

to cleistogamy, in its ordinary sense it is clear that there is no contradiction between the Knight-Darwin Law and the facts, as Loew has clearly pointed out ("Einführung," p. 144).

After the passage quoted above, Knuth goes on: "In the place of the one-sided law of the above-named naturalists (of which the general truth remains unproven) Müller set up a law, proved directly by Darwin's experiments and indirectly by the reproductive arrangements of plants in general, but especially by those of flowering plants. The law, namely, that 'when the offspring of cross-fertilisation come into serious conflict in the struggle for life with the offspring of self-fertilisation, the former (cross-bred) win the day. Only when this contest is absent can self-fertilisation suffice for reproductions for many generations.'

I confess that this law is to me unsatisfactory. We ask ourselves "when is the struggle between cross- and self-bred offspring<sup>1</sup> absent?" Clearly when all the offspring are of one kind, *i.e.* all cross-bred or all self-bred: in a dioecious plant where all offspring are cross-bred, there is no question of self-fertilisation. In a plant with purely cleistogamic flowers, all offspring would be necessarily self-bred, and the law would imply that cleistogamic perpetuation may suffice. The law, therefore, amounts to this: that self-fertilisation will suffice only when it is unavoidable. This is as much as to say that any form of fertilisation is better than none. It is best to neglect this form of Müller's hypothesis, and to seek his meaning in his simpler and broader statements. In summing up his discussion in the "Historical Introduction," he says ("Fertilisation of Flowers," p. 23): "There is a good foundation, therefore, for the demand that the explanation of floral mechanisms shall rest only on the sufficient and demonstrable assumption that cross-fertilisation yields more vigorous offspring than self-fertilisation."

We have therefore as the chief points in Müller's theory:

(1) Fertilisation at any price.

(2) The increased vigour of cross-bred offspring.

Let us consider these more fully, and first for the conclusion that self-fertilisation is better than no fertilisation. This is a proposition which Müller has insisted on in the most interesting and instructive way, but it surely is not very novel in principle.<sup>2</sup> In a passage already quoted, Darwin reviewing, in 1876, his work of 1862 ("Cross- and Self-Fertilisation," p. 8), says: "I should have added the self-evident proposition that the propagation of the species, whether by self-fertilisation or by cross-fertilisation . . . is of paramount importance. Hermann Müller has done excellent service by insisting repeatedly on this latter point." No one had a higher respect than my father for Müller's work, and he had no disrespectful intention in describing Müller's contribution to the theory as self-evident. The interesting point is that these views did not strike him as original, because they had already occurred to himself.

That Müller based the explanation of floral mechanism on the experimental results of cross-fertilisation cannot be considered as a new departure. I should have imagined it to be notorious that this was Charles Darwin's view, if it were not that we find Knuth and others describing Müller's theory (in which this is the essential thing) as a great law of nature.

In a letter ("Life and Letters," iii. p. 291) to the late Asa Gray (September 10, probably 1866), Charles Darwin wrote: "I have seen the young seedlings from the crossed seed exactly twice as tall as the seedlings from the self-fertilised seed. . . . If I can establish this fact . . . in some fifty cases . . . I think it will be very important, for then we shall positively know why the structure of every flower permits, or favours, or necessitates an occasional cross with a distinct individual."

It seems to me that Charles Darwin's generalisations in regard to flowers may be summed up thus:—

(1) First comes what he called the self-evident proposition that fertilisation of some sort is of paramount importance. This is of the nature of an axiom.

(2) Then comes the direct observation that the vast majority of flowers are open. From this fact alone we should be justified in concluding that there is some advantage in cross- as compared to self-fertilisation, which advantage makes it worth while for flowers to run the risks and incur the expenditure necessarily connected with openness, and avoidable by cleistogamy. The

<sup>1</sup> I use the words *cross-bred* and *self-bred* to denote the offspring of cross- and self-fertilisation; we thus avoid the slightly obscure phrases cross-fertilised and self-fertilised seedlings which occur in Darwin's books.

<sup>2</sup> I am far from wishing to suggest that H. Müller's work does not contain much that is new and valuable; I am here considering only its fundamental bases.

innumerable adaptations for pollen-transport suggest and strengthen the same conclusion. But this is, properly speaking, only an elaboration of the fact that flowers are open.

(3) Direct experiment demonstrates the nature of this surmised advantage of cross-fertilisation over self-fertilisation.

As already pointed out, the Knight-Darwin Law in its usual form, *i.e.* no plant is self-fertilised *ad infinitum*, or in its improved form—"Nature abhors perpetual self-fertilisation"—is a generalisation drawn from observations on structure and experiments on crossing, the value of which in Darwin's opinion was rather its applicability to the problem of sex in a wide sense, than its use as a basis for understanding the mechanisms of flowers.

The point which seems to me important in the history of the subject, is that the above generalisations, which are in substance to be found in Darwin's works, are still the foundation-stones of floral biology, and would stand as firmly if the Knight-Darwin Law had never been formulated. For the naturalist who takes a wider field, and studies the origin of sex and the action of changed conditions, the existence or non-existence of perpetual self-fertilisation must always be an important question; but the law in which its non-existence is formulated, is not a fundamental canon of floral biology.

FRANCIS DARWIN.

### BOTANY AT THE BRITISH ASSOCIATION.

THE subject of alternation of generations in plants played a prominent part in the work of the Botanical Section. The President (Prof. Bower) devoted a considerable portion of his address to the controversial questions connected with "the great enigma of the alternation of generations" in green plants. Mr. Lang, of Glasgow University, and Prof. Klebs, of Halle, contributed important papers on this subject, and these were followed by a general discussion on the problems of alternation. Mr. Lang gave an excellent summary and critical review of our present knowledge concerning alternations of generations in the Archegoniata. The recent work of this investigator on some striking cases of deviation from the normal life-history of ferns, must be ranked among the most important contributions germane to this subject which have appeared in recent years. In concluding his account of some of the main factors in alternation, the author suggested three subsidiary questions as worthy of attention—the probable line of descent in archegoniate plants, the bearing of the cytological facts on the question, and the significance to be attached to apospory and apogamy.

Prof. Klebs' paper dealt with the alternation of generations in the Thallophyta, a subject which he was particularly well fitted to discuss from a critical standpoint. After taking a general survey of the various divisions of the Thallophyta, Prof. Klebs referred more especially to certain cases which have a more direct bearing on the question of the first appearance of a regular alternation of generations. The majority of the Algae and Fungi have two or more kinds of propagation, each of which necessarily depends upon definite external conditions. According to the conditions the different kinds of propagation may appear on the same or on different individuals, independently or in any succession. The fertilised ovum in sexual forms does not differ essentially on germination from another propagative cell. In none of these cases is there any reason for speaking of an alternation of generations. In conclusion, the author briefly referred to the possible connecting links between the Algae and Archegoniata. Sir Edward Fry, Dr. Scott, Profs. Marshall Ward and Marcus Hartog took part in the discussion which followed the two contributions by Mr. Lang and Prof. Klebs.

Another important item in the programme of Section K was a semi-popular lecture by Dr. F. F. Blackman, on the breathing mechanism of plants. The lecturer gave a clear and interesting summary of the progress of experimental work on the phenomena of gaseous exchange between a green plant and the medium in which it grows, concluding with an account of some recent investigations which have not yet been published.

*Algae and Fungi.*—The Committee on Fertilisation in the Phaeophyceae reported very satisfactory progress in the researches on the Fucaeae and Dictyotaceae. Mr. Lloyd Williams, of Bangor, whose researches have been carried out under the auspices of the Committee, gave an account of his important work on the reproduction of *Dictyota dichotoma*. *Dictyota*, an annual brown seaweed, germinates during the

summer and begins to form its reproductive cells in July. The tetraspores are produced throughout the season, but the sexual cells show a remarkable periodicity. The author described the fertilisation of the oospheres by the motile antherozoids, and expressed the opinion that there are strong reasons for concluding that the factor which determines the maturation and liberation of the sexual cells, and the fertilisation of the oospheres, is the amount of illumination to which the plants are exposed.

Prof. Phillips, of Bangor, contributed a paper on the form of the protoplasmic body in certain Floridææ. In *Ceramium rubrum* and other species a strong strand of protoplasm runs along the axial cells from pit to pit. In *Dasya coccinea*, the branches of limited growth run out into pointed uncurticated filaments, the cells of which are large. Across the vacuole of these cells running from pit to pit occurs a thread of protoplasm much more delicate than the corresponding structure in *Ceramium*. In *Callithamnion byssoides*, threads of protoplasm, which exhibit incessant movement, radiate from a cushion lying over the pit and end blindly on the vacuole. All these phenomena point to the great physiological importance of the pit-communication between cell and cell.

Prof. Errera, of Brussels, communicated the results of some recent work on the structure of the yeast cell; his investigations led him to the following conclusions: (1) a relatively large nuclear body exists in each adult cell; (2) young cells contain no such body; at a later stage the old nuclear body divides, one of its two daughters wanders through the narrow connecting channel into the young cell; (3) after the division is complete, the two cells are kept together by a mucilaginous neck-shaped pedicel; (4) carbohydrates are stored up in yeast in the form of glycogen, which accumulates or disappears from the vacuoles very rapidly, according to conditions of nutrition and growth.

Mr. Harold Wager also presented a communication on the same subject; he referred to the existence of a deeply stainable body, regarded by most observers as a nucleus, and of a vacuole in close contact with the nucleus. During the division of a cell a portion of the nucleus and of the vacuole passes into the daughter-cell. Mr. Wager pointed out certain errors in the work of Hieronymus; and expressed the opinion that the "nucleus" of the yeast possibly represents an early stage in the development of the vegetable nucleus; it might be fitly designated a proto-nucleus. Mr. Wager also gave an account of his researches on the rare fungus *Polyphagus euglenæ*, a parasite on *Euglena viridis*. The material was obtained from a filter-bed at Keighley. Mr. Wager was able to follow in detail the methods of spore and zygospore formation; he noted the interesting fact that the male cell is larger, and possesses a larger nucleus than the female cell.

Prof. Marshall Ward gave an account of a new potato disease which appears to be fairly common, but has hitherto usually been confounded with the disease caused by *Phytophthora*. The pathology of the disease was dealt with, and the author referred to certain external symptoms which enable a practised eye to distinguish diseased plants from those suffering from the attacks of *Phytophthora*. An interesting feature of the disease is that the fungal hyphæ appear to prepare the way for the entrance of bacteria and other organisms into the tissues of the host-plant. The same author contributed a second paper, in which he described the action of *Penicillium* as a wood-destroying fungus.

Mr. Trow, of Cardiff, gave an account of the cytology and reproduction of *Achlya americana* var. *cambrica*. He described the nuclear division in the oogonium and antheridium; also the occurrence of fertilisation as in *Saprolegnia mixta* and *S. dichina*.

Mr. Ellis, of Cambridge, contributed a note on a method of obtaining material for illustrating smut in barley.

*Pteridophytes and Gymnosperms (Recent and Fossil).*—Mr. Lang announced the discovery of the prothallus of *Lycopodium clavatum*. A few prothalli were found wholly imbedded in the peaty soil underlying a patch of moss; three of them bore young plants, and a number of slightly older plants, the prothalli of which had disappeared, were found in the same spot. The prothalli, which present a general resemblance to those of *Lycopodium annotinum*, are of considerable size, completely devoid of chlorophyll, and fairly well provided with rhizoids. Their form is that of a thick fleshy cake, which soon becomes thrown into folds by the unequal growth of the margin. The

sexual organs are borne on the upper surface; both antheridia and archegonia may be present at the same time.

Dr. Scott gave a short account of some of his recent work on the anatomy of Coal-measure plants; the most important of his contributions was a description of the structure of a new form of the genus *Medullosa* from the Lower Coal-measures of Lancashire. This extinct type of Palæozoic plants has not hitherto been recorded from a British locality, and has not previously been found in rocks of Lower Coal-measure age. The material on which the description was founded was obtained by Mr. Lomax, and the excellent sections, of which micro-photographs were shown on the screen, were prepared by this able worker. Dr. Scott showed that the type of structure represented by the Lancashire *Medullosa* is that of a polystelic *Heterangium* which bore *Myeloxylon* petioles. The same author exhibited photographs of an unusually fine specimen of the Halonial branch *Lepidodendron*, allied to *L. fuliginosum*, recently discovered by Mr. Lomax. Other contributions by Dr. Scott dealt with an English example of the interesting Palæozoic fern *Botryopteris*, and with a remarkably fine example of *Zygopteris* from the Williamson Collections of Coal-measure plants in the British Museum.

Mr. A. C. Seward described the external features, internal structure and geological history of the Malayan fern *Matonia*. The anatomical investigation was founded on some material received through the kindness of Mr. Shelford, of the Sarawak Museum. The stem of *Matonia pectinata* is characterised by an arrangement of vascular tissue which appears to be unique among recent ferns; there are two annular steles, and occasionally also an axial strand of xylem and phloem traversing the creeping rhizome. The genus *Matonia* has usually been regarded as a type apart, and the anatomical characters emphasise the isolated position of the genus. The two living species of *Matonia* are no doubt the survivors of a tribe of ferns widely distributed during the Rhætic and Jurassic periods.

Mr. C. E. Jones, of Liverpool, contributed a paper on the anatomy of the stem of certain species of *Lycopodium*; his communication was of the nature of a preliminary note on the subject of the general anatomical investigation of *Lycopodium*, on which he is at present engaged.

Mr. Pearson, of Cambridge, described the apogeotropic roots of the Australian Cycad *Bovenia spectabilis*; he drew attention to the occurrence of colonies of *Anabena* in the intercellular spaces of the cortex.

*Physiology and Natural History.*—Prof. Errera discussed the theoretical calculation of an osmotic optimum. Recent researches made by Dr. F. Van Rysselberghe, of Brussels, have shown that vegetable cells generally answer an osmotic stimulus by an appropriate osmotic reaction, and that the relation between stimulus and reaction follows, within wide limits, the "law of Weber." Hence results the possibility of predicting the existence and value of an osmotic optimum. The same author also contributed a note on the unit to be adopted for osmotic measurements.

Mr. Francis Darwin read a paper of special interest on the Knight-Darwin Law. (This paper is printed in full in another part of the present number.)

Prof. Reynolds Green gave an account of some results which he had obtained confirmatory of Buchner's work on the enzyme of the yeast plant. Prof. Green found that if the yeast experimented on is in a state of active fermentation, the alcohol-producing enzyme can be procured as Buchner has stated. He described the method of investigation adopted, and concluded by stating that the enzyme obtained from yeast agrees in an important respect with other enzyme.

Prof. C. de Candolle, of Geneva, gave the results of a comprehensive comparative study of peltate leaves, with special reference to the number of species possessing such organs, their distribution among the various natural orders, and their mode of growth.

Mr. Burkill, of Kew, dealt with changes in the sex of willows. In the genus *Salix* flowers of both sexes are occasionally present in the same catkin, and the sexual organs are sometimes found to be intermediate in structure between stamens and carpels. Mr. Burkill gave the results of his examination of an extensive series of specimens and published records.

Mr. S. T. Dunn contributed some notes on the origin of railway-bank vegetation.