THE ORIGIN

OF A

LAND FLORA

A THEORY

BASED UPON THE FACTS OF ALTERNATION

BY

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WITH NUMEROUS ILLUSTRATIONS

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PREFACE

In the year 1874 apogamy was discovered in Ferns by Farlow: and in 1884 instances of apospory in Ferns were demonstrated before the Linnaean Society of London by Druery. These events stimulated a fresh enquiry into the nature and origin of Alternation in Archegoniate Plants. My own observations on apospory confirmed my interest in this question: it seemed to me probable that some biological cause had determined the prevalence and constancy of the alternation, to which apogamy and apospory appear as occasional exceptions. The theory was entertained that the change of conditions involved in the invasion of the Land by organisms originally aquatic had played a prominent part in the establishment of those alternating phases of the life-cycle which are so characteristic of Archegoniate Plants. As early as 1889 I had already written several chapters of a treatise on this subject: but the necessary facts were found to be then so imperfectly known that the work was abandoned, and instead of a full discussion of the matter, the Biological Theory of Antithetic Alternation was briefly stated in a paper published in the *Annals of Botany* in 1890 (vol. iv. p. 347). The main position of Celakovsky in discriminating between Homologous and Antithetic Alternation was adopted; but the latter type, as seen in Archegoniate Plants, was recognised as having been fixed and perpetuated in accordance with the adaptation of aquatic organisms to a Land-Habit. The *Studies in the Morphology of Spore-producing Members* were then entered upon as preliminary investigations to elucidate the facts requisite for a more full statement, and they were published in five parts, from 1894 to 1903. Meanwhile, in 1894 Strasburger contributed to the Meeting of the British Association in Oxford his paper on the "Periodic Reduction of Chromosomes." He brought together a wealth of facts establishing the cytological distinction of the alternating generations, and his theoretical position was virtually identical with that of my paper of four years earlier.

Now, after the lapse of seventeen years, it has been possible to state the biological argument more fully in the present volume, strengthened by many new facts. The First Part (pp. 1-254) deals with the general theory. The Second Part (pp. 255-657) is taken up with a detailed statement of the facts, together with comparison of the constituents of the several phyla *inter se*. The Third Part (pp. 658-717) is devoted to general comparisons and conclusions. The attempt has been made to work in the results of Palaeontological research with those of the comparative analysis of living forms. The enquiry has related to all the characters, both vegetative and propagative, of the sporophyte generation: these include the external form, the embryogeny, and anatomical features, and especially the structure and development of the Spore-producing members, while the characters of the gametophyte have also been taken into account. It is found that the conclusions arrived at are supported by general convergence of the lines of evidence derived from all of these sources.

The method adopted in the preparation of this work has been to examine not only the mature structure, but also the development of the organisms, and of their several parts. While fully utilising the results of Palaeontological and anatomical study, considerable weight has throughout been given to the facts of the individual development: sometimes the latter appear to oppose the former. It is not held that the ontogenetic history will always serve as an infallible guide, and opportunity has been taken to point out that conclusions based upon it are liable to be overruled by the results of wide comparison (pp. 159, 636, and 660, footnote). But it is felt that in much of the recent work on Pteridophytes, and especially where fossil comparisons come in, the arguments from individual development have been accorded less than their due share of attention.

I have made no attempt to give comprehensive or complete bibliographical references: from Campbell's *Mosses and Ferns* and from other sources such references can readily be obtained. But wherever a quotation is made, or where a substantial body of information derived from another author has been embodied in the text, the reference is fully given. While thus acknowledging my indebtedness to those whose work is published, I desire also to record the continuous personal help so willingly given by three friends and colleagues, who have all allowed me the use of unpublished drawings and facts. Mr. Kidston's peculiarly exact knowledge has greatly strengthened and amplified the Palaeontological statements, while Dr. Lang and Mr. Gwynne-Vaughan have given me throughout the assistance of friendly criticism, and the support of their special knowledge of certain branches of the matter in hand.

In conclusion, I am well aware that the chief question dealt with

lies outside the realm of possible proof under present conditions: the theory is submitted as a working hypothesis. Naturally it is applicable with greater readiness to those organisms which are less advanced, but less readily to those which have departed furthest along the lines of adaptation to life on exposed Land-Surfaces. Other opinions on the origin and nature of Alternation have come into fresh prominence in recent years, and especially the view that the present condition of the Archegoniatae has originated by differentiation of phases of a life-cycle originally Homologous. This theory has not been disproved any more than the theory of Antithetic Alternation has been proved. Whatever view be ultimately taken of the prime origin of the alternating generations, many of the conclusions arrived at here as to the morphological progress and phyletic grouping of the Archegoniatae will stand: they have a validity of their own quite apart from any question of the ultimate origin of the sporophyte, which has finally become the dominant factor in the Flora of the Land.

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TABLE OF CONTENTS

PART I.

STATEMENT OF THE WORKING HYPOTHESIS

PART II.

DETAILED STATEMENT OF FACTS

PART III.

CONCLUSION

INTRODUCTION.

Of the two branches of the Organic World, the Vegetable Kingdom might be expected to present a simpler problem of Descent than the Animal Kingdom, on account of the prevalent non-motility of the mature individual. That fixity of position which the Higher Plants show, should tend to a more obvious record of previous events than the ambulatory habit of Animals, and especially of their higher types, would seem to allow. It is reasonable to expect that organisms of fixed position should demonstrate in their distribution some traces of their past history; these would be specially valuable in the elucidation of the problem of the Origin of a Land Flora, and of the relation of the Land-growing Plants to those of the water.

But this *primâ facie* probability is largely discounted by the extraordinary facility shown by Plants for the distribution of their germs. A comparison of the Higher Animals with the Higher Plants in respect of motility shows that the motile parent in the former is without special provision for distribution of its germs, while the Plant with its fixity of station shows high elaboration and variety in the methods of their dissemination. In consequence of this there will be a natural tendency in the vegetable kingdom, as there is also in that of animals, towards the obliteration of any such genetic record as the fixity of position of the individual plant during its active vegetation might otherwise have been expected to have left. Accordingly, on examination of the vegetation of any ordinary country-side, its uplands and lower levels, its swamps, streams, and pools, plants of the most varied affinity are found to be promiscuously shuffled together, and show little sign of ranking in their position according to their descent. For instance, the Flora of still fresh waters may be found to consist of such plants as various green Algae and Characeae; of *Isoetes* and *Pilularia*; together with Angiosperms, such as *Littorella*, *Lobelia*, and *Subularia*. In flowing mountain streams, in addition to green Algae may be found *Chantransia* and *Lemanea*, associated with *Fontinalis* and sundry Angiosperms. Conversely, in various positions on land, along with certain Algae in moist spots, representatives

of the great groups of Bryophytes, Pteridophytes, and Seed-plants may be found in close juxtaposition, and sharing the same external conditions. On the sea-littoral it is otherwise: there Algae are found associated together almost to the exclusion of other plants. Nevertheless, occasional Phanerogams do invade the belt between tide-marks, and thus even this limit between the Vascular Flora of the land and the Algal Flora of the sea-littoral is apt to be blurred.

It is plain, then, from such simple examples as these, which might be indefinitely varied and extended, that the problem of the origin of a Land-Flora is not to be solved by any mere reading of the facts of distribution into terms of the evolution of the characteristic plants of the land. Some other basis than that of distribution at the present day must be found for the solution of the problem. It is to be sought for in their comparison as regards structure and function, and that not only in the most complete condition of full development, but also in the successive phases of the individual life-cycle.

The study of the form and structure of plants, as well as of their physiology, directs attention naturally to the water-relation: this more than any other single factor dominates the construction of land-living plants, while comparison with kindred aquatics shows how profoundly land-living plants are influenced by the necessity of adequate water-supply. But not only is this dependence of land-plants on water a general feature of the whole life-cycle: in certain large groups of plants it is found that leading events in the individual cycle are directly dependent upon the presence of external fluid water. The importance of such matters in relation to the present problem of the Origin of a Land-Flora will be gauged by their prevalence and constancy in large groups of organisms. Now in the whole series of Archegoniate Plants (Mosses and Ferns), and in some Gymnosperms the act of fertilisation can only be carried out in presence of fluid water, outside the actual tissue of the organism: their spermatozoids are for a time independently motile in external water, and it is a mere detail that in the higher and more specialised forms, the distance to be traversed is only short from the point of origin of the spermatozoid to the ovum which it is to fertilise. The importance of fertilisation need not be insisted on here: everyone will admit it to be a crisis, perhaps the most grave crisis, in the life-cycle of the plant. When this critical incident in the life is found, in so large a series of allied plants as the Archegoniatae, to be absolutely dependent on the presence of external fluid water for its realisation, that fact at once takes a premier place in any discussion of the relation of plants to water.

A comparison of the Seed-Plants with the Archegoniatae leads without any doubt to the conclusion that their method of fertilisation by means of a pollen-tube is a substitution for that by means of the motile spermatozoid. The Seed-Plant by adopting this siphonogamic mode of fertilisation becomes thereby independent of the presence of external

fluid water at this critical period: it may thus be held to have broken away from a condition of life inconvenient and embarrassing to organisms which live on exposed land-surfaces: and to have established itself in this character, as well as in its vegetative development, as a typical land-living organism. If this view of the matter be adopted, it follows that the Mosses and Ferns occupy a middle position in the relation to water: they may almost be described as amphibious, since, though they vegetate mostly on land, and show certain advanced structural adaptations to such life, they are nevertheless dependent upon external water for the important incident of fertilisation in each individual life-cycle. The strange feature is that they have retained so persistently this aquatic type of fertilisation.

Looking further down in the scale of vegetation, attention is naturally directed towards the Algae, plants resembling, in some superficial characters of cell-structure and of colouring, the simpler terms of the Archegoniate series, though still more dependent than they upon external fluid water for the completion of their life-cycle. It may well be that the affinity which such features suggest is at best only a remote one; but at least the existence of such forms would seem to justify the view as a probable one, that the great Archegoniate series, which has had so large a share in initiating that Land-Flora which we now see occupying the exposed land surfaces of the globe, has had its origin in aquatic forms: that from these a gradual adaptation to a land-habit has provided those forms of vegetation which we group together under the terms, Liverworts, Mosses, Club-mosses, Horsetails, and Ferns: and finally, with further adaptation to the land-habit, came the Seed-Plants—first the Gymnosperms and subsequently the higher Flowering Plants. The latter culminated in the Gamopetalous Dicotyledons, which are essentially of Flowering Plants the most typical elements of a Land-Flora, since they include a smaller proportion of aquatic species than either the Monocotyledons or the Archichlamydeae.

This, then, is the general position adopted at the outset: it is in accordance with the known facts of Palaeontology, and is the view generally entertained by modern morphologists. It will be the object of the present work to enquire into the details of such progressions as those above mentioned; especially it will be our duty to see how far the life-histories of Archegoniate forms will justify the view that the present Land-Flora has originated from an aquatic ancestry, and that there has been a migration from the water to the land: in that case, it will be a further object to ascertain how this has been carried out, and to trace those methods of specialisation to a land-habit, which have led to the establishment of the higher terms of the series as the characteristic representatives of the Flora of exposed land-surfaces.

It is no new view which is thus to be put forward; for it has long ago been concluded that the origin of life, whether animal or vegetable,

has been in the water, and that the higher forms of either kingdom have assumed such structural and physiological characters as enable them to subsist in greater independence of aquatic surroundings than their simpler progenitors. The present attempt will be to fill in certain of the details into this general scheme, as applied to the vegetable kingdom, and to present some connected story of how the transition may have come about, as it may be seen reflected in the plants themselves, whether of the present day or of the remote past.

CHAPTER I.

THE SCOPE AND LIMITATIONS OF COMPARATIVE MORPHOLOGY.

CONFRONTED with the great variety of plant-types which exist living and fossil on the earth's crust, the Botanist may regard them in various ways with a view to reducing them to some general conception of order. He may be satisfied with the mere cataloguing and description of the divers forms which he is able to distinguish, and with the grouping of those together which show characters in common:—this is the work of the Descriptive Botanist, and it naturally took the first place in the historical development of the science. Or he may attempt to find in such similarities of form as are shown by organisms thus grouped together some consecutive account of their probable origin:—this is the work of the Scientific Systematist, or student of Phylogeny, and it is the ultimate aim of all current Morphology.

In the earlier periods the student of form understood himself to be enquiring into the details of the Divine plan, as illustrated in a series of isolated creations: and any similarities which species might show would demonstrate for him merely the underlying unity of that plan. But in these later days he believes that the comparative study of form will lead him towards a knowledge of the main lines of descent. Contributory to this, which can only result in a balancing of probabilities, or often of mere surmises, is the study of the Fossils: Palaeophytology gives the only direct and positive clue to the sequence of appearance of plant-forms in past time upon the earth. Unfortunately the results acquired as yet along this line of observation are so fragmentary that they do not suffice to indicate even the general outline of the true picture: they must for the present be used rather as a check to phyletic theories than as their constant guide. The field is thus left in great measure open to other lines of enquiry.

A second line of evidence which bears upon the evolutionary history may be derived from the geographical distribution of plants upon the

earth's surface. This is, however, applicable only within certain limits: one of those limits is imposed by the wide distribution of germs which is so prevalent in plants. Wherever the mechanism for dispersion of germs is highly elaborated, and successful, the traces of evolutionary history, as shown by geographical distribution, are apt to be obliterated. The consequence is that in practice such distribution is only available as evidence of descent within restricted limits. The great geographical barriers, such as the tropics, the greater oceans, and the more continuous mountain ranges, it is true, delimit at present certain areas of vegetation, within which evidence of value as contributory to a knowledge of descent may be gathered; but at best this applies only to the later phases of evolution, and geographical distribution of plants at the present day gives little clue, or perhaps none at all, to the origin of the great groups which constitute the Vegetable kingdom at large. The fact that such genera as *Equisetum*, *Lycopodium*, *Selaginella*, *Isoetes*, *Marattia*, *Marsilia*, and *Pilularia* are, within their several limits of temperature, virtually cosmopolitan shows how little can be expected from geographical distribution of living forms as a key to the evolution of early types. Among fossils, *Lepidodendron* is virtually cosmopolitan. Plants of the *Glossopteris* flora, long thought to be distinctively southern, have recently been recognised from Russia. Such examples suggest that neither does the geographical distribution of fossils as yet give any certain evidence as to descent of the main phyletic lines.

Another closely related branch of Botanical science is the study of organisms from the aspect of function and circumstance, as tested by physiological experiment. The intimate connection between form and environment is too obvious to need insistence here; but though the individual shows a high degree of plasticity under varying conditions, still there is a large field, embracing the very fundamentals of plant-form, such as the evolutionary origin of leaves, of roots, or of sporangia, which lies as yet outside the region of physiological experiment. Thus, however interesting the branch of physiological morphology may be, its scope is still narrowly limited. The method of experiment, with a view to ascertaining the effect of external agencies in determining form, is now nascent, and carries with it high possibilities. But it is well in the enthusiasm of the moment to keep in view the limitations which must always hedge it round. It is to be remembered that the effect of external conditions upon form is always subject to hereditary control, and that thus a large field is left open still for speculation. This seems to have been forgotten by a recent writer, who remarks that "the future lies with experimental Morphology, not with speculative Morphology, which is already more than full blown."[1] Though we may question the cogency of this antithesis, still the assertion contains an important truth, inasmuch as it accords prominence to experiment; but the case is overstated. All who follow the development

[1] *Flora*, 1903, p. 500.

of morphological science will value the results already obtained from the application of experiment to the problems of plant-form. But it is necessary at the same time to recognise that the two phases of the study, the experimental and the speculative, are not antithetic to one another, but mutually dependent: the one can never supersede the other. The full problem of Morphology is not merely to see how plants behave to external circumstances *now*—and this is all that experimental morphology can ever tell us—but to explain, in the light of their behaviour now, how in the past they came to be such as we now see them. To this end the experimental morphology of to-day will serve as a most valuable guide, and even a check to any more speculative method, by limiting its exuberances within the lines of physiological probability. But present-day experiment can never do without theory in questions of descent. Experiment by itself cannot reconstruct history; for it is impossible to rearrange for purposes of experiment all the conditions, such as light, moisture, temperature, and seasonal change, on the exact footing of an earlier evolutionary period. And even if this were done, are we sure that the subjects of experiment themselves are really the same? There remains the factor of hereditary character: there is also the question as to the circumstances of competition which cannot possibly be put back to the exact position in which they once were. Consequently there must always be a margin of uncertainty whether a reaction observed under experiment to-day would be the exact reaction of a past age. So far, then, from experiment competing with, or superseding speculation in Morphology, it can only act as a potent stimulus to fresh speculation, whenever the attempt is made to elucidate the problem of descent. It will be only those who minimise the conservative influences of heredity, or, it may be, relegate questions of descent to the background of their minds, who will be satisfied by the exercise of the experimental method of morphological enquiry, apart from speculation.

The relations of Morphology and Physiology have been variously recognised in the course of development of the science. In the earlier periods the two points of view rarely overlapped. Even Sachs, the great pioneer of modern experimental physiology, kept the two branches distinct in his text-book, recognising the "Difference between Members and Organs." But later, in his lectures, he brought them more closely together, and habitually regarded morphological facts in their physiological aspect. This is indeed the natural position for any adherent of Evolution: and it has been concisely said that morphology deals with the stereotyped results of physiology. Such a statement may, however, be criticised as assuming too much, in that it accords all initiative in, and determination of form, as well as its selection and perpetuation, to the influence of circumstance and function. A more apposite summing up of the relations of the two branches of Biological science has lately been given by Goebel[1]

[1] "Die Aufgaben und Probleme der heutigen Pflanzenmorphologie," *Biol. Centrbl.*, Bd. xxv., No. 3.

when he said that "Morphology includes such phenomena as are not yet physiologically understood." He further indicates that the separation of the two points of view has not any foundation in the nature of the case, but it is only a preliminary aid to a clear view amid the multiplicity of phenomena. The limits between morphology and physiology must necessarily fall away as advances are made. But meanwhile Morphology must continue to exist, even though it is not and cannot be an exact science: it deals comparatively with phenomena imperfectly explained as regards their origin in the individual or the race. The history of development of plant-form is an ideal to be approached experimentally, and the final object will be not merely a knowledge of the phylogenetic development, but of the very essence and cause of the development itself. It will be obvious how far present phylogenetic theory falls short of this ideal of Causal Morphology, but that is no sufficient reason for discontinuing its pursuit as a progressive study.

For the present the comparative study of plant-form from the point of view of descent, as exhibited in the various phases of the individual life-cycle, must be pursued as in itself a substantive branch of the science: it is clear from what has been said above that it is not co-extensive with either Palaeophytology, Plant-Geography, or Plant-Physiology: nevertheless it overlaps with all of these, and must be liable to be checked by the results of any of these branches. Furthermore, the extension of knowledge of any of these branches will inevitably lead to further overlapping, till in the end the knowledge derived from the various methods of investigation should coincide in conclusions which will be general for them all, and constitute a true perception of the evolutionary story. But at the moment this consummation is so far from being attained that there is still room for the theoretical treatment of the evolution of plants as based on the formal comparison of their life-cycles. This must take due cognisance of the other branches of study, but will still rest upon its own footing of fact and conclusion.

There is one assumption involved in such comparative study which should be clearly apprehended and considered, rather than tacitly passed over. An evolutionary argument based on comparison of life-cycles is only valid if the organisms compared have retained the main incidents in their individual life unchanged throughout descent. In the main argument of this work, the assumption is deliberately made that such constancy existed, or, rather, the argument proceeds upon the conclusion derived from broad comparison, that the main incidents once initiated have been pertinaciously retained. It may be held, and reasonably defended, that sexuality may have arisen in many distinct phyletic lines. It is not our present purpose to distinguish those different origins, or defend their distinctness. But comparison leads us to conclude that, once initiated in an evolutionary sequence, sexuality remained throughout descent substantially the same process in normal life-cycles. It may be modified in mechanism,

as indeed there is good reason to see that it was; but it consisted still in the fusion of two cells together, bringing, as we believe generally, and see proved already in so many cases, a doubling of the chromosome-number as a consequence. Seeing sexuality of this nature a constantly recurring feature in the life-cycle of various definite phyla leads to the conclusion that in those phyla it was also constant during their descent. Similarly, a reduction of chromosome-number has been found to be regularly associated with normal spore-production, and spore-production is found to be a constantly recurring event in large series of plants. In these it is concluded that reduction and spore-production have also been constantly recurring incidents throughout the descent of those series. It is hardly right to designate this opinion as an assumption: it seems rather to be a natural and valid outcome of comparative study. But if, on the other hand, such constancy of the leading events of the life-cycle in any phylum during descent were to be clearly disproved, then it will follow with equal clearness that the comparative argument based upon such facts will have to be revised for that phylum. It may seem hardly necessary to put down *in extenso* reasoning which is so obvious; but, on the other hand, it is well to see clearly the basis upon which the main argument will proceed. The constancy of the events of sexuality and of spore-production in normal life-cycles of the several ascending series of green plants is itself the cardinal point of the theory to be advanced in relation to the origin of a Land-Flora. In so far as inconstancy of either of these events occurs in them it will be shown that there is good reason to believe such exceptions to be of relatively late origin.

The further facts which form the basis of Comparative Morphology include those relating to the mature external form of the plant, as seen in the successive phases of the individual life-cycle: the internal structure, as shown by its anatomical study: the form and structure of the parts involved in propagation, and the embryology of the individual. Such facts relating to living organisms are to be read in the light of comparison with the fossils, and the validity of any conclusions tested as far as possible according to the results of physiological experiment.

It has been customary from the earliest times of natural classification to group together as akin, according to their degree of similarity, those organisms which correspond in form. Such alliances, long ago recognised, received a new significance in the light of evolutionary theory: the likeness thus comes to be attributed to community of descent, the nearness of the kinship being held proportional to the similarity of form, structure, and development of the individual. It is essential, however, to bear in mind always that this is only an hypothesis, incapable of complete proof under present conditions of study, and that the extent of direct evidence as yet available is small indeed. It is true that variation in different degrees is widespread, that, whatever the causes or methods involved, new races may be, and indeed have been established, which come true in more or