Seven Decades of Botany.[1]

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"The future of Biology lies not in generalisation but in closer and closer analysis."—BATESON (Birkbeck Lecture, 1924).

DEATH sudden and wholly unforeseen has stepped between Section K (Botany) and the president of its choice. Dr. Bateson had presided over the whole Association at its meeting in Australia, and partly on that account he had been specially selected for the chair of this Section in Oxford. From him we might have expected a broad outlook upon biological science. His address would have been instinct with wide experience in both of the branches of living things, the interests of which interweave in enthralling and often most perplexing ways. We should have heard a fearless statement of his mature views. Something constructive would certainly have justified the congratulations with which some of us had already welcomed his nomination. A great figure has been taken from the arena of biological science. A career still full of the promise of further achievement has closed prematurely.

This is not the time or the place for any comprehensive obituary of Bateson. I will only allude briefly to four leading events in his scientific career. He felt in early life the lack of facts bearing on variation, and sought to extend their area in his great work "Materials for the Study of Variation," published in 1894. This was the year when the British Association last met in Oxford. I do not remember that its contents came into the discussions in Section D, though the book centred upon the vital question of continuity and discontinuity. The second event was the publication in 1902 of "Mendel's Principles of Heredity," in which, though essentially a controversial statement, Bateson perceived latent in the rediscovered writings an expanding vista of advance. "Each conception of life," he says, "in which heredity bears a part must change before the coming rush of facts." In a third stage of his work Bateson expanded this theme into a fuller statement under the same title, and it was published in 1909. Passing from this period of high hopes to the fourth phase of 1924, we see in his address at the Birkbeck Centenary a chastened attitude. He there remarks: "We must frankly admit that modern discoveries have given little aid with the problem of adaptation," and that, much as Mendelian analysis has done, "it has not given us the origin of species." But that analysis having "led to the discovery of transferable characters, we now know upon what to concentrate. . . . Henceforth the study of evolution is in the hands of the cytologist acting in conjunction with the experimental breeder. Every appeal must ultimately be to the mechanics of cell-division. The cell is a vortex of chemical and molecular change. . . . The study of these vortices is biology, and the place at which we must look for our answer is cell-division." I would ask you to mark that last word. It is cell-division, not nuclear division; and earlier in his address we find the pregnant sentences: "As to what the rest of the cell is doing, apart from the chromosomes, we know little. Perhaps the true specific characters belong to the cytoplasm, but these are only idle speculations." Such extracts from Bateson's latest public pronouncement may suggest to you what the Section has lost by his death. They show the mind still elastic and perceptive: still both constructive and critical.

Any address that follows such a tragedy of disappointment as the Section has suffered can only fall short of what we had hoped to hear. Instead of attempting to fill the broad biological rôle that naturally fell to Bateson, I propose to centre my remarks upon three dates when the Association has met in Oxford, namely, 1860, 1894, and 1926. It happens that these dates mark approximately periods of transition in the progress of biological science, and particularly in botany.

1860.

I need scarcely recall that the meeting in Oxford of 1860, the year after the publication of the "Origin of Species," witnessed the clash between the new view and the opposition it was certain to arouse. The story has been often told of the aggressive attack and the crushing retort. But it is not sufficiently recognised that, though Huxley bore the first brunt of the fight, a large part in the contest was taken by Hooker. The meeting closed after he had spoken, and in his own words he was "congratulated and thanked by the blackest coats and the whitest stocks in Oxford."

Two generations have passed since the Oxford meeting of 1860: and still the "Origin of Species" holds its place as a great philosophical pronouncement. As the methods of research passed into greater detail, the area of fact has been extended through the labours of an ever-growing army of inquirers, and naturally divergences of view have arisen. Some authors appear to demand that for all time the "Origin" must cover every new aspect of biological inquiry, or else the whole theory crumbles. That is to demand a prophetic vision for its author. We need not for the moment follow these or other criticisms, but rather recognise that the theory rested essentially on facts of heritable variation, without defining their magnitude, limitations, or origin; and that it explained a means of their summation so as to produce progressive morphological results.

Before we leave the historical aspect of evolution a moral may be drawn from the lives of its four protagonists of 1860. Darwin, Wallace, Hooker, and Huxley were all equipped for the battle from the armoury of personal experience in the great world. The theory of evolution was born and bred of foreign travel, and upon foreign travel quite as much as upon quiet work at home its future still depends. We should not for a moment minimise the great developments of laboratory study and of breeding experiment in recent years that bear upon its progress. But it is not thence alone that the fullest achievement can be anticipated. The cytologist and the breeder, just as much as the abstract theorist, should know Nature

[1] From the presidential address to Section K (Botany) of the British Association, entitled "1860—1894—1926," delivered at Oxford on August 5.

face to face, not merely through a glass darkly. To those who believe in the close relation between environment and variation, which is to me the very core of evolution, this seems essential to any well-balanced view. The open forest, the sea-coast, steppe, and mountain-side should be regarded as the natural complement to the laboratory and the breeding-station. No one, morphologist or physiologist, should hold himself equipped for research or fully qualified to teach unless he have at least some experience of travel through wild Nature. This can best be acquired in the tropics.

What, however, do we find? In 1886 a committee of the British Association was appointed to assist the visits of botanists to Ceylon for study. Several well-known botanists availed themselves of its aid; but after a few years the scheme flickered out through inanition. In 1909 I visited the Cinchona Station in Jamaica, and again a scheme for continued use of the station by British botanists was initiated; but it has since died out for want of consistent support. Why did these efforts fail? We may set these failures down to under-valuation of the importance of foreign, and particularly of tropical, study; and the lack of full perception that open Nature is the greatest laboratory of all. Our future botany seems in danger of becoming myopic by reason of study being concentrated at too short focus. To correct this, young aspirants should travel early, as free lances, hazarding the fortune of the wild, as Darwin and his fellows did.

HOMOPLASY.

I have already alluded to the tempestuous meeting of 1860 in Oxford. Shortly after it an undergraduate came up to Christ Church who, before he was of standing to take his M.A. degree, had himself made a real contribution to the philosophy of evolution. It was Ray Lankester, who in 1870 published a short paper "On the Use of the term Homology in Modern Zoology, and the distinction between Homogenetic and Homoplastic Agreements." Its author was only twenty-three years of age, and its date barely a decade after the publication of the 'Origin.' This short paper went far to clear up the vague ideas surrounding the term 'homology' in the minds of early evolutionists. Lankester introduced the idea of 'homogeny,' substituting in a more strict sense the word 'homogen' for 'homologue.' He also suggested, to avoid confusion, the use of another new term, namely, 'homoplasy.' He defined homogeny as simply the inheritance of a common part, while homoplasy depends upon the common action of evoking causes or of a moulding environment upon homogonous parts, *or* upon parts which for other reasons offer a likeness of material to begin with.

This definition was at once adopted in the morphological study of animals, but Lankester did not himself apply it at the time to the morphology of plants. In point of fact the conception of homoplasy and the use of this clarifying term made its way but slowly into botanical literature. There is reason to believe that we are as yet only beginning to recognise in the evolution of the plastic plant-body how far-reaching has been the influence of homoplasy, not only upon external form, but also in the internal evolution of tissues. We are only now beginning to realise how far-reaching have been its results in plants as we see them. On the other hand, such realisation when well assured cannot fail to react upon our estimates of affinity of the organisms in which homoplasy appears. It may be going too far to trace all such results as consequences of the meeting of 1860; but the initiative was certainly given by Lankester in the years that followed.

1894.

Passing from the stormy period of 1860, when the whole outlook of biological science was being transformed by the advent of evolution, to 1894, we see that the atmosphere had cleared. One result was that the evidence of descent tended to become too definite in the minds of some enthusiasts, and there was even a disposition to argue deductively from the accepted position, a tendency that is much too prevalent to-day.

The outstanding feature of the Oxford meeting of 1894 was Strasburger's generalisation on the periodic reduction of chromosomes. This shed a new light on the vexed question of alternation, which, based on the brilliant results of Hofmeister, by this time held the field not only as an objective fact but also as an evolutionary problem. The effect of Strasburger's communication was to establish the chromosome-cycle as general for plants that show sexuality. It provoked comparison with a similar cycle in animals. The recognition of both cycles took its origin in the discovery by van Beneden in 1883 that in sexual fusion the number of chromosomes is the same in both of the conjugating nuclei. Later observers have confirmed this in a multitude of instances, and disclosed the correlative reduction, or meiosis. The existence of a nuclear cycle alike in animals and in plants cannot, however, be held as establishing any homogenetic unity of the two kingdoms. Comparison of the simpler forms of each indicates that the divergence of the kingdoms, if they ever had a common origin, was very early indeed, and probably antedated sexuality in either. Such similarities as they show in propagative detail, and particularly in the nuclear cycle, would be homoplastic, not homogenetic. If this be so for the two kingdoms of living things, may it not be equally true for the several phyla of plants that show sexuality; for we are not justified in assuming that sexuality arose but once in plants?

Historically this generalisation of Strasburger fell like a bomb-shell into the midst of the old controversy between the rival theories of alternation, styled in the words of Celakovsky 'homologous' and 'antithetic.' But it must be remembered that at the moment there was no complete demonstration of a cytological alternation in any one Alga, though the facts soon followed for Fucus and for Dictyota. We need not recite again the arguments for and against that old discussion. It soon lost its intensity in face of the obvious deficiency of crucial facts, which alone could lead to some final conclusion. Loose comparisons between organisms not closely allied are but the long-range artillery of morphology. Comparisons between organisms closely related are its small arms. The discussions of the 'nineties of last century on alternation were all engagements at long range, which could not be decisive

without the use of close comparison. As the necessary facts were not then in our hands, those premature engagements might be held as drawn; and it was open to both parties still to entertain their own opinions.

Before discussing the relation of somatic development to that cycle, it will be well to revise the terminology then in use. It would be well to drop those old terms, which are neither exact nor explicit, and to support a more general use of the words 'interpolation theory' in place of 'antithetic' and 'transformation theory' in place of 'homologous.' These words accord better with current views, and are explicit.

1926.

From the time that the periodic reduction of chromosomes was recognised as general in organisms showing sexuality, the nuclear cycle has formed a natural foundation for the comparison of the life-histories of plants. The normal cycle may be figured to the mind as a closed circular thread with two knots upon it, syngamy and reduction. Between those knots beads may be strung, one or more than one, or none. These represent somatic developments, which are normally diploid between syngamy and reduction, haploid between reduction and a fresh act of syngamy. They follow in alternate succession in any normal cycle, but either may be repeated indefinitely by vegetative propagation.

Certain questions arise with regard to the evolution of these somata as we see them. The first is, how far are the diploid and haploid somata of the same cycle comparable one with another? The reply will turn upon the constancy of the events of syngamy and reduction throughout descent. If they were constant, then it appears a necessary consequence that the alternating diploid and haploid somata must have been distinct throughout their history; and any similarity which they may show, as in Dictyota or Polysiphonia, would be homoplastic. It would indeed appear natural that they should be alike in Algæ, since they are parts of the same organic life and live in identical circumstances. It has, however, been suggested that reduction may not be a fixed but a movable event in the individual life: liable to be deferred or carried over to a later phase, in which case a diploid generation might arise by transformation from an already existent haploid phase. The monospores of the Nemalionales have been cited as possibly convertible in other red seaweeds into tetraspores, by some sudden deferring of the act of reduction.

I am not aware that this has been advanced by close comparison beyond the position of tentative suggestion, though the existence of a diploid gametophyte and of a haploid sporophyte in certain abnormal ferns would indicate the possibility of the suggestion being true. Pending the advance of a closely reasoned argument it is best to keep an open mind. Meanwhile the weight of facts hitherto known from plants at large may be held to support the stability of the events of syngamy and reduction during normal descent. The two generations of the same life-cycle would, in the absence of a carry-over of reduction, be homoplastic, not homogenetic.

No one has yet made out a closely reasoned case for the descent of the Archegoniatæ from the green, the brown, or the red algæ. The old view that they originated from the green algæ has never recovered from the blow delivered by Dr. Allen, when he showed that the reduction in Coleochæte takes place in the first divisions of the zygote, and that the presumed primitive sporophyte is really haploid, and not cytologically a sporophyte at all. It is a perfectly tenable position to hold that the Archegoniatæ sprang directly from none of these groups, as we know them. In the absence of definite comparative evidence, the field appears to be open to an origin of alternation in the Archegoniatæ by interpolation of a sporophyte *de novo*, developed not in water but in relation to a land-habit.

DEVONIAN FOSSILS AND A LAND FLORA.

Palæobotanical discovery has been greatly advanced within the period under review. The features of the vegetation of Mesozoic time are becoming clearer than ever before under the hands of Prof. Seward. The Carboniferous flora has been richly presented to us by Williamson, Scott, Oliver, and Kidston in Britain, and by continental workers such as Renault, Zeiller, Bertrand, Nathorst, and Solms-Laubach. We are now able to substitute something positive in place of vague surmisings. Not only do the new facts illuminate our knowledge of plants now living, but they also apply a check upon theories as to their origin.

Latterly a vision is becoming ever more and more real of a Devonian flora, revealed by Kidston and Lang in Britain, and by other workers in Scandinavia, in Germany, and in America. Given more extended collecting, an improving technique, and the fortune of finding more material as well preserved as that at Rhynie, who knows but what the coming decades may see the land of the Devonian period clothed before our eyes by a flora no less stimulating and even more suggestive than that of the coal? But though Devonian lands are the earliest yet known to have supported a sub-aerial flora, the highly advanced structure of such a fossil as *Palæopitys Milleri* suggests that we are still far from visualising the actual beginnings of land vegetation. Moreover, the mixture in the Rhynie Chert of algal types with vascular land-plants presents at the moment a problem as perplexing as it is ecologically strange.

It is always difficult to estimate justly the times in which we live; but we may well believe that the future historian of botany will note the present period as one specially marked by successful study of the floras of past ages, and by the increasing cogency of their comparison with the vegetation of the present day.

THE *ANNALS OF BOTANY* AS AN HISTORICAL DOCUMENT.

Perhaps too much time has been claimed for morphological questions, which are closely related to the dates of the three meetings of the British Association in Oxford. The brief space that remains may be devoted to a more general survey of the period which these dates cover. In this we could not do better than to take as an index the pages of the *Annals of Botany*, for the existence of which we owe a deep debt to the Oxford Press. In 1860 there was no organised laboratory

teaching of botany in any university in Britain; and as yet there was no journal of the nature of the *Annals*. But the revival of close observational study in botany under Huxley and Thiselton-Dyer at South Kensington in the early 'seventies, recorded last year by various writers in the *New Phytologist*, was beginning to take effect in 1881, when the British Association met in York. There the outstanding feature was the address of Hooker on geographical distribution. This and the papers by Bayley Balfour on Socotra and by Baker on Madagascar were all that really mattered botanically, and almost all the contributions were systematic or regional in subject. The revival of the laboratories had not yet fructified.

At this time all the work that was done in laboratories was called 'physiology,' as distinct from systematic botany, which was conducted on dry specimens in the herbarium. In 1887, six years after the York meeting, the *Annals of Botany* was founded through the activity of the late Sir Isaac Bayley Balfour, and a small committee of guarantors whose personal security induced the Clarendon Press to make the venture. From the start that journal has paid its way. The forty stately volumes form a record, between the pages of which may be read the history of botanical progress in Britain, and in some degree also in the United States, for American botanists have always been with us in its pages.

In the first issues of the *Annals*, morphology and systematic botany preponderated, and from the proceedings of the meeting of the British Association in Oxford in 1894 we see that this was still so. That meeting witnessed a crisis in the affairs of botany in Britain. A newly established Section I of Physiology assumed that the functional activities of plants would be swept, together with those of animals, into its hands. Up to this time Section D had been the undivided section of Biology. An irregular cleavage of interests was set up by this claim, for the zoologists were mostly willing to give up their physiology, but the botanists were not. Their refusal to accept divorce of form from function contributed to, or at least coincided with, the foundation of a separate Section K of Botany, and has dictated the policy of British botany ever since.

As we pass from 1894 to the current period we perceive a marked shifting of the interest of botanists from the study of form to that of the intimate constitution and functional activity of plants. Whole fields of colloidal chemistry and physics, of quantitative physiology, of cytology and genetics, of ecology, of fungology and bacteriology, have been opened up. The present century has been specially marked by the extension of opportunities for physiological research, by better equipment of departments in the universities, and by the foundation of independent establishments carrying on experimental inquiry in its broadest application. This is rapidly bringing the science into closer relation with Imperial and social aims.

It is needless to specify, but the effect of it all is plainly written in the pages of the *Annals*. Experimental results have gradually taken the preponderant place over description and comparison, as is amply shown in the last January number. 'For better, for worse,' the pendulum has definitely swung over from the extreme systematic position of half a century ago, through a phase of prevalent morphology (or perhaps we should better say of organography), to an extreme physiological position at the present time. Some may even have felt that this address is in itself an anachronism, in that it has not touched upon the moving physiological questions of the day. While I may claim none the less to sympathise with physiological aspirations, I do not assent to any ultra-physiological aspect of botany that would degrade or minimise the comparative study of form. *Medio tutissimus ibis* is still a true maxim. The laboratory physiologist, dealing with the things of the moment, cannot safely detach himself from the things of the past as recorded in heritable form. He should not allow himself to be immersed in statistics and neglect history. The pendulum has gone full swing, within a period of about half a century; but we may confidently anticipate a return towards some middle position.

Power Alcohol and other Petrol Substitutes.

ALTHOUGH opinions differ concerning the extent of the world's petroleum reserves, it is generally agreed that if the consumption of petrol continues to increase at its present rate, available supplies will soon become inadequate. Thirty years ago, it is said, there were but four motor cars in the United States; to-day there are nearly twenty million, and the consumption of petrol in that country has risen to about 900 million gallons a month. The demand for aviation shows every sign of expanding, and when we consider that petroleum is very unequally distributed in the earth's crust, and that economic independence is still a watchword in international politics, we can readily understand the vigorous efforts that are being made to produce liquid fuels by artificial means.

So far as we can see to-day, there are not many possible alternatives to petrol. There are, indeed, immense supplies of liquid fuel lying dormant in the oil-shales that are so abundantly distributed over the earth, but until methods of extraction and purification are devised that are both technically and economically successful, we shall continue to look to other fossil fuel, coal or peat, to vegetable matter, and to the mixture of carbon monoxide and hydrogen known as 'water-gas,' to supplement our present supplies of petrol, and to replace them when the day of extinction draws nigh.

Benzol is an excellent motor-fuel, but its production is comparatively small; and it is required for other purposes: for example, for dyes and explosives. Acetone is the ideal liquid for mixing with other motor-fuels, but at present it is too costly to compete with them, although its commercial production through the acetic acid made by fermenting cellulose may be achieved at an early date, and so bring it into the foreground. Alcohol is of especial significance, because the raw materials of its manufacture, cellulose and sugar, are renewed incessantly by a bountiful Nature, and also because its value as a motor-fuel, particularly in admixture, has been proved beyond a doubt. Hydrocarbon