The Unification of Pure Botany.

By A. G. TANSLEY, F.R.S.

THE history of the development of the science of botany in Great Britain since the great revolution in biological thought brought about by Darwin is an interesting and instructive study. Botany now represents so vast a field of knowledge and research that it is quite impossible for any single individual to gain an intimate first-hand acquaintance with all its different branches. Many research workers spend their lives in cultivating a small area of one portion of this immense territory. Nowadays many of them have very little interest in or understanding of the work of their fellow "botanists." The taxonomy of flowering plants and of the various lower groups, the ecology and general natural history of all this multitude of forms, their gross and their minute anatomy, histology, and cytology; the study of variation and heredity; the great and varied field of modern plant physiology, with its interest more and more centred in the chemical and physical characters of protoplasm and its derivatives; the study of the characteristic aggregates of plant life that we call vegetation; the applications of botany to agriculture and to industry—we need only pass these fields of study rapidly before our minds to realise their enormous range, and the want of connexion in practice between the topics with which a modern botanist may occupy himself.

Yet the whole of the vast field of our knowledge of plant life continues to be called by one name, and most of those who labour in it are still possessed of some sense of community with their fellow-workers. There has always been strong, and hitherto successful, opposition to proposals for formal division of the subject into separate parts, though both logic and practical convenience would seem to dictate such a course. There seems to have been an intuition that division would involve the loss of something too important and too precious to be lightly sacrificed. We have to ask ourselves whether this intuition can be justified on reasoned grounds, whether there is any rallying point from which the science of plants can be regarded as a whole, and presented to those who are beginning its serious study. In order to approach this question intelligently we must cursorily review the historical factors that have determined the existing position.

In recent centuries, that is, after the revival of learning, botany has developed as a result partly of man's natural interest in plants, the living beings which form so great a part of his natural environment and on which he depends so largely for his food, but very markedly as a specific result of interest in the collections of medicinal herbs grown in special gardens attached to the medical schools. The earliest professors of botany in western and central Europe were the curators of these Herb or Physic Gardens, and they taught their students the nature and properties of the plants under their care, and how to distinguish the various kinds. Gradually the scope of these collections widened to include non-medicinal plants, and the effort to bring order into the multitude of forms led to the study of their structure—morphology—and to the creation of systems of classification.

The early professors of botany, while they acquainted themselves with the properties of plants, were necessarily also taxonomists and morphologists—they had to be, in order to cope with the material with which they were concerned. They mostly possessed the type of mind which finds its satisfaction in the study and comparison of objects which present various kinds and degrees of similarity and difference—the type of mind which naturally *observes* and *classifies*—well exemplified by that great pioneer Linnæus. But alongside this primary development of pure botany, another kind of interest showed itself, interest in how plants work, how they get the material which enables them to increase in bulk, what is the nature of this material, how they grow and reproduce themselves. This second type of mind, which naturally *observes* and *experiments*, was notably exemplified by our own countrymen, Andrew Knight and Stephen Hales, forerunners of the modern plant physiologists.

About the middle of the nineteenth century, in Germany especially, there was a great quickening of scientific interest in plants, a great outburst of investigation into the minute structure and life history of plants, and also of experimentation. The two types of interest in plants were both strongly represented in this new movement of "wissenschaftliche Botanik," and they were reflected in the foundation, beside the old professorships of botany, of new chairs of plant physiology, a duplication which exists in most of the larger German universities. But there was no sharp separation of the kinds of study, and the great German pioneers of modern botany were certainly not narrow specialists. In Great Britain, fifty years ago, botany was still almost exclusively represented by systematists and morphologists, among whom were some of our greatest names. Meanwhile Darwin's work had inspired the whole of biology with new life, and there arose a group of eager young men who wanted a different kind of material, which traditional British botany could not give them. They saw in Germany a great mass of new knowledge of the internal structure, life histories, and physiology of plants, and several became pupils of great German botanists who had taken leading parts in the new discoveries. On their return they helped to found in Great Britain the new school of laboratory botany which marked the later seventies and the eighties of last century.

In this school the divergence of the two types of human interest in plants showed itself very plainly from the first. One group of the younger British botanists took up with enthusiasm the work of exploring the structures and life histories of the various groups of plants, another—a much smaller one—the experimental study of function. The influence of Darwin had now become overwhelming. The origin of species by means of natural selection was generally accepted by biologists—it had become biological orthodoxy, but was still in the first flush of its effectiveness. Hence the natural morphologists among the younger men were inspired by a desire to apply the Darwinian theory of evolution to the detailed development of the plant kingdom—to the tracing of the phylogeny of different groups as illustrating the continuous adaptation of plants to environment. Much of this work was carried out by comparative study of the structures and life histories of living plants, and prominent examples were the great series of comparative studies of the spore-bearing organs of Pteridophytes—the great middle grade of the plant kingdom including the more primitive vascular plants—and of the phenomenon of alternation of sexual and spore-bearing generations which the life histories of these plants regularly show.

Another important factor now came into play. The masterly pioneer work of Williamson had at this time added greatly to our knowledge of the rich flora of the English coal measures, and these beautifully preserved fossils offered a rich field to the trained anatomist, who was able to apply his newly acquired knowledge of the details of structure of living plants to the elucidation of the fossil forms which reached the culmination of their development towards the close of the Palæozoic age. Many of the fossil plants in question clearly belonged to the same order of Pteridophyta—the horsetails, the clubmosses, and the ferns—of which representatives still exist, though in greatly diminished size and numbers. Others, on the contrary, could not be placed in any existing order, though they clearly belonged to the same general grade of organisation. Others again, the vegetative structure of which had long been known, were eventually proved, about the beginning of the new century, to be fern-like plants bearing seeds (Pteridospermeæ), though seeds of a type differing in important respects from those of existing seed plants.

Most of this work, together with the concurrent, energetically pursued comparative investigations of the detailed structure of living forms, was undertaken under the influence, and inspired by the ideal, of tracing out the "genealogical tree" of the plant kingdom, an ideal which was the direct result of the doctrine of organic evolution. The newly discovered facts of structure in both recent and fossil forms of Pteridophytes, among others those relating to their vascular systems, suggested that there were two main lines of descent among vascular plants; one including the cone-bearing small-leaved forms, the other with typically large leaves including the ferns and probably also the seed plants. There seemed a probability that the Pteridosperms had an origin in true ferns, some of which, especially the wholly fossil group of Primofilices, and also existing ferns believed on other grounds to be relatively primitive, they resembled in vascular structure more or less closely. Though their seeds differed in important characters from the seeds of modern plants, there was perhaps a natural tendency to the assumption that "a seed was a seed," and that from some plants not unlike the Pteridosperms the modern seed plants might be descended.

The facts, however, did not carry the same phylogenetic convictions to every one. There was a good deal of difference of opinion as to the connexion or want of connexion between the various groups of Pteridophytes, and as to the lines of descent of the seed plants. It has become more and more clearly recognised that particular, well-characterised plant structures, such, for example, as the archegonium (the type of female organ found in all the Pteridophyta as well as in the non-vascular group of mosses and liverworts), or the seed itself, are not (as was too often assumed, if only implicitly and unconsciously) necessarily homogenetic, *i.e.* indicating community of descent between the plants possessing them. Such organs may well have taken origin independently—and the same conclusion may be extended even to such fundamental structures of vegetative organisation as leaf, stem, and root—along many different lines of descent. On general biological grounds we should indeed expect this to be the case. The conception of homoplasy, or parallel evolution of similar organs under similar external conditions of life, has of course long been familiar to biologists, but we should be prepared for a far wider interpretation of this principle than was originally contemplated. It is not only a question of *particular* external conditions, but also of the limited number of ways in which protoplasm can react to constantly recurring conditions. It is not of course suggested that an organ should not be regarded as strictly homologous within a small well-defined natural group, but that wide phylogenetic conclusions, relating to large series of forms showing gaps in continuity, are rendered additionally unsafe when we consider the likelihood of independent development of what have often been assumed to be phyletically the same structures.

As a matter of fact the search for common ancestors has turned out to be disappointing. The better the different groups of fossil Pteridophyta and of primitive seed plants have become known, the more definitely they have shown themselves independent, and this conclusion has recently been quite clearly stated by the leaders of this branch of botany. One authority goes so far as to doubt whether "missing links" have ever existed, and to suggest that the different groups of vascular plants may have had their origin in primitive water plants (Algæ) at different times in the history of the earth. To put the matter shortly, morphologists have not succeeded in establishing the phylogenetic connexions of the different groups of vascular plants, or even whether they have any connexions. Different groups appear in the geological record, reach a culminating point, and disappear again, either completely, or leaving a few diminished representatives behind. The older (Palæozoic) groups reached a high degree of complexity and show many features strikingly parallel with those of modern plants, but it is only these latter, especially the Angiosperms or modern seed plants, which have developed that flexibility which has enabled them to dominate the highly varied environments presented by the earth's surface. The vast amount of careful and accurate investigation of structure that has been carried out in the effort to establish positive phylogenetic conclusions has, however, immensely increased our detailed knowledge of structure. It has also established that within undoubtedly homogeneous groups there have been certain types of progression, both in vegetative and reproductive structures, and that these have been repeated again and again in different phases of geological history.

Meanwhile the physiologists, in accordance with their different kind of interest in plants, worked on wholly different lines. Thirty years ago plant physiology consisted very largely of quantitative studies of the functions of the adult plant, such as transpiration, respiration, photosynthesis, etc., under different conditions, and there was a sharp separation between the metabolic functions and the phenomena of "irritability" such as the tropisms—changes in the direction of movement. Each function was studied, deliberately, as much as possible in isolation, and the records were necessarily extreme examples of specialisation, often as little interesting to any one but the specialist as purely morphological studies of particular forms. Morphology and physiology, as practised in those days, were not only essentially divergent but also practically unconnected pursuits, and neither had any immediate bearing on the central problems of plant life. This state of things was conspicuously reflected in botanical teaching, morphology and physiology being generally taught independently, and presented to the student as if they had little or no connexion, as indeed was the fact. This divorce was even crystallised into a formula which stated that the object of morphology was the elucidation of phylogeny, while that of physiology was the study of function. It must often have seemed to the student a mere accident, as it were, that they both happened to deal with plants.

Together with the widening of our knowledge of the functions of the adult plant, a deepening of plant physiology has also been in progress, depending very largely on important advances in physical chemistry, and the application of the results to the activities of living substance which has resulted in the rise of the modern science of biochemistry. This has placed tools in the hands of the plant physiologist of which he is now making good use. Very great advances have been made in our understanding of the real nature of protoplasm and of the modes of action of the living cell. More and more we are able to study these modes of action in terms of actual identifiable substances and their chemical and physical changes, instead of referring them to "functions" of a mysterious entity, protoplasm. In recent years too, *developmental* physiological studies, from different points of view, have been inaugurated, and these are gradually giving us new light on the conditions obtaining in the germinating seed, the seedling, and the young growing plant, and how these conditions lead up to the processes of the adult organism. We are thus beginning to get a real picture of the plant as a developing complex of substances and structures, and of the way in which they act and react upon one another. Recent work upon the actual determination of substances, tissues and organs within the individual plant, such as endodermis, cork, and cuticle, and on the relation of the differences between the primary meristems of root and shoot to the construction of these organs, though still in its infancy, has already begun to throw light on these problems of development.

Here, in the causal study of ontogeny, the development of the individual plant, we have a line of work that should unite the interests, too long widely divorced, of morphologists and physiologists. There have not been wanting far-sighted morphologists who have long been dissatisfied with the tracing of doubtful phylogenies, and have sought in the study of the causal factors of ontogeny a starting point for an attack on the problems of form. But they have seldom had the training necessary for successful advance in this direction. We should boldly claim, as has been claimed by Prof. D'Arcy Thompson, that since the problems of form are in the first instance mathematical problems, the problems of growth essentially physical problems—and, we may add, since the problems of tissue differentiation are essentially biochemical problems—"the morphologist is *ipso facto* a student of physical science." If we are to obtain real solutions of these problems we must get away altogether from the point of view of the Darwinian morphologist, and work on other lines, in which physical and chemical training is essential. Meanwhile, we cannot underrate the great services rendered under the stimulus of the effort to work out the phylogeny of plants, which have enormously increased our detailed knowledge of structure, and thus provided us with numberless unanswered questions.

Some of these questions can be approached with the means now at our disposal; for example, questions of the general form: How do the actual substances and structures of the young growing plant of any given species or strain produce the characteristic structures and properties of the adult? But when we ask how the substances and structures of the embryo, and eventually of the zygote, come to produce those of the young plant, we have to confess that the means of dealing with the problem are at present quite beyond us. When we get back to the zygote we are brought up against its inaccessibility to useful chemical analysis, and we are confronted with the still mysterious "genes" of the Mendelian, those hypothetical entities which the geneticist finds it necessary to postulate in order to explain the results of cross-breeding. It is the stock of genes possessed by the zygote, seated in the chromatin of the cell-nucleus, which are conceived as determining, in the last analysis, the characters of the individual organism derived from the zygote. The cytoplasm of the zygote also plays an important part in its development, and since the cytoplasm of different species is different, and is continuous from mother to offspring, we cannot deny that it must also transmit hereditary characters. The genes of the chromatin only produce their effect in development by interaction with the surrounding cytoplasm, and it is in the cytoplasm, in the vacuoles and in the cell walls that the larger part of the chemical and physical changes, which bring about development, are carried out. We are thus far from being able to ignore the cytoplasm in considering development.

Nevertheless it is primarily the genes of the chromatin that determine the specific characters of the organism. We do not know what genes are. They may be definite chemical substances, they may be molecular complexes, or some may be of one, some of the other nature. But we do know that within the periods of exact breeding experiments carried on for many generations, the genes show themselves as invariable entities, heritable changes in the adult organism occurring as the result of the redistribution or loss of genes at the "reduction division," and not by any demonstrable alteration in the genes themselves. The process of ontogeny ultimately rests on the way in which the genes and their derivatives in the developing organism produce the characters of the adult under the influence of a particular environment. We can only hope to approach the fundamental problem of how this happens slowly and by degrees. Great as have been recent advances in our knowledge of the physics and chemistry of protoplasm, we are still seriously hampered by want of knowledge in attacking even the easier problems of ontogeny. But a successful beginning has already been made, and ultimately, with deeper knowledge and improved technique, we may get back to the embryo, and perhaps eventually to the zygote and the mysterious genes.

Thus it seems that in the causal study of ontogeny lies the nexus which is capable of reuniting the divided branches of pure botany—taxonomy, morphology, physiology, genetics; and this seems to be equally true of the zoological field. Taxonomy is the natural arrangement of the end results of divergent developments: on one side it rests on descriptive morphology, on the other on genetics. Morphology, as a branch of science, should no longer be described merely as a comparative study of structure with the object of tracing phylogeny: it must take cognisance of the causal explanation of forms and structures. Physiology is not adequately described as the study of function, in the sense of the particular "functions" of the adult organism. It is a study of all the *processes* of the organism in terms of chemistry and physics. Supported by increasing biochemical knowledge, it is the essential means of explaining ontogeny. Genetics, during the last quarter of a century, has performed the great service of making clear the mechanism of heritable variation, which, as Bateson long ago said, is the primary problem of evolution. But the secret of the production and variation of organic structure can never be discovered until we know the real nature and the working in development of the genes themselves; and this mighty problem, the ultimate solution of which must lie in the distant future, can only be approached through the biochemical study of individual development. Substantial advance in this direction is necessary before we shall be in a position to determine the real nature of possible factors in evolution other than the redistribution and dropping out of genes—how, for example, the environment can, as it almost certainly does, affect the hereditary constitution of a race of organisms.

From a point of view such as this, botany—and indeed biology at large—should be presented to the student, if his imagination is to be stimulated to the greatest advantage. Thus he will be placed in the best position to understand the real significance of the subject, perhaps to add to it by his own work. It is unnecessary to say that the main material for teaching cannot be derived from the direct causal study of ontogeny, for the very good reason that we know extremely little about it. But the material used in teaching can be selected with the object of constantly laying stress on the facts and problems of development, of insisting on the search for causal explanations, and of the necessity of seeking them by experiment, of abandoning the deep-rooted and sterilising fallacy—still unfortunately instilled into our school children—that usefulness to the plant is any explanation of the appearance of a structure. In this way the student will be brought from the outset to view the science of plants in the right perspective; he will be led to interest in the most fruitful lines of research, and his training will stand him in good stead no matter what kind of plant study he may take up, whether it be a branch of pure botany, or one of its manifold applications to agriculture or to industry, remote as these may be, to all appearance, from the central problems of plant life. So perhaps we may hope to retain in the future that sense of community between botanists which can only be real if it is based on some real underlying unity of outlook.

British Geological Photographs.

By Prof. S. H. REYNOLDS, Secretary of the British Association Geological Photographs Committee.

FROM time to time articles and notes have been published in NATURE on the work of the British Association Committee for the collection of British photographs of geological interest. It is, however, twenty-five years (March 10, 1898, vol. 57, p. 437) since the last of these articles, by Prof. W. W. Watts, appeared. The collection at that time numbered 1750 prints; it now numbers 6310. It might perhaps be thought that this large number would afford a fairly complete record of the subject. This is very far from being the case. Even in the districts most fully illustrated, such as the Belfast district, Yorkshire, and parts of the south and west of England, there is still much to be done, while many parts of Ireland and some of Scotland are still quite unrepresented. It is, in fact, only when a district is so fortunate as to possess a resident who is keenly interested in such work (as Mr. G. Bingley for Yorkshire and Mr. R. Welch for Antrim) that a really adequate series of photographs has been taken. The photographic survey of the Island of Eigg carried out by Mr. A. S. Reid should be mentioned in this connexion.

Probably one of the most important pieces of work of the committee has been to preserve a record of temporary geological features. Particularly instructive examples of such records are Mr. C. Buckingham's photographs of the nailbournes of Kent and Mr. P. B. Roberts's series illustrating the progress of a wave of erosion at Bexhill. The nailbournes or winterbournes so characteristic of many chalk districts are temporary streams, which in some cases only flow when an exceptionally wet season has raised the level of saturation. Some years may pass between the successive appearances of a bourne, and during such a period the possibility of its reappearance may be lost sight of and buildings may be erected in its path. This happened, for example, at Croydon during the first few years of the present century. Mr. Buckingham's photographs, two of which are reproduced (Figs. 1 and 2), show in a most instructive fashion the contrast in appearance of