THURSDAY, FEBRUARY 15, 1877

DARWIN ON FERTILISATION

The Effects of Cross- and Self-Fertilisation in the Vegetable Kingdom. By Charles Darwin, M.A., F.R.S., &c. (London: John Murray, 1876.)

FEW as are the students of vegetable physiology in this country, it is very far from a mere boast to say that, with Mr. Darwin's aid, we have no reason to shrink from comparing English work in this subject with that done abroad. Mr. Darwin has sometimes lamented that he is not a botanist, yet it would be difficult to name any scientific man with an accepted claim to that description who could point to more valuable botanical work than his studies of heterostyled plants, the fertilisation of orchids, and the habits of climbing and insectivorous plants. As to the present volume, there is no risk whatever in stating that it at once takes and will always retain a classical position in botanical literature. And when one considers that these are not the only things which have come during late years from the same apparently inexhaustible treasury, and when one remembers also that the great student who has filled it has throughout struggled with difficulties which would have effectually quenched the energy of most men, one may allow oneself to wonder whether Mr. Darwin's own scientific activity is not itself a more than remarkable biological problem.

There can be no doubt that the publication of the present work is extremely opportune. An enormous body of observations, of which a great part have been brought together by Dr. Hermann Müller, have solidly confirmed the well-known induction stated by Mr. Darwin in 1862, that "nature abhors perpetual self-fertilisation." Most persons who have studied the subject have been satisfied that the facts safely covered the conclusion that the varied adaptive contrivances in flowers really had for their object the prevention of self- and the promotion of cross-fertilisation, even if nature chose to preserve an impregnable silence as to the reason of her abhorrence of the former process. There have not, however, been wanting those who have attempted to explain away the significance of all that had been stated. Not seeing the mischief of self-fertilisation, they have hastily assumed that it had none, and thence have arrived at the conclusion that the cause of the adaptive modification of flowers must be sought for elsewhere.

At any one period the area of knowledge is always bounded by a wall too high to see over, and against which it is easy but not profitable to bruise one's head. It is difficult to say whether it requires more genius to scale the wall at one dash or to pass out by the doors which are everywhere provided for those with eyes to see them. And though no one would have the rashness to suggest that there was anything defective in Mr. Darwin's scientific vision, yet there is some comfort to be derived from the fact that he gives from his own experience a most instructive instance of the real difficulty that even the greatest of investigators may feel in emancipating himself from the limits which prepossession—conscious or unconscious—constantly opposes to the progress of research. Without, of course, having a shadow of doubt that nature had some need to satisfy in so laboriously struggling to prevent self-fertilisation in plants, Mr. Darwin was content to suppose that it might be injurious in the long run, in some way difficult, at present—if ever—to be analysed, and, to use his own words:—

"That it would be necessary, at the sacrifice of too much time, to self-fertilise and intercross plants during several successive generations in order to arrive at any result. I ought [he continues] to have reflected that such elaborate provisions favouring cross-fertilisation, as we see in innumerable plants, would not have been acquired for the sake of gaining a distant and slight advantage, or of avoiding a distant and slight evil" (p. 8).

In fact an observation almost accidental led the way to the remarkable discoveries recorded in the present volume. Of these an article in the *Academy* (August 28, 1875) by Mr. George Darwin gave, I believe, the first intimation, and raised in the highest degree our expectations. "My father," he stated, "has now been carrying on experiments for about nine years on the crossing of plants, and his results appear to him absolutely conclusive as to the advantages of cross-fertilisation to plants." Mr. Darwin informs us that he was led to the investigation by the manifest contrast presented by "two large beds of self-fertilised and crossed seedlings from the same plant of *Linaria vulgaris*" (p. 9), in which he found to his surprise that "the crossed plants when fully grown were plainly taller and more vigorous than the self-fertilised ones." His "attention was now thoroughly aroused," and two-thirds of the present volume are devoted to the very extended course of experimentation, the results of which Mr. Darwin puts forward in confirmation of the conclusion which his first and accidental observation suggested. These results deserve and will receive the most careful study at the hands of botanists, but it would be scarcely useful within the limits of this notice to examine them in any detail. They appear, however, to me, to demonstrate completely the advantage which cross-fertilised plants obtain in all that concerns their struggle for life—in increase of size, of bulk (as measured by weight), and of fertility, as well as in precocity of flowering and capacity of resisting adverse external influences.

The remainder of the volume is, however, occupied with general discussions, upon which it may be interesting to make some remarks. The process of gamogenesis essentially consists in "the physical admixture of protoplasm derived from two sources." Mr. Darwin's investigations have left no room for even a shadow of a doubt that the object of nature in bringing about this result is to secure for the starting-point of the new organism a protoplasmic mass made up of elements which have been independently individualised or differentiated by exposure to different external conditions. Mr. Herbert Spencer explains this by the need which the manifestation of life involves for continually disturbing the condition of molecular equilibrium to which all things in nature gradually tend. But as Mr. Darwin hints, this mode of explanation scarcely does more than restate the empirical facts which we may now sum up by saying that for gamogenesis to give the best result a certain mean differentiation—varying much for different organisms—in the sexual elements which take part in it is necessary. And in so far as Mr. Spencer's theory suggests an analogy to chemical change, it is perhaps leading us away from the direction of real explanation altogether.

The use of the phrase "mean differentiation" perhaps conveniently expresses Mr. Darwin's ingenious and most probable correlation of the facts of hybridisation with those of self-fertilisation.

"It is an extraordinary fact that with many species, flowers fertilised with their own pollen are either absolutely, or in some degree, sterile; if fertilised with pollen from another flower on the same plant they are sometimes, though rarely, a little more fertile; if fertilised with pollen from another individual or variety of the same species, they are fully fertile; but if with pollen from a distinct species, they are sterile in all possible degrees until utter sterility is reached. We thus have a long series with absolute sterility at the two ends; at one end due to the sexual elements not having been sufficiently differentiated, and at the other end to their having been differentiated in too great a degree, or in some peculiar manner" (pp. 455, 456).

In this mode of regarding phenomena which at first hardly seem to have anything in common, and embracing them under a single "expression," there is a neatness quite mathematical. Mr. Darwin admits, however, with characteristic frankness that in thus breaking down the fundamental difference between species and varieties, he traverses a prejudice which "it will take many years to remove" (p. 467).

But it is possible to go even further and regard gamogenesis and agamogenesis themselves as particular cases of a generalised process. Every organism, whether sexually produced or not, may be regarded as an aggregate of cells derived from a single mass of protoplasm which has undergone repeated division. Fertilisation, as Prof. Huxley has remarked,[1] is only "one of the many conditions which may determine or affect that process." And this remark probably supplies the explanation of the undoubted fact that amongst flowering plants as in every other part of the vegetable kingdom, there is every gradation between plants which are simply incapable of self-fertilisation and therefore would die out if they were not perpetually crossed, and others in which self-fertilisation is the rule.

"Some few plants, for instance, *Ophrys apifera*, have almost certainly been propagated in a state of nature for thousands of generations without having once been intercrossed; and whether they would profit by a cross with a fresh stock is not known. But such cases ought not to make us doubt that, as a general rule, crossing is beneficial, any more than the existence of plants which in a state of nature are propagated exclusively by rhizomes, stolons, &c. (their flowers never producing seeds), should make us doubt that seminal generation must have some great advantage, as it is the common plan followed by nature" (p. 439).

Still there is room for believing that nature may be able to give more or less freely to plants, but in some other way, those benefits which gamogenesis, especially in its more differentiated forms, undoubtedly confers. It may be one of nature's favourite expedients, and yet not the only one. It is highly important to bear this in mind and to keep clearly in view what it is exactly that Mr. Darwin has done. He has explored, and in a manner which had never been attempted, much less accomplished before, the precise utility of cross-fertilisation, and has consequently given enormously increased force to all arguments drawn from the adaptive arrangements that promote it by demonstrating their extreme urgency. But he has not tied nature's hands to doing her work with this implement alone, and therefore he is not open to the objection which some persons will probably urge, that cross-fertilisation cannot be so important, seeing that many plants get on apparently very well without it. This is, indeed, as if one were to argue that the printing-press cannot have had the influence attributed to it, seeing that there have been those who expressed their meaning excellently well with the help of the fore-finger and some sandy soil.

The evidence which Mr. Darwin has collected leads almost irresistibly to the conclusion that the benefit derived from gamogenesis does not depend upon any mysterious property inherent in the process itself, but that "change" is to be regarded as at the bottom of the benefit derived from it; intercrossing, in fact, ceases to be beneficial if the plants crossed have been for many generations exposed to the same conditions. The advantage is, in fact, of the same kind as that which all organisms seem to derive from "an occasional and slight change in the conditions of life." "But the offspring from a cross between organisms which have been exposed to different conditions [and therefore differentiated] profit in an incomparably higher degree than do young or old beings from a mere change in their conditions" (pp. 454, 455), and the reason is that "the blending together of the sexual elements of two differentiated beings will affect the whole constitution at a very early period of life, whilst the organisation is highly flexible." But as change may be of the most variable amount, the corresponding differentiation may be equally variable. In some cases it must be exceedingly small; amongst the *Conjugatæ*, for example, in *Rhynchonema*, two adjacent cells of a filament unite by small lateral processes which bridge over the intervening septum. And the bridge being very narrow, one cell is forced to become the recipient of the contents of the other and the sexual differentiation of the two conjugating cells is thereby established. In *Vaucheria*, where the protoplasm is continuous through the whole vegetative portion of the filamentous organism, the sexual organs are formed by small adjacent processes which are merely parted off from the common protoplasm of the filament which bears them. This must also be an extremely close case of self-fertilisation, but as fertilisation is effected by motile antherozoids, there is a remote possibility of an occasional cross. The hermaphrodite condition in such cases may easily be conceived to have been developed from a stage in which conjugation alone obtains.

It would not be difficult to show that all through the vegetable kingdom the hermaphrodite condition precedes the diœcious. Thus in ferns where the sexual organs are developments of epidermal processes on the peculiar intermediate generation known as the prothallium, there is almost every condition which is met with in flowering plants. The female organs (archegonia), however, require more than one layer of cells for their ultimate development, and are consequently matured later than the male organs (antheridia). Hence ferns tend to be proterandrous and therefore functionally diœcious; and as it fre-

[1] "Encyclopædia Britannica," Art. Biology, p. 687.

quently happens that the young prothallium gets arrested in its development without reaching the stage in which archegonia are produced, such prothallia will be exclusively male by arrest of development. It can hardly be doubted that in an analogous manner male flowers have arisen in diclinous flowering plants. In *Osmunda* amongst ferns the complete diœcious condition is reached. There can, in fact, be no doubt that ferns are habitually cross-fertilised, and there is also good reason to believe that they are even hybridised. It is further noteworthy that whilst in *Osmunda* there is an agamic reproduction of the prothallial generation, in a few rare cases, as pointed out first by Dr. Farlow, the process of gamogenesis is wholly in abeyance and the prothallium gives rise to the spore-bearing stage agamogenetically. One might remark here that the probable absence of true gamogenesis amongst the larger fungi might be compared with this abnormal occurrence in ferns. But another explanation suggests itself. Amongst the *Myxomycetes* the continuous masses of protoplasm which constitute the plant in its active state, segregate into spores which eventually set free zoospores. These swim about to again coalesce into a plasmodium. Sachs has suggested that this coalescence is of a sexual character, and in fact a kind of multi-conjugation; and no doubt the zoospores, in their motile condition, will undergo a certain amount—inconceivably minute it may be—of differentiation, due to slight differences in exposure to external conditions such as heat and light, and thus the end of a more regular sexual process may be attained. In the higher fungi there is nothing exactly comparable with this unless we compare with the fusion of zoospores in the *Myxomycetes* the habitual inosculation and intergrafting of the mycelial threads, the result of which must be to bring about an intermixture of somewhat differentiated protoplasm.

Perhaps, therefore, on a review of Mr. Darwin's remarks on the subject of hermaphroditism (pp. 409, 410), one may demur to his conclusion that the monœcious condition "is probably the first step towards hermaphroditism." It seems not improbable that precisely the converse may be the more true. Mr. Darwin thinks "that as plants became more highly developed and affixed to the ground they would be compelled to become anemophilous in order to intercross. Therefore all plants which have not since been greatly modified would tend still to be both diclinous and anemophilous." But it does not appear that it is intended to limit this statement to flowering plants; yet it would certainly require some modification amongst *Pteridophyta* for example. As we have seen, ferns, at any rate, are not diclinous, nor are they anemophilous, yet they escape all the evil results possibly attending the hermaphrodite condition. The fact is that as long as plants possess motile antherozoids, and their sexual processes take place not in mid-air, but on damp soil, there is no need for the intervention of agencies like the wind or insects to bring about cross-fertilisation. The natural locomotive powers possessed by the antherozoids are sufficient to secure that. The difficulty began when the very limited mobility of the pollen tube was substituted for the amazing activity of the antherozoid. And it will throw a great deal of light on the question as to whether the primordial flower was diclinous or not if one considers the manner in which it probably originated.

In the first place, it must be remembered that the processes which take place in a "flower" are, in a vascular cryptogam, spread over two distinct generations. The drama which once had two acts is now compressed into one. Bearing this in mind, we shall find little difficulty in seeing in the sporangiiferous cone or spike of *Selaginella* the homologue of the flower. For, like that, it is composed essentially of an axis bearing modified lateral appendages, some of which, in this case the upper ones, produce male structures—microspores—and the lower—female ones—macrospores. These bodies fall to the ground, and those from adjacent plants are more or less commingled by the wind before sexual interaction begins to take place. Now, comparing a flower, we find that it also consists of an axis with modified lateral appendages, and if we call the embryo-sac a macrospore and the pollen-grain a microspore, as we are thoroughly justified in doing, then the only important difference between a "*Selaginella*-fructification" and a "flower" is that the position on the axis of microspore- and macrospore-producing structures is inverted.

How, then, do we proceed from one to the other? Simply by prolonging the period during which microspores and macrospores remain attached to the parent plant. Instead of fertilisation being effected on soil moist enough to allow the antherozoids to move, suppose it take place on the parent plant in a comparatively dry atmosphere. Antherozoids are no longer set free by the microspore, which simply puts out processes (of which those from the microspore of *Salvinia*—forming the very rudimentary male prothallia—are a kind of foreshadowing) towards the female organs developed from the macrospore. And there is precedent, for example, amongst the *Saprolegnieæ*, for such a reversion to a mode of fertilisation resembling conjugation (which fertilisation by a pollen tube really is) from a phase of motile antherozoids.

There is a probability, then, that a flower originated by the retention of macrospores (more especially) within the structures of some plant-form not distantly related to *Selaginella*—such a flower would be extremely inconspicuous, destitute of colour—these modifications being only subsequently acquired—and, what is more important, hermaphrodite. Diclinous flowers would arise simply by the arrest of development of either the male or female organs, and this arrest would be only one of the several modes by which nature determines the cross-fertilisation which we now know to be beneficial, and therefore likely to be secured by the self-adjusting process of natural selection. This view, by which flowers are regarded as originally hermaphrodite, instead of, as Mr. Darwin suggests, monœcious, further supplies a very simple explanation of the otherwise almost inexplicable nature of cleistogene flowers. These being inconspicuous and self-fertilising—are probably survivals of the original type.

I am happy to be able to support what I have urged by the following passages from Mr. Bentham's presidential address to the Linnean Society in 1873. Criticising Strasburger's views as to the pedigree of phanerogams (which derived them from the diclinous Conifers), he remarks that if we accept them,

"We must suppose that races, after having once secured the advantages of a total separation of the two sexes and undergone modifications suited to their separate requirements, have again returned to their primitive state of sexual proximity, and commenced a totally different series of modifications destined to counteract the evil effects of that proximity. A much more simple hypothesis would be that Conifers separated from the parent stock before the development of floral envelopes, *the higher Dicotyledons before the separation of the sexes*."

The anemophilous fertilisation of the arborescent plants of cool countries is perhaps rather a climatic adaptation than a survival of a primitive condition, while the cases, of which many have been recorded, in which diclinous plants have produced hermaphrodite flowers—such as the papaw and pitcher-plant in the Glasnevin Botanic Garden described by Dr. Moore—would be easily explicable as the results of atavism, *i.e.*, of reversion to a former hermaphrodite condition. On the other hand Mr. Darwin's suggestion (p. 410) that "if very simple male and female flowers on the same stock each consisting of a single stamen or pistil, were brought close together and surrounded by a common envelope, in nearly the same manner as with the florets of the *Compositæ*, we should have an hermaphrodite flower," offers very considerable morphological difficulties. As a further argument that the flower originates like the fructification of *Selaginella*, by the sexual specialisation of adjacent lateral appendages, one may point out that the early stages in the development of macrospores and microspores are indistinguishable, while in flowering plants there is a reminiscence of this in the case of ovules occasionally being polleniferous.

Difficult as it is to resist discussing the suggestions which everywhere present themselves in this most interesting book, the limits of a review compel me to stop. I will merely point out that here, as in so many cases, investigations undertaken from a purely scientific point of view are not without their practical utility. The precise conditions which Mr. Darwin has ascertained as sufficient to fix in a fleeting variety any particular quality, will be of the last importance in the hands of cultivators.

Just two centuries before the date of this book Sir Thomas Millington, at Oxford (1676), laid the foundation of this branch of investigation by assigning to pollen on theoretical grounds its hitherto unknown function. This it only remained for Bobart, in the Oxford Physick Garden, to experimentally verify (1681). Science is the property of no nation, nevertheless one may feel some pride that the first and the last of the capital discoveries that have been made in respect to plant fertilisation belong to Englishmen.

W. T. THISELTON DYER

OUR BOOK SHELF

Bulletin des Sciences Mathématiques et Astronomiques. Tome dixième. Mars-Juin, 1876. (Paris: Gauthier-Villars.)

WE have no mathematical publication in this country covering quite the same ground as this admirable *Bulletin*. Indeed we hardly think such a journal could survive the issue of half-a-dozen numbers here. The late Mr. T. T. Wilkinson, in an interesting series of notices of "Mathematical Periodicals," points out that such periodicals have "formed a distinguishing feature in our scientific literature for upwards of a century and a half," and quotes a remark of Prof. Playfair (*Edinb. Rev.*, vol. xi.) to the effect that "a certain degree of mathematical science, and, indeed, no inconsiderable degree, is, perhaps, more widely diffused in England than in any other country of the world." These observations have reference principally to such journals as the *Lady's and Gentleman's Diary*.

A very limited circulation, we fear, rewards the editors of the *Quarterly Journal of Mathematics* and the *Messenger of Mathematics*. Nor do we think the state of things would be greatly altered if such a publication as the one before us were started here. The division is mostly a triple one—a review, or reviews, of new mathematical works, followed by an analysis of the contents of current mathematical publications, occasionally supplemented by an original paper.

In the March number we have a long account of Dr. Lindemann's edition of Clebsch's "Vorlesungen über Geometrie" (ersten Bandes erster Theil), a review of Rear-Admiral Sands's "Astronomical and Meteorological Observations" (1871, 1872), an analysis of Dr. Günther's "Lehrbuch der Determinanten—Theorie für Studirende." We have also in this and the other numbers descriptions of the contents of Bellavitis' *Rivista di Giornali*, Catalan and Mansion's *Nouvelle Correspondance Mathématique*, *Mathematische Annalen*, *Giornale di Matematiche*, *Monatsberichte*, and like periodicals. Just noticing the interesting discovery that the Gaussian logarithms (logarithmes d'addition et de soustraction) were first treated of by Leonelli (Avril No., p. 164), his work having been translated into German in 1806, and Gauss having published his table in Zach's *Monatliche Correspondenz* in 1812, we pass on to two notices of mathematical histories. M. E. Hoefer's "Histoire des Mathématiques, depuis leurs Origines jusqu'au Commencement du XIX^{e} Siècle" (Mars No.), comes in for strong condemnation. At the end of the critique we read "nous terminerons cette analyse en exprimant le désir de voir bientôt paraître dans notre langue un ouvrage sur l'histoire des mathématiques, écrit par un mathématicien avec tout le soin que réclame une tâche aussi difficile, et s'adressant, non à *tout le monde*, mais à ceux qui ont intérêt à connaître cette histoire et que leurs études mettent à même de la comprendre." The importance of Hankel's "Zur Geschichte der Mathematik im Alterthum und Mittelalter" in the eyes of the editor may be gathered from the fact that the notice of it takes up thirty-four pages out of the forty-eight. Judging by the extracts and comments the work is one of much research, originality, and interest. "Tel est le résumé bien incomplet du remarquable volume dont nous avons cherché à rendre compte. Nous espérons que ce que nous venons de dire suffira pour engager tous ceux qui s'intéressent à la science à lire le livre de Hankel, et pour en faire désirer une traduction dans notre langue." Is it too much to hope that now we have living amongst us a mathematician whose "great historical treatises are so suggestive of research and so full of its spirit" this country will produce a work to rival M. Hankel's? If it is too much to expect then we hope some one will do for us what the writer in the *Bulletin* desires for his own country.

LETTERS TO THE EDITOR

[The Editor does not hold himself responsible for opinions expressed by his correspondents. Neither can he undertake to return, or to correspond with the writers of, rejected manuscripts. No notice is taken of anonymous communications.]

The Obsidian Cutlers of Melos

DURING a tour in Greece in the past summer I obtained a small number of stone implements chiefly from the Island of Kythera (cerigo) and the Isthmus of Corinth, consisting of a few corn-crushers or pounders, and some celts. The latter are particularly clumsy and very thick in section, and are usually a beach or torrent pebble of suitable form ground to a cutting edge, and sometimes roughened by pecking at the other extremity, as if to afford a firmer grasp for the hand. Their shape