The Present Outlook on Descent.¹

By Prof. F. O. BOWER, F.R.S.

A ROUGH periodicity may sometimes be seen in the progress of science. After a stirring time of advance may come a period of lethargy, or even of negation, followed again by some fresh spurt of activity. At the present moment we seem to have reached a phase of negation in respect of the achievements of phyletic morphology, and in conclusions as to descent. This is suggested by the presidential address in Section K at the British Association at Liverpool. Already Prof. Seward in the Hooker Lecture, 1922, had said, "It may be that we shall never piece together the links of the chain of life, not because the missing parts elude our search, but because the unfolding in all its phases cannot be compared to a single chain. Continuity in some degree there must have been, but it is conceivable that plant life viewed as a whole may best be represented by separate and independent lines of evolution, or disconnected chains which were never united, each being initiated by some revolution in the organic world."

From this and like passages, Mr. A. G. Tansley in his address at Liverpool concludes that such a picture of the history of evolution makes the search for common ancestors literally a hopeless quest, the genealogical tree an illusory vision. As Prof. W. H. Lang once remarked, the most recent graphic representations of the inter-relationships of plants look more like a bundle of sticks than a tree. Contemplating the hypothetical tree thus reduced to a bundle of sticks, Mr. Tansley is further impressed by the growing evidence of homoplasy. He remarks on the increasing doubt whether many organs formerly regarded as homogenetic are of common origin by descent, or really homologous in this sense at all, and he concludes that the more such suspicions effect permanent lodgment in our minds the more uncertain all wide positive phylogenetic conclusions must become. He then states that the whole of this branch of botany seems to leave the great majority of the younger botanists cold. Of course it does when so presented to them. There is nothing more repellent to the aspiring mind than sheer negation, especially if it follows on a period of hope, however ill-founded that hope may have been. This is the present position regarding morphology as sketched from the chair of the Botanical Section at Liverpool. I believe that a similar negative attitude is also to be found among those who pursue zoological science.

How, then, are we to proceed in the inquiry as to the origin of living things as we see them? My reply is, by the continued study of morphology. In Darwin's own words ("Origin," chap. xiv.) this is "the most interesting department of natural history, and it may be said to be its very soul." We must remember that behind the facts of homoplasy, which appear to frighten off the young aspirants, the causes are still to be found, just as much as behind true homologies. The point that they are probably different from what we had thought need not be any deterrent. It is a feeble mind that is daunted by the difficulty of the quest. But we are told nowadays that morphology itself is not one;

that different parts or aspects of it exist; that certain aspects are outworn, others herald a golden age that is coming; that the day of the formal morphologist is already past; the day of the causal morphologist is with us. Is this a true antithesis? In the first place, what do we mean by formal morphology? I understand it to mean, in the broadest sense, the comparative study of form. There can be no argument for evolution at all without such formal morphology, for form is the visible record of what physiology does, and without that record, argument on evolution would be impossible. It is in the interpretation of that form in the light of function, and in relation to the conditions external and internal, that formal morphology—perhaps better designated organography—still has, and will always have, its real value. The day of the formal morphologist in this sense will never be past, and in present practice that is the scope which his cult actually possesses. In fact, those who pursue organography have been anticipating this golden age for years.

An example was recently submitted to the Royal Society of Edinburgh of the newer formal morphology, in certain contributions on size. It was shown that complexity of vascular structure is closely related to actual dimensions. In particular it was found that increase in size, whether of stems or of leaf-stalks, is followed by decentralisation, and often by disintegration of the vascular tracts. Such changes following on enlargement have appeared repeatedly in distinct types, and in different parts of the plant body. In fact, certain characteristic vascular structures appear to depend on actual dimensions rather than on affinity of the plants showing them. Accordingly they lose grade as a basis for phylesis. This argument, which follows directly from the facts of the formal morphology of internal tissues, may be held as falling under the name of causal morphology; for whatever the cause may be, it is certainly related to actual size, as is brought out by the measurements submitted. Accordingly, we learn from this illustration that in present-day practice the distinction between formal morphology and causal morphology is not valid. The modern study of form is in practice inseparable from the study of the causes which bring it into existence.

A close comparison of related genera and species, which would in its execution be ranked as dead formal morphology, is often found to spring into life as disclosing some clear evolutionary trend. In my view no one is properly fitted to investigate questions of evolution unless he should have acquired, by practical study of some natural group of organisms, sufficient experience of formal morphology to classify them himself, or to criticise the classification already advanced by others. I very much doubt whether all of those who write on cytological detail, and rush from extreme minutiae to far-reaching evolutionary conclusions, have passed through any such school. In the discussion of the phyletic relations of classes, I know that generalisations are light-heartedly handled by those who have no detailed systematic experience. This is altogether unsound. An architect would never dare to build a cathedral, or an engineer a bridge, without adequate

¹ Opening address delivered before the Royal Society of Edinburgh on October 22, 1923.

knowledge of the strength of the materials he uses. But the collapse of an ill-constructed theory is a less imposing catastrophe than that of a bridge or a building; so the evolutionist who fails through ignorance or inexperience gets off scot-free. He is not taught in the severe school of public condemnation.

An example of the near relation of specific knowledge of form to moving evolutionary questions of the moment is seen in what have been styled "phyletic drifts." These, which give a fertile stimulus to the inquiry into causes, depend largely for their recognition upon comparison of generic and specific differences of related forms. By the term "phyletic drift" (which may be held to connote a special type of convergent evolution) it is meant to convey that along a plurality of nearly related evolutionary paths, parallel but independent, a similarity of structure has been reached. Phyletic drifts are particularly well illustrated in the ferns, and the similarity of the results in them is sometimes so great that systematists have placed plants now known to have had distinct phyletic origin in the same genus. In no feature is this more impressive than in the slide of the sorus from the margin of the leaf to the under surface. There is no doubt that the primitive position was marginal; but along many distinct phyletic lines it may be traced how the sorus has passed, sometimes early in descent, sometimes later, to a superficial position, and it may be firmly fixed there by inheritance. Another example is seen in the old genus *Acrostichum*, which included representatives of as many as six different phyletic sequences, these having been grouped together on the ground of similarity of soral character. Again, the mixed sorus, which is the prevalent type of modern times, has been acquired along not one line only, but a plurality of them. Another widespread example of a phyletic drift is seen in the diminishing output of spores in the more advanced ferns, and this has been carried out by parallel progression in many distinct lines of descent. But more remarkable still is the reduction in number of the spermatocytes in the antheridia of ferns, which proceeds along lines parallel to those of their reduced spore-production. Many examples of similar parallel progressions are to be found also in the vegetative organs.

Here is indeed ample material for causal inquiry, all brought to light by formal observation. What is it that has affected all of these separate phyletic lines in the same way? Have these striking results originated by inner impulse, or are they the consequence of impress of similar external conditions upon the plants in question? Are these phyletic drifts to be held as evidence of some occult form of inheritance of acquired characters? Such insistent questions of causality are the direct outcome of that purely formal comparison which has brought the phyletic drifts to light. Such results may be described as "homologies of organisation," and, as Prof. W. H. Lang has so well said, "the critical study of homologies of organisation over as wide an area as possible becomes of primary interest and importance" (Address, British Association, Section K, Manchester, 1915). Questions of this sort would never have been raised but for the detailed comparisons of form combined with phyletic argument. Any one who reads my recently published volume on the ferns with ordinary care and intelligence will see that all through

the detailed descriptions the relation to function and to the problem of causation is kept constantly in view. This illustrates once more how the formal and causal aspects of plant organs are inextricably united in modern writing, and how erroneous it would be to regard such writing as a mere summing-up of a past period of formal observation. The facts disclosed have themselves already opened up new lines of causal inquiry.

Another phase of morphology that promises to bring interesting results is experiment, already made fruitful by Goebel (*"Einleitung in die experimentelle Morphologie der Pflanzen,"* Leipzig, 1908). It was said a good many years ago that the future lies with experimental morphology. But those who take this hopeful view appear to forget that present-day experiment cannot possibly reconstruct history, for it is impossible to re-arrange all the conditions as they were in a previous evolutionary period; and even then, are we sure that the subjects of experiment are really the same as they were then? Moreover, those subjects must always react under the limitations of their present-day hereditary character. Hence it is highly improbable that any modern reaction under experiment can be the exact reaction of a former age. The results may be suggestive, but it must always be a question how far they throw real light upon earlier events.

Returning now to the president's address at Liverpool, Mr. Tansley advocates in place of the mere pursuit of phyletic the study of "process of development." But he recognises clearly how "process and structure continually act and interact," and, accordingly, he concedes that "there should be no division of elementary Botany into morphology and physiology." That is surely in essentials the position introduced by Sachs forty years ago under the title of organography. Many of us have thought we were pursuing this all the time, not only in elementary teaching, but also in our research. This study of process of development can only be carried out effectively where there is adequate knowledge of the details of the thing developed. You must visualise your problems before you can hope to solve them. Their complete visualisation in all aspects is what I understand as the scope of morphology; and so I find myself substantially at one with the president. But this is not yet the universal view.

Morphology suffers still under depreciation at the hands of some whose special interest lies in other directions: they would give it only a subordinate place; but it will command its sustained value in the eyes of all those who survey the whole area of biological science with well-balanced view. Its limitations must, however, be clearly recognised. Where genera and species are few and isolated, and the fossil record is scanty, comparative morphology becomes proportionately more speculative, and the opportunity for developing its causal aspect is limited. But where there is an ample present-day representation of allied genera, well filled with species, and where the fossil record is rich and continuous, the scope of comparative morphology expands: any conclusions derived from comparison of living forms will acquire added weight so far as they are found to accord with the fossil record of related types. The most trustworthy line of argument will be the reverse of the line which evolution is presumed to have taken. It will start from an adequate

knowledge of the strength of the materials he uses. But the collapse of an ill-constructed theory is a less imposing catastrophe than that of a bridge or a building; so the evolutionist who fails through ignorance or inexperience gets off scot-free. He is not taught in the severe school of public condemnation.

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knowledge of the living types by study of closely related genera and species. It will progress backwards to earlier geological horizons. Frequently the line of affinity may be found to be more or less seriously interrupted, and gaps may have to be bridged by hypothesis rather than filled in by demonstration. But in favourable instances, and probably the ferns are more favourable than any other phylum of plants, the lines can be traced back with reasonable assurance of affinity of the plants compared to the fossils of the Primary Rocks.

Comparative morphology as applied to the Filicales may be held to have amply justified itself, and to have presented in a coherent and natural phylum a convincing evolutionary picture. Much of the detail may be wanting, and it may be far from being worked out satisfactorily into all its modern ramifications. But the main outline is becoming clear, so that working back comparatively we can build up from the converging downward lines a picture of an archetypic fern. It comes out as a type of vegetation not very different from those plants that constituted the vegetation of the Rhynie Chert. We need not assume that these plants were actual fern-ancestors, but it is not difficult to imagine how from such a type of vegetation as they present a plant might have been derived which would rank as an early Cenopterid.

The Filicales are, however, an exceptionally favourable instance. From what has been said, it will be seen that even this phylum vanishes downwards into uncertainty, and other lines are still less clear. We arrive finally at that *terra incognita* of the early Palæozoic Period sketched by Seward. In this I see nothing that

is deplorable and little that need be held as depressing. Why should we pledge our sense of satisfaction in phyletic study to an evolutionary tree with a single trunk? Why should failure to find such a tree lead any one endowed with a spirit of adventure to sheer off from formal morphology? However many the starting-points of new phyla may have been, or the separate lines of origin of such parts as leaves, the general position of evolutionary theory remains as sound as before this wave of pessimistic negation struck it. Evolutionary history must depend as before primarily upon formal morphology: the study of the "process of development" cannot be held as satisfactory without the "record of development." I am glad to find a somewhat similar opinion expressed from the chair of the Zoological Section at Liverpool in the words that "Morphology must be the forerunner of Physiology."

These two aspects of the study of organic nature should be held to be more than ever inseparable and co-ordinate in the modern developments of biological science. Though specialism may threaten divorce, this should be resisted by all who entertain broad views. A school based primarily on the study of "process of development," and with the "record of development" relegated to the background, might turn out good statisticians, but it would probably fail in converting them into historians. This is what we have been threatened with in recent years. But the president of the Botanical Section of the British Association gives his adhesion to the only sound line when he advocates the co-ordination of physiology and morphology—that is, of the studies respectively of "process" and of "record."

Oysters and their Nutritive Value.

By J. R. NICHOLLS.

THE natural oyster beds of England are a valuable part of British fisheries, and English oysters have been held in high repute from time immemorial. It is interesting, therefore, to find that scientific attention has been directed towards the oyster and its problems. Dr. E. S. Russell has produced an interesting paper based on an elaborate series of analyses carried out by the Government Chemist's Department, whose report is included in the publication.¹

As a rule, monthly samples were examined from Burnham, Ipswich, Mersea and Whitstable during a period of a year. In all, 49 complete analyses are recorded. The average weight of meat per oyster was found to be greatest in the autumn or early winter, and the heaviest meats came from Whitstable, the order of the other districts being Ipswich, Mersea, Burnham. The proportion of water was practically constant. No clearly marked seasonal variation was observed in the percentage of fat, although it appeared to fall off in the autumn and winter. Proteins showed a well-marked change, being highest in the spring months and lowest in the second half of the year, but the total quantity of protein per oyster showed an increase during the growth period and remained nearly constant thereafter.

¹ Report on Seasonal Variation in the Chemical Composition of Oysters. By Dr. E. S. Russell (Ministry of Agriculture and Fisheries, Fishery Investigations, series 2, vol. 6, 1923, No. 1). H.M.S.O. 3s. net.

The most prominent feature was the change in glycogen, which showed a fall in the spring and a rise in the autumn. A general correspondence was observed between the variations in dry weight and variations in glycogen, indicating that the fattening of oysters in the autumn was due to accumulation of this carbohydrate. Glycogen occurs mainly and perhaps exclusively in the large vesicular cells of the connective tissue, and is the main, if not the sole, carbohydrate. As emphasised in the Government Chemist's report, it was found necessary to analyse a special portion of each sample for glycogen immediately after opening the oysters, as glycogen rapidly alters during the preparation of samples for analysis. It seems clear that surplus food material is stored mainly in the form of glycogen, and that this reserve is utilised certainly for the development of the sexual products, and probably also to maintain metabolism during periods of scarcity of food. The part played by glycogen in oysters is therefore similar to that played by fat in vertebrates.

The nutritive value is greatest in the autumn and early winter, hence oysters are then best as an energy-producing food. This period roughly corresponds with "the months with an τ " in accordance with the popular idea.