapted for its dissemination." That the crossing is beneficial, and consequently the want of it injurious, is a teleological inference from the prevalence of the arrangements which promote or secure it,—an inference the value of which increases with the number, the variety, and the effectiveness of the arrangements for which no other explanation is forthcoming. That the good consisted in a re-invigoration of progeny, or the evil of close-breeding in a deterioration of vigor, was the suggestion first made (so far as we know), or first made prominent, by Knight, from whom Darwin adopted it. However it be as to animals, there

* *The Effects of Cross- and Self-Fertilization in the Vegetable Kingdom*; by CHARLES DARWIN, M.A., F.R.S., etc. London: Murray. (New York: D. Appleton & Co.) 12mo, pp. 482. 1876.

was until now no clear and direct evidence that cross-fertilization in the vegetable kingdom did re-invigorate. Indeed, the contrary might be inferred from the long and seemingly indefinite perpetuation of bud-propagating varieties, which have no fertilization at all. But the inference from this is not as cogent as would at first appear. For, although bud-propagation is, we think, to be considered as the extreme of close-breeding, yet in it the amount of material contributed by parent to offspring is usually vastly more than in sexual reproduction; and, accordingly, the diminution to an injurious degree of any inherited quality or essence might be correspondingly remote. Yet, as sexual reproduction may be and often must be much closer in plants than it can be in most animals, the ill effects of self-fertilization, or the good of cross-fertilization, might the sooner be noticeable. Mr. Darwin arranged a course of experiments to test this question, prosecuted it as to some species for eleven years; and the main object of this volume is to set forth the results.

Ipomœa purpurea, the common Morning Glory of our gardens, was the leading subject. The flowers of this species self-fertilize, but must also be habitually cross-fertilized, as they are visited freely by humble-bees and other insects. Ten flowers of a plant in a greenhouse were fertilized with their own pollen; ten others were crossed with pollen from a different plant. The seeds from both were gathered, allowed to germinate on damp sand, and as often as pairs germinated at the same time the two were planted on opposite sides of the same pot, the soil in which was well mixed, so as to be uniform in composition. "The plants on the two sides were always watered at the same time and as equally as possible, and even if this had not been done the water would have spread almost equally to both sides, as the pots were not large. The crossed and self-fertilized plants were separated by a superficial partition, which was always kept directed towards the chief source of the light, so that the plants on both sides were equally illuminated." Five pairs were thus planted in two pots, and all the remaining seeds, whether or not in a state of germination, were planted on the opposite sides of a third pot, so that the plants were crowded and exposed to a very severe competition. Rods of equal diameter were given to all the plants to twine up, and as soon as one of each pair had reached the summit, both were measured. But a single rod was furnished to each side of the crowded pot, and only the tallest plant on each side was measured. This was followed up, for ten generations; the close fertilization being always self-fertilization, i. e., by pollen to stigma of the same flower; the crossing, between individuals in successive generations of this same stock, except in special instances,

when an extraneous stock was used as one parent,—to eminent advantage, as will be seen.

The difference in vigor between the cross-bred and the close-bred progeny, as measured by early growth, was well marked throughout. In the mean of the ten generations it was as 100 to 77. In the tenth generation it was 100 to 54, that is, five cross-bred plants grew to the average height of 93·7 inches while the close-bred were reaching the average of 50·4 inches. This was a notably greater difference than in any previous generation. But this was probably accidental or anomalous; for it was not led up to by successive steps. Indeed, the difference in the first generation was a trifle greater than the average of all ten, being as 100 to 76. The second generation was as 100 to 79; the third as 100 to 68; the fourth as 100 to 86; the fifth as 100 to 75; the sixth as 100 to 72; the seventh as 100 to 81; the eighth as 100 to 85; the ninth as 100 to 79; the tenth, as already stated, 100 to 54. The general result is made striking in the following illustration.

“If all the men in a country were on an average six feet high, and there were some families which had been long and closely inter-bred, these would be almost dwarfs, their average height during ten generations being only four feet eight and one-quarter inches.” (p. 53.)

It is remarkable that the difference between the close-bred and the cross-bred individuals should have been as great as it was in the first generation; and, this being the case, it might have been expected that the difference would have gone on increasing in the succeeding generations. If self-fertilization is injurious, the ill effects would be expected to be cumulative. “But,” instead of this, “the difference between the two sets of plants in the seventh, eighth, and ninth generations taken together is less than in the first and second generations together.” Upon this Mr. Darwin remarks: “When, however, we remember that the self-fertilized and crossed plants are all descended from the same mother plant, that many of the crossed plants in each generation were related, often closely related, and that all were exposed to the same conditions, which, as we shall hereafter find, is a very important circumstance, it is not at all surprising that the difference between them should have somewhat decreased in the later generations.” (p. 56.)

Further light was thrown upon these points by two kinds of subsidiary experiments. In one case, the cross was made between two flowers of the same plant of *Ipomœa*, while other flowers were self-fertilized as before. On raising seedlings from the two lots, it was found that such crossing gave no superiority: indeed, the offspring of the self-fertilized flowers appeared to be rather more vigorous than the close-crossed. And other experi-

ments led to the same conclusion, namely, that there was no particular benefit from cross-fertilization on the same plant. In the other case, the cross was made not only between the flowers of distinct plants, but between those from different sources, and which had presumably grown under somewhat different conditions. For instance, several flowers of the ninth generation of crossed plants of *Ipomœa* were crossed with pollen taken from the same variety, but from a distant garden. The resulting seedlings showed the benefit of the fresh stock remarkably, being as much superior in vigor to those of the tenth inter-crossed generation as the latter were to the self-fertilized plants of the corresponding generation. In height they were as 100 to 78, over the ordinary inter-crossed; and in fertility, as 100 to 51. Indeed, Mr. Darwin's main conclusion from all his observations is, "that the mere act of crossing by itself does no good. The good depends on the individuals which are crossed differing slightly in constitution, owing to their progenitors having been subjected during several generations to slightly different conditions, or to what we call in our ignorance spontaneous variation."

The greater constitutional vigor of the crossed plants of *Ipomœa* was manifested in other ways than their rate or amount of growth; they better endured exposure to a low temperature or sudden changes of temperature; they blossomed earlier; and they were more fertile. The difference in fertility varied greatly in degree (the extremes in different experiments and in different generations being 100 to 99 and 100 to 26), but was always sustained. Also, "the impaired fertility of the self-fertilized plants was shown in another way, namely, by their anthers being smaller than those in the flowers on the crossed plants. This was first observed in the seventh generation, but may have occurred earlier. . . . The quantity of pollen contained in one of the self-fertilized was, as far as could be judged by the eye, about half of that contained in one from a crossed plant. The impaired fertility of the self-fertilized plants of the eighth generation was also shown in another manner, which may often be observed in hybrids—namely, by the first-formed flowers being sterile."

Similar experiments were made, but not carried to the same extent, upon fifty-seven other species of plants, belonging to fifty-two genera, and to thirty great natural families, the species being natives of various parts of the world. The results—the details and discussion of which occupy the bulk of this volume—vary greatly, some plants making a better, and others a less good showing for the advantage of cross-fertilizing, and this advantage manifesting itself in different ways, some in vigor or amount of growth, some in hardiness, most in fertility; but

with twelve cases in which the crossed plants show no marked advantage over the self-fertilized. There were, however, fifty-seven cases in which the crossed exceeded the self-fertilized by at least five per cent, generally by much more.

Increase of vigor, as evinced in growth, appears generally to be accompanied by increased fertility; but sometimes the good of crossing was manifested only in productiveness, i. e., in a larger amount of seed. This proved to be the case in *Eschscholtzia*, in which—strange to say—self-fertilized plants of several generations were superior in size and weight to inter-crossed plants, even when the crossing was between flowers derived on one side from American, on the other from English seed, from which, upon Mr. Darwin's view, the maximum benefit should be gained. This instance, however, stands alone. Yet it is approached by several others, in a manner which might have negatived the general conclusions of the research, if they had been hastily gathered from a small number of trials.

For example, in the sixth self-fertilized generation of *Ipomœa purpurea*, one of these plants took the lead of its competitor, kept it almost to the end, and was ultimately overtopped only by half an inch on a total height of several feet. To ascertain whether this exceptionally vigorous plant would transmit its power to its seedlings, several of its flowers were fertilized with their own pollen, and the seedlings thus raised were put into competition with ordinary self-fertilized and with inter-crossed plants of the corresponding generation. The six children of Hero (the name by which this individual was designated), beat the ordinary self-fertilized competitors at the rate of 100 to 84, and the inter-crossed competitors at the rate of 100 to 95; and in the next generation the self-fertilized grand-children beat those from a cross between two of the children at the rate of 100 to 94. In the next generation the seedlings were raised in winter in a hot-house, became unhealthy, and the experiment terminated without marked result. Moreover the remarkable vigor of growth in Hero and its progeny was attended by somewhat increased fertility. Here, then, an idiosyncrasy arose, from some utterly unknown cause,—a spontaneous variation of constitution, which was transmitted to posterity, and which gave all the benefit of cross-fertilization, and somewhat more, both as to vigor and fertility. A similar idiosyncrasy made its appearance in the third generation of seedlings of *Mimulus luteus*.

Discordant or anomalous facts like these seem confusing, even though too few to affect seriously the grand result of the numerous experiments; but upon Darwinian principles, in which adaptations are ultimate results, they are to be expected, as a consequence of the general and apparently vague proclivity to vary.

In Foxglove,—the flowers of which are naturally self-sterile or nearly so, and in which crossing gave a marked advantage over self-fertilizing, both as to growth and productiveness,—a decided, though small advantage, appeared to come from the crossing of flowers on the same plant.

In *Origanum vulgare*, crosses were made between different plants of a large clump, long cultivated in a kitchen-garden, which had evidently spread from a single root by stolons, and which had become in a good degree sterile, as is usual under such conditions. The crossing caused rather more seed to form; but the seedlings from the crossed did not surpass in growth those of the self-fertilized; “a cross of this kind did no more good than crossing two flowers on the same plant of *Ipomœa* or *Mimulus*. Turned into the open ground, and both self- and cross-fertilized the following summer, and equal pairs of the resulting seeds planted on opposite sides of two very large pots, the crossed plants from seed showed a clear superiority over their self-fertilized brethren, at the rate of 100 to 86. But this excess of height by no means gives a fair idea of the vast superiority in vigor of the crossed over the self-fertilized plants. The crossed flowered first and produced thirty flower-stems, while the self-fertilized produced only fifteen, or half the number. The pots were then bedded out, and the roots probably came out of the holes at the bottom, and thus aided their growth. Early in the following summer, the superiority of the crossed plants, owing to their increase by stolons, over the self-fertilized plants, was truly wonderful. . . . Both the crossed and the self-fertilized plants being left freely exposed to the visits of bees, manifestly produced much more seed than their grandparents,—the plants of original clumps still growing close by in the same garden, and equally left to the action of bees.”

These few cases must here suffice, and they give a fair general idea of the main results reached,—somewhat qualified, however, by certain instances in which little or no benefit was observed. Let it be remarked that while most of the cases show decided and unequivocal good from the crossing, none of them unequivocally tell to the contrary, as the advantage appears sometimes in one direction, sometimes in another. “Thus, the crossed and self-fertilized plants of *Ipomœa*, *Papaver*, *Reseda odorata*, and *Limnanthes* were almost equally fertile, yet the former exceeded considerably in height the self-fertilized plants. On the other hand the crossed and self-fertilized plants of *Mimulus* and *Primula* differed to an extreme degree in fertility, but by no means to a corresponding degree in height or vigor.”

We must wholly omit—among many other things—the interesting account of self-sterile plants, meaning here

not those in which the pollen does not reach the stigma unaided, but those in which it is impotent, or nearly so, when applied, although efficient upon the stigma of another individual. *Verbascum*, *Passiflora*, *Corydalis*, and many Orchids afford instances of this sort. In these the advantage of cross-fertilization rises to a necessity. A noteworthy fact respecting them (of which Mr. Darwin makes much) is, that such self-sterility, or the reverse, is influenced by slight changes in the conditions, such as difference in temperature, grafting on another stock, and the like. In South Brazil, Fritz Müller found that for six generations all his plants of *Eschscholtzia Californica* were completely sterile, unless supplied with pollen from a distinct plant, when they were completely fertile. This was not the case in English plants, which, when covered by a net, set a considerable number of capsules, the seeds of which, by weight, were as 71 to 100 of those on plants intercrossed by bees. These Brazilian seeds, sent to England, yielded plants with moderately self-fertile flowers, and this limited self-fertility was increased in two generations of English growth. Conversely, seeds from English plants grown in Brazil were more self-fertile than those reared in Brazil for several generations; yet "one which did not flower the first year, and was thus exposed for two seasons to the climate of Brazil, proved quite self-sterile, like a Brazilian plant, showing how quickly the climate had acted on its sexual constitution." Having observed that certain individuals of Mignonette were self-sterile, Mr. Darwin secured several such plants under separate nets, and by inter-crossing these for a few generations, obtained plants which inherited this peculiarity, so that "without doubt a self-sterile race of Mignonette could easily have been established."

Nine of the twelve chapters are devoted strictly to the effects of cross and self-fertilization. The tenth considers the "means of fertilization." Cross-fertilization is favored or ensured by: 1, the separation of the sexes; 2, the maturity of the male and female sexual elements at different periods; 3, dimorphism or even trimorphism; 4, various mechanical contrivances; 5, the more or less complete inefficiency of a flower's own pollen on its stigma, and the prepotency of pollen from any other individual over that from the same plant. We understand that Mr. Darwin is just now occupied in revising and extending his various papers upon these topics, with a view to their publication in a volume. Here he gives a list of plants which, when insects are excluded, are either quite sterile or produce less than half the number of seeds yielded by unprotected plants. This is followed by a list of plants which, when protected from insects, are either quite fertile or yield more than half the number of seeds produced by unprotected plants.

“Each of these lists contains by a mere accident the same number of genera, viz., forty-nine. The genera in the first list include sixty-five species, and those in the second sixty species; the Orchideæ in both being excluded. If the genera in this latter order, as well as in the Asclepiadeæ and Apocynaceæ, had been included, the number of species which are sterile if insects are excluded would have been greatly increased; but the lists are confined to species which were actually experimented on. The results can be considered as only approximately accurate, for fertility is so variable a character, that each species ought to have been tried many times. The above number of species, namely, 125, is as nothing to the hosts of living plants; but the mere fact of more than half of them being sterile within the specified degree, when insects are excluded, is a striking one; for whenever pollen has to be carried from the anthers to the stigma in order to ensure full fertility, there is at least a good chance of cross-fertilization. I do not, however, believe that if all known plants were tried in the same manner, half would be found to be sterile within the specified limits; for many flowers were selected for experiment which presented some remarkable structure; and such flowers often require insect-aid.” (p. 370.)

It is worth noticing that *Trifolium repens* and *T. pratense* (the common white and red clovers) have a place in the first list; *T. arvense* and *T. procumbens* in the second. Darwin refers to Mr. Miner's statement that “in the United States, hive-bees never suck the red clover,” and says it is the same in England, except from the outside through holes bitten by humble-bees; yet that H. Müller has seen them visiting this plant in Germany, for the sake both of pollen and nectar, which latter they obtained by breaking apart the petals. Darwin has not qualified his statement, long ago made, of the complete sterility of red clover protected from insects; but Mr. Meehan asserts that protected plants are fertile in this country, without, however, giving details or the rate of fertility. In *T. arvense*, “the excessively small flowers are incessantly visited by hive and humble-bees; when insects were excluded the flower-heads seem to produce as many and as fine seeds as the exposed heads.”

As to cross-fertilization, “the most important of all the means by which pollen is carried from the anthers to the stigma of the same flower, or from flower to flower, are insects, belonging to the orders of Hymenoptera, Lepidoptera, and Diptera; and in some parts of the world, birds.” In a note the author cites all the cases known to him of birds fertilizing flowers. These are chiefly humming-birds. “In North America they are said to frequent the flowers of *Impatiens*” (for which Gould, Trochilidæ, is referred to as authority, and a reference is given to the Gardeners' Chronicle, which we find relates to something else in South

America); and this is all concerning the United States. Can it be that there are no references in print to the most familiar fact that our humming-bird is very fond of sucking the blossoms of Trumpet Creeper (*Tecoma radicans*) and of Honey-suckles? Both these are, in size and arrangement of parts, well adapted to be thus cross-fertilized.

Flowers are rendered conspicuous to birds and still more to insects, by bright colors. And as "almost every fruit which is devoured by birds presents a strong contrast in color with the green foliage, in order that it may be seen, and its seeds disseminated," so the proportionally large size and the bright colors of the corolla, or in some cases the equally bright hues of adjoining parts of the flower, or of the inflorescence, are correlated to visiting insects,—have come to pass, as Darwin would say, in consequence of the visits of insects, through the advantages in vigor and productiveness gained by cross-fertilization. He is ready to adopt even the idea of Conrad Sprengel, which seemed to be so fanciful, that marks and streaks on the corolla serve as guides to the nectary: for, although insects are well able to discover the nectar without the aid of guiding marks, yet they are of service by facilitating the search and enabling insects to suck a greater number of blossoms within a given time, which is tantamount to greater opportunity for cross-fertilization.

That odors attract insects is certain and many flowers are both conspicuous and odoriferous, while others make up in fragrance what they lack in show. "Nägeli affixed artificial flowers to branches, scenting some with essential oils, and leaving others unscented; and insects were attracted to the former in an unmistakable manner."

"Of all colors white is the prevailing one; and of white flowers a considerably larger proportion smell sweetly than of any other color, namely, 14·6 per cent; of red, only 8·2 per cent are odoriferous. The fact of a larger proportion of white flowers smelling sweetly may depend in part on those which are fertilized by moths requiring the double aid of conspicuousness in the dusk and of odor. So great is the economy of nature, that most flowers which are fertilized by crepuscular or nocturnal insects emit their odor chiefly or exclusively in the evening. Some flowers, however, which are highly odoriferous depend solely on this quality for their fertilization, such as the night-flowering stock (*Hesperis*) and some species of *Daphne*; and these present the rare case of flowers which are fertilized by insects being obscurely colored."

"The shape of the nectary and of the adjoining parts are likewise related to the particular kinds of insects which habitually visit the flowers; this has been well shown by H. Müller by his comparison of lowland species, which are chiefly visited by bees, with Alpine species belonging to the same genera, which are visited by butterflies."

“Pollen contains much nitrogen and phosphorus—the two most precious of all the elements for the growth of plants—but in the case of most open flowers, a large quantity of pollen is consumed by pollen-devouring insects, and a large quantity is destroyed during long-continued rain. With many plants this latter evil is guarded against, as far as is possible, by the anthers opening only during dry weather, by the position and form of some or all of the petals, by the presence of hairs, etc.; also, as Kerner has shown in his interesting essay, by the movements of the petals or of the whole flower during cold and wet weather. In order to compensate the loss of pollen in so many ways, the anthers produce a far larger amount than is necessary for the fertilization of the same flower. I know this from my own experiments on *Ipomœa*, given in the Introduction; and it is still more plainly shown by the astonishingly small quantity produced by cleistogone flowers, which lose none of their pollen, in comparison with that produced by the open flowers borne by the same plants; and yet this small quantity suffices for the fertilization of all their numerous seeds. Mr. Hassall took pains in estimating the number of pollen-grains produced by a flower of the Dandelion, and found the number to be 243,600, and in a *Pæony* 3,654,000 grains. The editor of the ‘*Botanical Register*’ counted the ovules in the flowers of *Wisteria sinensis*, and carefully estimated the number of pollen-grains, and he found that for each ovule there were 7,000 grains.” (pp. 376, 377.)

These are probably fair averages of the numerical ratio of pollen to ovules in flowers which are adapted to be fertilized by insect agency. Their meaning in “the economy of nature” is seen by a comparison on the one hand with *anemophilous*, i. e., wind-fertilized, flowers, in most of which there is a vastly greater disproportion between the numbers—compensating for inevitable waste—and on the other with *cleistogenous* flowers, namely those small and less developed blossoms which some plants produce in addition to the ordinary sort, and which fertilize as it were in the bud, necessarily by their own pollen. Here is no waste, and accordingly the anthers are very small, and the pollen-grains not many times more than the ovules: also such flowers are never brightly colored, never odoriferous, and they never secrete nectar.

The only advantages of this close-fertilization which we can think of are sureness and strict likeness; both of which are quite as well secured by budding-reproduction. Now, as cleistogone flowers are borne, we believe, chiefly and perhaps only, by species whose normal blossoms are adapted for insect-fertilization, they must be regarded as a subsidiary arrangement, a safeguard against failure of proper insect-visitation. As the volume before us amply shows, this failure is in general provided for by a more or less wide margin of self-fertilization

in the very flowers which are adapted for crossing. In *Impatiens*, *Viola*, and the like, it is provided for by separate flowers, the special adaptations of which are unmistakable.

H. Müller appears to have shown "that large and conspicuous flowers are visited much more frequently and by many more kinds of insects than are small inconspicuous flowers. He further remarks that the flowers which are rarely visited must be capable of self-fertilization, otherwise they would quickly become extinct." Mr. Darwin's list seems to show that, as a rule, they are so; yet many very small flowers, like those of *Trifolium arvense*, and small and dingy ones, like those of *Asparagus*, are freely visited by bees; and, conversely, many large and conspicuous flowers which are frequented by insects are none the less self-fertilizable. Throughout we find that such things do not conform to arbitrary or fixed rules; and this favors the idea that the differences have been acquired. Mr. Darwin conjectures that the self-fertilizing capabilities of many small and inconspicuous flowers may be comparatively recent acquisitions, on the ground that, if they were not occasionally intercrossed, and did not profit by the process, all their flowers would have become cleistogenous, "as they would thus have been largely benefited by having to produce only a small quantity of safely protected pollen."

Mr. Darwin's experiments tending to prove that cross-fertilization between flowers on the same plant is of little or no use, he is naturally led to consider the means which favor or ensure their fertilization with pollen from a distinct plant. This must needs take place with dioecious plants, and is likely to occur with the monoecious, and is in some cases secured (as in Walnut and Hazelnut) by some trees being proterandrous and others proterogynous, so that they will reciprocally fertilize each other. In ordinary hermaphrodite species the expansion of only a few blossoms at a time greatly favors the intercrossing of distinct individuals, although, in the case of small flowers it is attended with the disadvantage of rendering the plants less conspicuous to insects. Our common Sundews furnish a good illustration of this. They abound wherever they occur, and are for a long while in blossom, but each plant or spike opens but one flower at a time. The fact of bees visiting the flowers of the same species as long as they can, instead of promiscuously feeding from the various blossoms nearest within reach, greatly favors such intercrossing. So does the remarkable number of flowers which bees are able to visit in a short time (of which mention will be made), and the fact that they are unable to perceive without entering a flower whether other bees have exhausted the nectar. Then dichogamy (the maturation of one sex in a hermaphrodite flower earlier than

the other) is so prevalent that it may almost be regarded as the rule; and this ensures such crossing between few-flowered plants, and greatly favors it in the case of spikes, racemes, and the like. For, proterandry being the commonest arrangement, so that the younger flowers act as male, and the older as female, and bees habitually alighting at the bottom and proceeding upward, they carry the pollen from the upper and younger flowers to stigmas of the lower and older flowers of the next spike, and so on. Heterogonism (see this Journal for December, p. 82), which is less common, operates precisely like complete dioecious separation of the sexes in this respect, and with the advantage that all the individuals are seed-bearing. Most of the special arrangements peculiar to certain families, such as Orchids, or to plants—such as *Posoqueria*, with its wondrous mechanism for quickly stopping out access to the stigma when the pollen is violently discharged upon some insect, but opening the orifice the next day—are of a kind to favor the crossing of distinct plants. Prepotency of other pollen, which may accompany the other arrangements or exist independently, acts largely and powerfully toward the same end. Our author investigates this at some length: we cite for illustration a single but a strong case. The stigmas of a long-styled Cowslip were supplied with pollen from the same plant, and again, after twenty-four hours, with pollen of a short-styled, dark-red Polyanthus, a variety of the same species: from the resulting seeds twenty seedlings were raised, and all of them bore reddish flowers; so that the effect of the plant's own pollen, though placed on the stigmas twenty-four hours previously, was destroyed by that of the red variety. The same thing is shown by the impossibility in many cases of raising two varieties of the same species pure if they grow near each other. "No one who has had any experience would expect to obtain pure cabbage-seed, for instance, if a plant of another variety grew within 200 or 300 yards." And a veteran cultivator once had his whole stock of seeds seriously bastardized by some plants of purple Kale which flowered in a cottager's garden half a mile away. Mr. Gordon records a case of the crossing between Primroses and Cowslips through pollen carried by bees over more than two kilometers, or an English mile and a quarter.

We must copy the close of this section—long though it be—because of its capital illustration of the topic in hand, and for the teleological lesson which it teaches.

"The case of a great tree covered with innumerable hermaphrodite flowers, seems at first sight strongly opposed to the belief in the frequency of intercrosses between distinct individuals. The flowers which grow on the opposite sides of such a tree will have been exposed to somewhat different conditions, and a cross

between them may perhaps be in some degree beneficial; but it is not probable that it would be nearly so beneficial as a cross between flowers on distinct trees, as we may infer from the inefficiency of pollen taken from plants which have been propagated from the same stock, though growing on separate roots. The number of bees which frequent certain kinds of trees when in full flower is very great, and they may be seen flying from tree to tree more frequently than might have been expected. Nevertheless, if we consider how numerous are the flowers, for instance, on a Horse-chestnut or Lime-tree, an incomparably larger number of flowers must be fertilized by pollen brought from other flowers on the same tree, than from flowers on a distinct tree. But we should bear in mind that with the Horse-chestnut, for instance, only one or two of the several flowers on the same peduncle produce a seed; and that this seed is the product of only one out of several ovules within the same ovarium. Now we know from the experiments of Herbert and others that if one flower is fertilized with pollen which is more efficient than that applied to the other flowers on the same peduncle, the latter often drop off; and it is probable that this would occur with many of the self-fertilized flowers on a large tree, if other and adjoining flowers were cross-fertilized. Of the flowers annually produced by a great tree, it is almost certain that a large number would be self-fertilized; and if we assume that the tree produced only 500 flowers, and that this number of seeds were requisite to keep up the stock, so that at least one seedling should hereafter struggle to maturity, then a large proportion of the seedlings would necessarily be derived from self-fertilized seeds. But if the tree annually produced 50,000 flowers, of which the self-fertilized dropped off without yielding seeds, then the cross-fertilized flowers might yield seeds in sufficient number to keep up the stock, and most of the seedlings would be vigorous from being the product of a cross between distinct individuals. In this manner the production of a vast number of flowers, besides serving to entice numerous insects and to compensate for the accidental destruction of many flowers by spring-frosts or otherwise, would be a very great advantage to the species; and when we behold our orchard-trees covered with a white sheet of bloom in the spring, we should not falsely accuse Nature of wasteful expenditure, though comparatively little fruit is produced in the autumn."

The Horse-chestnut is not altogether a well-chosen example, for in it, as in our Buckeyes, a very large proportion of the flowers in the thyrsus are usually male, with barely a vestige of pistil. These serve, however, to increase the show, in the manner here illustrated, as well as to furnish abundance of pollen.

The section on anemophilous (wind-fertilized) plants,—their interest as survivals of the earlier phænogamic vegetation,—the speculation as to how, when flying insects came to prevail, an anemophilous plant may have been rendered entomophi-

lous,—how pollen, being a most nutritious substance, would soon have been discovered and devoured by insects, and by adhering to their bodies be carried from anthers to stigma and from one flower to another,—how a waste secretion, such as honey-dew or glandular exudations, may have been developed into nectar and utilized as a lure,—the interesting illustrations of the vast amount of pollen produced by anemophilous plants, and the great distances to which their light pollen is often carried by the wind,—all these inviting topics we must now pass by.

In passing we note the remark that “the excretion of a sweet liquid by glands seated outside of a flower is rarely utilized as a means of cross-fertilization by the aid of insects;” and the sole exception alluded to is that of the bracts of *Marcgraviaceæ*. But a parallel case is afforded by many species of *Euphorbia*, and notably in a striking species cultivated in conservatories, under the name of *Poinsettia*. Here the attraction to the eye is supplied by the intense red coloration of ordinary leaves placed next to the inflorescence, and that to the palate or tongue (if either term may be allowed), by a large cup-shaped gland on the side of the involucre, which contains or surrounds the naked and greatly simplified flowers of both sexes.

That anemophilous plants are prevailing diclinous (either monœcious or dioecious) is speculatively connected with their antiquity; that they are very largely trees or shrubs is because “the long life of a tree or bush permits of the separation of the sexes with much less risk of evil from impregnation occasionally failing, and seeds not being produced, than in the case of short-lived plants. Hence it probably is, as Lecoq has remarked, that annual plants are rarely dioecious.” The number of anemophilous species is comparatively small, but that of individuals of the species strikingly large, so that they form of themselves, in cold and temperate regions, where plant-fertilizing insects are fewer, either vast forests, as of Coniferæ, birches, beeches, etc., or meadows, and glades, as of grasses, sedges, and rushes. Being thus either necessarily or prevailingly cross-fertilizable and gregarious, it is not wonderful that they should hold their own unchanged in various parts of the world. Still their advantage is gained at the expense of the production of an enormous superfluity of pollen, a costly product; and, when dioecious, half the individuals produce no seed. Hermaphroditism with dichogamy, or some equivalent, and transportation by an appeal to the senses and appetites of insects, secures all the advantages with least expenditure. The earliest fertilization in plants took place by the locomotion of the fertilizing or even of the fertilized material, in manner of most of the *Algæ*: mainly losing this as vegetation became terrestrial, the transpor-

tation was committed to the winds, and finally in the higher plants more economically consigned to insects.

The eleventh chapter, on the habits of insects in relation to the fertilization of flowers, is one of the interesting and readable, although the shortest. It appears that the prince of naturalists, Aristotle, had observed more than 2000 years ago that the hive-bee visited the flowers of the same species as long as possible before going to a different species. This holds true of all kinds of bees and certain other insects, generally, but not absolutely. Although, as Lubbock has recently proved, bees are much guided by color, yet they hold to the practice just mentioned in spite of difference in this respect, being botanists enough to know that color is not a good specific character. Mr. Darwin has repeatedly seen humble-bees flying straight from a red *Fraxinella* to a white variety, from one Larkspur to a different colored variety, and the same as to Primroses and Pansies. But two species of Poppy were by some bee treated as one; and H. Müller traced hive-bees from blue hyacinths to blue violets. On the other hand, Darwin's bees fly straight from clump to clump of a yellow *Oenothera* without turning an inch from their course to *Eschscholtzias* with yellow flowers which abound on either side. This constancy to species, however, is manifested only when their flowers abound; a fact which may have led Mr. Darwin to his explanation of the reason of it.

“The cause probably lies in insects being thus enabled to work quicker; they have just learnt how to stand in the best position on the flower, and how far and in what direction to insert their proboscides.* They act on the same principle as does an artificer who has to make half-a-dozen engines, and who saves time by making consecutively each wheel and part for all of them. Insects, or at least bees, seem much influenced by habit in all their manifold operations; and we shall presently see that this holds good in their felonious practice of biting holes through the corolla.” (p. 420.)

As to this latter practice —

“The motive which impels bees to gnaw holes through the corolla seems to be the saving of time, for they lose much time in climbing into and out of large flowers, and in forcing their heads into closed ones. They were able to visit nearly twice as many flowers, as far as I could judge, of a *Stachys* and *Pentstemon* by alighting on the upper surface of the corolla and sucking through the cut holes, than by entering in the proper way. Nevertheless each bee before it has had much practice, must lose some time in making each new perforation, especially when the perforation has to be made through both calyx and corolla. This action therefore implies foresight, of which faculty we have abundant evidence in

* H. Müller had come to the same conclusion.

their building operations; and may we not further believe that some trace of their social instinct, that is, of working for the good of other members of the community, may here likewise play a part? Many years ago I was struck with the fact that humble-bees as a general rule perforate flowers only when these grow in large numbers near together," etc., etc. (p. 433.)

It appears that the cutting of these holes is done only by humble-bees, never by hive-bees. Yet the latter are quick to take advantage of them.

"In the early part of the summer of 1857 I was led to observe during some weeks several rows of the scarlet kidney-bean (*Phaseolus multiflorus*), whilst attending to the fertilization of this plant, and daily saw humble- and hive-bees sucking at the mouths of the flowers. But one day I found several humble-bees employed in cutting holes in flower after flower; and on the next day every single hive-bee, without exception, instead of alighting on the left wing-petal and sucking the flower in the proper manner, flew straight without the least hesitation to the calyx, and sucked through the holes which had been made only the day before by the humble-bees; and they continued this habit for many following days. Mr. Belt has communicated to me (July 28th, 1874) a similar case, with the sole difference that less than half of the flowers had been perforated by the humble-bees; nevertheless, all the hive-bees gave up sucking at the mouths of the flowers and visited exclusively the bitten ones. Now how did the hive-bees find out so quickly that holes had been made? Instinct seems to be out of the question, as the plant is an exotic. The holes cannot be seen by bees whilst standing on the wing-petals, where they had always previously alighted. From the ease with which bees were deceived when the petals of *Lobelia Erinus* were cut off, it was clear that in this case they were not guided to the nectar by its smell; and it may be doubted whether they were attracted to the holes in the flowers of the *Phaseolus* by the odor emitted from them. Did they perceive the holes by the sense of touch in their proboscides, whilst sucking the flowers in the proper manner, and then reason that it would save them time to alight on the outside of the flowers and use the holes? This seems almost too abstruse an act of reason for bees; and it is more probable that they saw the humble-bees at work, and understanding what they were about, imitated them and took advantage of the shorter path to the nectar. Even with animals high in the scale, such as monkeys, we should be surprised at hearing that all the individuals of one species within the space of twenty-four hours understood an act performed by a distinct species, and profited by it." (pp. 430, 431.)

But we must cut short our citations and remarks; passing by one of the most important points, relative to the amount of fertilizing work done by insects, namely, the evidence of the

extraordinary industry of bees and the number of flowers visited within a short time; which, as well as the distance to which pollen is sometimes transported, is far greater than one would have supposed. But the volume is reprinting by the Appletons, and will soon be within the reach of all,—along with a new edition of the orchid-fertilization book, the proper supplement to the present work, relating as it does to the class of plants in which the adaptation for fertilization by insects is carried to the highest degree of specialization and perfection.

ART. XVII.—*Note on Microdiscus speciosus*; by S. W. FORD.

IN my original description of this interesting Trilobite (this Journal, August, 1873) it is stated that the thorax is composed of four equal segments. The description, in so far as relates to this part of the animal organization, was drawn up from the study of a single specimen, showing the head, thorax and pygidium in nearly their natural positions, and apparently offering decisive testimony as to the true number of body-rings. Somewhat more than a year ago, however, I obtained from the Troy beds another specimen, of almost precisely the same dimensions, showing clearly but *three* segments in the thorax; and, subsequently, a much larger specimen showing the same number. This led me to re-examine, more critically, the specimen employed in the original description, when it was found that the head had slipped slightly forward, and that what I had regarded as the first pleura (all of the pleuræ of one side, as well as one-half of the head, being enveloped in the matrix) was a fragment of some foreign body that had fallen into the gap thus made. The deception, in the first instance, was rendered all the more complete from the fact that, by the displacement of the head alluded to, the articular fold of the first body-ring, which is ordinarily wholly hidden from view by the backward prolongation of the glabella, was exposed, thus making a very good case for a fourth segment. I now consider it certain that this species has never more than three body-rings. I have in my collection a small rolled-up specimen showing the extremities of but two body-segments, and I was at first led to think it possible that we had in this species an example of the metamorphoses of Trilobites, concerning which Barrande has taught us so much. But as I have observed since this specimen was obtained, an individual of even smaller size, with three perfectly formed body-segments, this notion is without foundation at the present time. I should here also add that the last body-