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THE ORIGIN OF LAND PLANTS[1]

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THE problem of how the existing vegetation of the earth has come into being is one of perennial interest to the botanist, and I have chosen as my subject some of the conclusions to which botanists have come as to the history of the plant life which now occupies so large a part of the earth's surface.

The evolution of the plant kingdom always has had for me a special fascination, and since my first serious botanical studies nearly fifty years ago, the subject has occupied a prominent place in my scientific work. Not, perhaps, a particularly practical subject, as ordinarily understood, and no doubt some of my audience may think it a waste of time to have devoted so large a part of one's life to such investigations. "What use is it all?" one may ask, and the answer must depend on one's outlook on life.

I might reply that it has furnished me a livelihood—that I have been well paid for doing what I most wanted to do. This might be given as a "practical" result of my activities. I am afraid, however, that I have even encouraged some of my students to go ahead in similar unpractical lines of research, hoping that they might have some of the same satisfaction in their life work that I have found. If I have succeeded in some degree in this, I feel that I have as truly performed a service as if I had merely equipped them to go out into the world and fight for money and what it brings.

The pursuit of science for the love of it, and not primarily for the material rewards it may bring, has results that no money can purchase. Such a love of

[1] Address of the president of the Pacific Division of the American Association for the Advancement of Science, Eugene, Oregon, June 20, 1930.

science may well be put by the side of the other arts, music, literature or painting—those things which we feel must have a place in the life of every truly civilized being. Having these resources, one need not be afraid of one's own company, and is independent of the multiform devices for killing time which at the present day seem indispensable to so large a part of mankind.

If we glance at the plants about us, we soon realize that a very large majority live on land, the number of aquatic species being relatively small. Of the land plants the major part are the familiar flowering plants. Next in number are the many fungi, including a host of parasitic forms, rusts, mildews, etc., with which the farmer and gardener are only too well acquainted. These, however, I hardly feel competent to discuss. Since there is abundant evidence that the primitive plants were aquatics, the botanist has to meet the problem as to the factors concerned in the migration of the aquatic ancestors of the existing land plants to their present terrestrial environment, and the extraordinary evolution of new forms which has accompanied this radical change of life on land.

If all the plants, from the earliest times to the present, had left fossil remains throughout the successive geological ages, the story of the evolution of the plant kingdom would be a comparatively simple matter; but, unfortunately, the fossil record is extremely imperfect, especially as regards the more primitive plants, which are, for the most part, too perishable to have left recognizable fossil remains. Where more resistant structures are present, such as the lime or flint incrustations of some algae, or the woody tissues of the so-called "vascular" plants, like ferns and many flowering plants, these have often been preserved very perfectly, either as impressions, or less commonly as actual petrifactions, like fossil wood, where one may make thin sections for microscopic study which sometimes show the cellular structure almost as perfectly as if made from living tissue.

From such fossil remains much has been learned about the early history of many important groups of plants, and we may hope for much more assistance from further discoveries by students of fossil plants in deciphering the story of plant evolution.

Owing to the incompleteness of the fossil record, we must have recourse to a very thorough comparative study of the living plants in our endeavors to trace their relationships. If we compare any two plants, we shall find a greater or lesser degree of correspondence in their structure, and from the degree of similarity between them we assume an indication, to a great extent, of the degree of genetic relationship. This comparative morphology must include not only the adult structure, but also the development of the organs of the plant from their earliest stages. Such study may embrace the whole life history of the plant from the germ-cell, or egg, to its mature form. Such a study of the development of the individual we call ontogeny, and such ontogenetic studies are of great importance in the establishment of a natural system of classification, as the developing embryo repeats, to some extent, the history of the group to which it belongs—or its phylogeny.

While comparative morphology is probably the most important factor in determining relationships, it is by no means infallible, and one has to exercise great caution in drawing one's conclusions. This is especially true where certain superficial organs are concerned. Thus the leaves of some seaweeds, mosses and flowering plants have a marked similarity in form and function, but we are certain that they are independent developments in three entirely unrelated plant types. Such organs have been called "analogous" but perhaps a better term is the more recent one, "homoplastic" as opposed to "homologous" organs, which latter are assumed to be genetically related. It is often difficult, however, to decide with certainty whether certain structures are really homologous or merely homoplastic.

Geologists tell us that in the earliest periods of the earth's history the seas were much less salt than at present, and that the first organisms probably lived in fresh water. Some of the simplest living things, like certain Protozoa and simple Algae, may have persisted to the present, little changed from these remote ancestors, since they are perfectly adapted to their fresh-water environment, which has not altered materially from the earliest times. It is, therefore, among such relicts of ancient life that we must look for the nearest relatives of the ancestors of the modern vegetation.

The term alga is usually given to all the plants below the mosses which possess the characteristic green pigment chlorophyll. Several independent classes of algae are recognized by the most recent students of the algae, most of these classes having, in addition to chlorophyll, other pigments. Two of these classes, the brown algae and the red algae, the former including the giant kelps of the Pacific Coast, are with few exceptions inhabitants of salt water. It is these highly specialized forms that mark the culmination of the algae, and at the present time they are the dominant plants of the ocean and have evidently best solved the problem of life in salt water; to their peculiar environment are doubtless due their most marked characteristics. There is little reason to suppose that any of the land plants have arisen from these seaweeds.

The green algae, on the other hand, probably represent the remnants of the primordial fresh-water vegetation, which has persisted with little change to the present time. It is from forms related to these primitive green algae that there is a good reason to believe the first land plants are descended. One of these classes, the Chlorophyceae, have the chlorophyll unmixed with other pigments, and probably represent the nearest approach to the lower land plants, since the latter have much the same cell structure, including pure-green chromatophores, and with relatively few exceptions are dependent on fresh water for their existence. We may assume that the land plants, now the predominant type, are descended not from the large complex seaweeds but from much simpler fresh-water green algae. One order of the Chlorophyceae, the Ulothricales, show approximately, at least, what may have been the course of evolution in the ancestors of the earliest land plants.

Many algae are unicellular organisms, and sometimes are capable of locomotion closely resembling some of the simplest animals, Protozoa; but they differ from these animal cells in the presence of chlorophyll, which is associated with the power of utilizing the energy of sunlight for the manufacture of organic compounds, *e.g.,* starch and sugar from CO_2 and water. This power of photosynthesis is the essential character of all green plants.

Starting with this free-swimming green cell, the first step in the development of the plant-body is the loss of motility and the investment of the cell with a definite membrane, or cell wall. By repeated division in a single plane such a cell may give rise to a row of similar cells—a filament. Sometimes the contents of a cell may escape, as a naked free-swimming "zoospore"—or several zoospores may be formed from the cell contents. These later settle down, develop a cell wall and grow into a new filament.

This reversion of the reproductive cells to the motile condition is a feature which is retained even in some of the seed-plants, and is perhaps the strongest evidence of the aquatic origin of the land plants.

The simplest type of a multicellular plant is the simple filament, or cell-row. Should divisions occur in two planes, a cell-plate results, and if in three planes a solid plant body, which may assume various forms, and in such large algae as many red and brown seaweeds may reach a size and complexity rivaled only by some of the higher land plants. No fresh-water algae show anything comparable to these salt-water giants.

Unlike the sea with its constant water level, where no seaweeds are exposed to prolonged drying up, most bodies of fresh water are more or less subject to marked changes of level as well as to much greater range of temperature than prevails in the ocean, while shallow ponds and streams are often completely dried up for long periods. We find, therefore, that most fresh-water algae have developed means of surviving periods of stress due to cold or drought. Some can exist with a minimum water supply and survive long periods of complete desiccation. The little unicellular plant, Protococcus (to use the old name), which forms dark-green films on shady walls, old flower-pots, etc., may be cited as an example. A few green algae may even become true land plants, developing delicate roots which penetrate moist soil and absorb water to replace that lost by evaporation. The curious little *Botrydium* is an instance of such a terrestrial alga. However, the limitations of such a simple form are obvious, and so far as I know, none of the algae have developed a really successful land plant.

The problem of surviving cold and drought has been solved by many green algae in quite a different fashion. In addition to reproduction by simple cell division and growth, special reproductive cells, known as gametes, are developed. The gametes are sexual cells—that is, the fusion of two of them is necessary for their further development. This fusion cell, the zygote, in most cases, develops a heavy cell-wall and forms a "resting-spore" capable of resisting cold and drought, which would be speedily fatal to the parent plant. When conditions are favorable the zygote germinates, the contents usually divide into several cells which escape as free-swimming zoospores, each of which develops into a new plant.

The gametes may be alike, but in most cases there is a differentiation into large female gametes or eggs, and much smaller males, or sperms, the latter being always actively motile, while the female gamete is usually non-motile, and is retained in the mother-cell (oogonium), where it is fertilized by the active sperm.

Although it is generally assumed that the first land plants were derived from some fresh-water green algae, it must be admitted that at present we know of no forms which satisfactorily bridge the gap between the algae and the simplest land plants—the so-called archegoniates.

Of the algae, the genus *Coleochaete* shows the nearest approach to the archegoniates in the development of the zygote, which enlarges greatly after fertilization, and on germination produces a much greater number of spores than any other green alga. This is obviously a great advantage. However, the differences in the development of the reproductive organs and the zygote, which develops zoospores on germination, are too great to indicate any direct relationship between Coleochaete and any known archegoniate.

The first invasion of the land by the algal ancestors of the higher plants must be regarded as perhaps the most momentous event in the history of the plant kingdom.

In the comparatively uniform environment of aquatic life there is much less scope for variation and selection to operate; but once established on land, surrounded by air instead of water, the fundamental growth factors—moisture, temperature, light and gravitation—become far less stable and the range of variation is evidently greatly increased, with a correspondingly enlarged field for the operation of natural selection. The results we see in the enormously greater range of structure in terrestrial as compared with aquatic organisms, both plant and animal.

When the plant exchanges its aquatic habitat for life on land it must undergo radical changes in structure. First in importance is the solution of the water problem. The submersed aquatic, surrounded by water, has no need for special organs for absorbing water, which is taken in at all parts of the surface, nor is there need for protection against loss of water by evaporation. The land plant, on the other hand, must be able to extract water from the soil, both for obtaining food and for making good the loss of water by evaporation into the air.

We find, therefore, that the typical land plants develop special organs, roots, for water absorption, and the surface cells of the stem and leaves have their outer walls more or less perfectly water-proof, and thus check evaporation. It is true that some of the lower land plants, such as many mosses and lichens, and even some ferns, can absorb water directly by their surface cells—very much as an alga does—but such plants dry up completely and remain dormant in dry air.

A submersed plant—whether alga or such a flowering plant as a pond-weed—is buoyed up by the dense medium in which it is suspended. Taken from the water, it collapses completely. The land plant must develop special supporting or "mechanical" tissues to overcome the force of gravity, or else lie prone on the ground, as we see some liverworts, among the most primitive of the land plants, and in this respect they recall their kinship with the algae.

With the increasing size of the land plants, in addition to the purely supporting or skeletal tissues, there has been developed a very complete system of conducting tissues through which water and the substances dissolved in it are transported through the plant. The woody bundles extending through the root and stem and the elaborate network of veins in the leaves serve both for giving firmness to the organs and as routes for water transport.

Since atmospheric conditions vary greatly as to temperature and moisture, land plants have had to adjust themselves to such extreme conditions as those of the saturated equatorial forest, the burning desert and frozen Arctic tundra. The water needs of a banana growing in the jungles of Borneo are very different from those of a cactus in the Colorado Desert or a dwarf willow in northern Alaska, and the temperature requirements are equally diverse. The banana, with its high water demand, is very limited as to its tolerance of temperature changes, while the willow, able to exist with a very small amount of water, can endure a range of 150° F. or perhaps more—a condition quite inconceivable for any truly aquatic plant.

All the typical land plants, *i.e.*, mosses, ferns and flowering plants, have much in common, and their reproduction is essentially the same. The egg-cell, when fertilized, instead of developing a resting-spore, as it does in the green algae, at once begins to grow and divide, so that a multicellular embryo results. Hence the name embryophyte has been proposed to include all these higher plants.

Some of the lower moss-like plants, the liverworts, probably resemble pretty closely the first land plants. These are small plants of very simple structure, lying flat on the ground, to which they are fastened by delicate roots. Structurally some of these liverworts are less complex than many algae, being composed of almost perfectly uniform cells. The green algae which seem to show the greatest resemblance to the liverworts are the Ulothricales, already referred to. Among the liverworts, one order, the Anthocerotales, closely resembles the Ulothricales in usually having but a single chromatophore in the cell—a condition found in many green algae.

A few liverworts are true water plants, and the life history of one of these suggests what may have been the transition from the aquatic environment to life on land. This liverwort, *Ricciocarpus,* usually is a floating aquatic. If, however, the water dries up, the plant settles on the mud and grows more vigorously than it does in the floating condition. Roots are developed, and the form of the plant becomes quite altered. It suggests that in similar fashion the algal ancestors of the land plants, stranded by the evaporation of the water, may have developed roots as the result of the contact stimulus of the solid earth, and thus would be able to prolong their growing period. It is conceivable that in some such manner was inaugurated the line of land plants which was destined to become the dominant type of the future.

The essentially amphibious nature of all the more primitive land plants is shown by their dependence on free water for fertilization. In all these the reproductive organs are very characteristic structures. If we examine these in a liverwort, we find the egg-cell contained in a flask-shaped structure, the archegonium. Since this archegonium is very much the same in the mosses, ferns and even in some of the lower seed plants—these have been called archegoniates. The male gametes are also borne in multicellular organs, antheridia, but these are much less uniform than the archegonia. However, in all these forms, the male gametes or sperms are free-swimming, ciliated cells, like those of the green algae, and in order that they may function, free water is necessary. Only when they are covered with water can the reproductive organs open and permit the sperm to escape and penetrate the open neck of the archegonium, and thus reach the egg-cell.

The embryo resulting from the fertilized egg develops into a structure very different from the plant which bears the gametes, and which is therefore called the gametophyte or sexual plant. The one produced from the embryo does not become free, but remains attached to the gametophyte upon which it lives as a parasite. Sooner or later a large part of the inner tissue of the embryo develops into special reproductive "sporogenous" cells, each one of which gives rise by division to a group of four spores. The fully grown embryo, therefore, is the non-sexual or neutral plant, or sporophyte.

In the process of fertilization there is a fusion of the nuclei of the sperm and egg, and the fusion cell, or zygote, has twice as many chromosomes as the gametes. The chromosomes are those remarkable constituents of the nuclei, the supposed bearers of hereditary characters. The nuclei of the gametes are said to be haploid, while the zygote nucleus, with the double number of chromosomes, is diploid. In all embryophytes, the diploid character of the cells of the sporophyte persists until the first division of the spore mother-cell, when by a peculiar type of nuclear division—the reduction division, or meiosis—the haploid number is restored, and the gametes developed from the germinating spores have haploid nuclei.

This alternation of the sexual with the non-sexual or neutral phase, produced as the result of fertilization, characterizes all embryophytes.

Of these, the forms which most nearly resemble the algae are some of the liverworts and the gametophytes of some of the ferns, and there is no great difficulty in comparing these with algae; but when we consider the reproduction, the resemblances are not so obvious. The complex, multicellular archegonia and antheridia are very different from the usually unicellular organs of the green algae. It is true that in some of the algae—especially the brown algae, the cells containing the gametes are massed in groups of definite form, known as gametangia, and it has been suggested that possibly from similar gametangia in some green algae the archegonium and antheridium of the embryophytes have been derived. This, however, is only a guess.

The more critically the archegoniates are studied, the more evident it becomes that the living forms are remnants of a number of independent lines of development whose relationships with each other are to say the least uncertain. Two main groups are generally recognized: the bryophytes—mosses in a broad sense; and pteridophytes, of which the ferns are the typical representatives. This division is based upon the relative importance of gametophyte and sporophyte—the former predominant in the bryophytes, the latter in the pteridophytes. This classification, however, can hardly be accepted as an entirely scientific one.

While the gametophyte of many liverworts much resembles in appearance some of the algae, there are many others, and especially true mosses, in which the gametophyte may develop into a plant of relatively large size, in extreme cases forming leafy shoots a foot or more in length with specialized tissues for support and water conduction, suggesting the structures of the sporophyte in the so-called vascular plants. The root system, however, is deficient, and mosses depend largely upon the direct absorption of water through the leaves, behaving much as an alga would do.

The apparent inability of the gametophyte to develop adequate roots perhaps accounts for its failure to reach dimensions at all comparable to those of the higher plants, and in none of the larger ones are the skeletal tissues sufficient to enable them to maintain a truly upright position.

The gametophyte of the archegoniates is the descendant of some strictly aquatic plant, and it is not unlikely that there are limits beyond which such a type can not progress. The higher mosses, which represent the most perfect development of these originally aquatic organisms, can not be said to have quite satisfactorily solved the problem of a plant perfectly adapted to life on land.

The further evolution of the land plants is mainly bound up with the neutral generations, the sporophyte. The origin of this we believe is to be found in the zygote or resting-spore of some green algae. This zygote may be said to represent a terrestrial phase of the alga—a condition fitted to survive drought and thus carry the plant over from one growing period to another. The fact that the zygote, the equivalent of the sporophyte of a liverwort or fern, is from the very first a structure fitted for life outside the water must be borne in mind in following the further history of the higher plants.

In those algae which are assumed to be the nearest relatives of the archegoniates, the zygote on germination produces several (usually motile) spores, each of which gives rise to a new plant—an evident advantage over such forms as produce but a single plant from the zygote. In Coleochaete—already referred to—the increase in size of the zygote, subsequent to fertilization, and its development into a globular multicellular body, which to a certain extent resembles the young embryo of some of the archegoniates, have suggested a possible relationship between them. While it is highly improbable that there is any direct relationship, it is pretty certain that the sporophyte of the first archegoniates must have been derived from a structure not very different from that found in Coleochaete.

A study of the development of the sporophyte of the bryophytes shows the general trend of evolution leading to the higher so-called vascular plants. The evidence, however, is much too fragmentary to permit of more than general conjectures as to what were the ancestors of the pteridophytes.

The simplest known sporophyte is that of a liverwort, *Riccia*. The embryo becomes a globular body, all of whose cells, except an imperfect superficial layer, produce spores. In most liverworts, however, the embryo is divided into an upper sporogenous region, and a basal sterile region which later forms the foot, and a more or less conspicuous stalk connecting the foot and the sporogenous region, which becomes a capsule containing the spores. The foot penetrates the surrounding tissue of the gametophyte, from which it draws the water and food materials for the further growth of the sporophyte, which thus lives as a parasite upon the parent gametophyte.

In none of the true liverworts does the sporophyte attain any considerable degree of independence, but serves merely as an organ for spore production.

In the true mosses the sporophyte becomes much more important, and spore production is to a considerable extent subordinated to the vegetative life of the sporophyte. The growth of the sporophyte may continue for a long time before any sporogenous tissue is apparent, and the amount of this is small compared to the sterile tissue. Some of the latter develops chlorophyll, which enables the plant to utilize the CO_2 of the atmosphere and is therefore quite independent of the gametophyte for its organic food, although it still obtains water and mineral substances through the foot, and never becomes entirely independent. A well-developed conducting tissue may also be formed, and a very elaborate mechanism for the dispersal of the spores. These highly differentiated structures indicate that the true mosses form a very specialized class with little direct connection with any other plants.

The very early history of the fern embryo is quite like that of the simpler liverworts, but very soon a radical difference may be noted. Instead of the globular or cylindrical form of the liverwort sporophyte, terminating in a single spore-capsule, the fern embryo at a very early stage shows the development of special organs. A large foot is present, but instead of the spore capsule two prominent outgrowths appear, one of which grows upward and soon appears as a fan-shaped green leaf, while the other, bending down, is a true root, which fastens the young sporophyte to the ground and thus connects it directly with the water-supply. With the leaf, a special organ for photosynthesis, and the roots, furnishing water, the sporophyte for the first time becomes an independent plant. A definite stem apex is established and new leaves and roots continue to form, and it may reach a large size and live for many years.

During the early stages of development, the sporophyte receives nourishment from the gametophyte through the foot, exactly as in the liverworts; but with the establishment of the roots, the gametophyte dies, leaving the sporophyte established as an independent plant.

The production of spores is often delayed for many years, the sporophyte increasing in size and developing a complicated system of organs and tissues. Of the latter the most notable is the elaborate system of conducting tissues—the "fibro-vascular" bundles, a feature of all the higher or vascular plants. In the common ferns the spores are contained in special capsules—sporangia—which are borne upon the lower surface of the leaves. The form and position of the sporangia are important factors in the classification of the pteridophytes.

Of special importance in connection with the origin of the pteridophytes is the very peculiar order Anthocerotales, or horned liverworts, already referred to, and usually considered to be true liverworts. They differ so much from these, however, that their separation, as a distinct class, seems warranted. Of all the bryophytes, the gametophyte of the Anthocerotales, with its very simple structure and alga-like chromatophores, most nearly resembles the green algae from which it is assumed the archegoniates are descended. On the other hand, the gametophyte and reproductive organs show some striking similarities to the lower pteridophytes. We might perhaps say that in a sense the Anthocerotes represent a synthetic type, allied on the one hand to the green algae, on the other to several distinct lines of bryophytes and pteridophytes.

While the gametophyte is so simple in structure, in which it agrees with some of the more primitive ferns, the sporophyte may show a long-continued growth, and in exceptional cases may attain practical independence. In the genus *Anthoceros* the sporophyte is a slender cylindrical body which may reach a length of ten centimeters or occasionally even more. At the base is a large bulbous foot, and above the foot is a zone of actively growing tissue to which the elongation of the growing sporophyte is due. In the most highly developed cases the foot becomes much enlarged, and possibly may come into direct contact with the earth. As in the true mosses, there is a great reduction in the amount of sporogenous tissue, outside of which is a thick mass of green cells, active in photosynthesis, and as in the higher plants, stomata, or breathing pores, occur in the epidermis. Occupying the axis is a strand of elongated cells which in exceptional cases may be fairly described as a primitive vascular bundle—in short the sporophyte in *Anthoceros* may very fairly be compared with that of the most primitive pteridophytes.

In speculating upon a possible connection of the Anthocerotes with the origin of the pteridophytes, it is noteworthy that among the oldest fossil remains of land plants certain extremely simple vascular plants, the Rhyniaceae, from the lower Devonian formations of Scotland, were in structure extraordinarily like some large sporophytes of *Anthoceros*.

In the evolution of the sporophyte of the archegoniates, the most significant fact is the progressive reduction of the spore product and the increasing importance of the sporophyte as a whole, compared with the gametophyte. In the true liverworts the life of the sporophyte is brief, and its exclusive function is the production of spores. In the mosses and Anthocerotaceae, the growing period of the sporophyte is greatly prolonged on account of the production of green tissue which enables it to make its own food, but it is still dependent on the gametophyte for water, as it does not develop a root. The sporogenous tissue is greatly reduced in amount. Finally, in the ferns, by the development of a root which gets its water-supply directly from the earth, the sporophyte becomes a truly independent plant, in which the spore-function is more or less incidental.

The increasing importance of the sporophyte in the life cycle of the plant is thus bound up with transformation of potentially sporogenous tissue into sterile or vegetative tissue. The significance of this progressive sterilization of sporogenous tissue as a factor in the history of the land plants has been treated at length by the distinguished British botanist, Professor F. O. Bower.

FOSSIL RECORD

When the first land plants appeared we do not know. The earliest known fossil records are in the Devonian rocks, but these are of vascular plants related to some living forms, and it is evident that they must have had a long ancestry of simpler forms behind them.

Mosses and liverworts are too perishable to have left fossil traces, except under very unusual conditions, and fossils of these, even in more recent formations, are very scanty and fragmentary, and throw little light upon their early history.

Of the vascular plants, however, including ferns, club-mosses and other existing types, there are abundant fossils, extending from the lower Devonian formations to the present. These fossils include not only impressions of stems, leaves and fructifications, but in many instances petrifactions which make it possible to study their microscopic structure, and these have furnished much valuable information as to the nature of some of the oldest known vascular plants. All the existing classes of pteridophytes can be traced back to the early Devonian formations and indicate that they have probably originated from independent but similar bryophytic ancestors.

As is so frequently the case, the most specialized of these ancient types have disappeared before their still more perfect descendants, while the lower and more generalized have persisted, or have left descendants which have been able to occupy positions to which more specialized forms are not so well adapted. Thus the giant pteridophytes of the Coal Measures have given way to the more modern trees, and to-day the tree-ferns alone remain to remind us of their past glories. The more humble ferns and club-mosses still play an important rôle in the vegetation where conditions are favorable, as in New Zealand and the mountain forests of the tropics; and a few, like the field horsetail (*Equisetum*) and the common bracken fern, manage to hold their own against the predominant flowering plants, even in very unfavorable conditions.

Of the existing pteridophytes the ferns form a very large majority, but most of the types found in the older formations are now extinct and have been replaced by those now existing, which are of relatively recent origin and which have succeeded, like the still more recent flowering plants, in adapting themselves to existing conditions. Some of the modern tree-ferns rival in size their fossil prototypes. The other living pteridophytes, the horse-tails, club-mosses and Psilotales, are few in number, compared with the ferns, and are but poor relations of the giant Lepidodendrons and Calamites of the Coal Measures.

As the primitive land plants adapted themselves more and more perfectly to the increasingly diverse conditions associated with their new environment, the evidences of their aquatic ancestry became less apparent, and finally in the highest of all plant types, the seed plants, disappeared.

The mosses and ferns illustrate the transitional stages through which the seed plants have passed in their evolution from their primitive aquatic ancestors, the green algae. In the bryophytes the history of the gametophyte shows the limitations of this aquatic organism in adjusting itself to the radically different water conditions to which land plants are subjected. Even the most perfect gametophytes, such as those of the higher mosses, owing to their failure to develop adequate roots and efficient skeletal tissues, are unable to attain any but the most modest dimensions. Moreover, these plants are essentially amphibious and free water is necessary for fertilization.

In the ferns the development of the race centers in the sporophyte—the neutral generation. This, being the product of the fertilized egg-cell, is equivalent to the zygote or resting-spore of the ancestral green algae from which it is assumed that the mosses and ferns are descended. As the zygote of the algae is usually fitted to survive periods of drought, we may say that the sporophyte from its earliest beginning has been an organism fitted for life on land. It evidently has a potentiality for development on land that is not shared by the essentially aquatic gametophyte. It might be said that nature, having in the mosses exhausted her resources in the endeavor to transform the aquatic gametophyte into a successful land plant, turned to the spore-bearing generation as a more promising subject for experimentation. In the ferns, therefore, we meet for the first time a sporophyte which has true roots with sufficient capacity for water absorption to provide for the further development of the sporophyte, which thus becomes a perfectly developed land plant, with stem, leaves, roots and elaborately developed tissues.

With the increasing importance of the sporophyte there is a gradual reduction in the gametophyte, which becomes more and more insignificant, finally resulting in its reduction to minute, almost microscopic size in what are known as the "heterosporous" pteridophytes. These heterosporous forms occur in several unrelated groups, and it is evident that heterospory has been developed quite independently in these.

Heterospory is the first step toward the development of the seed habit. In the ordinary ferns the spores are all alike, and the gametophytes developed from them bear both male and female gametes. Occasionally from similar spores gametophytes of two sorts—male and female—are produced, and in such cases the male plants are smaller than the females. In the heterosporous forms, such as the water fern, *Marsilia,* sporangia of very different sizes are developed: large ones, in which only one very large spore—the megaspore—comes to maturity; and small sporangia, in which all the spores—microspores—develop. The gametophytes in both cases are reduced to a few cells and are retained within the spores, and the whole development of the gametophytes is completed within less than twenty-four hours. From the megaspore, the female gametophyte is formed; from the microspores, the male.

In the club-mosses of the genus *Selaginella,* the macrospores remain within the sporangium until the development of the gametophyte is far advanced and may even be retained permanently within it, and the growing gametophyte draws upon the tissues of the sporophyte for its nourishment, thus reversing the relation of sporophyte to gametophyte as compared with the lower archegoniates.

The seed is a further elaboration of the megasporangium. In the seed plants the megaspore is retained permanently within the sporangium, where it completes the development of the gametophyte and fertilization is effected. The embryo plant, enveloped in the double covering of the spore membrane and the sporangium wall, which becomes the shell of the seed, is very effectively protected from external vicissitudes, and during its development can draw upon the parent plant for its food supply. It moreover stores up in the ripe seed the reserve food which is necessary during germination. The advance of the resting stage of the plant, from the simple spore in the fern to the embryo within the seed, gives the seed plants a great advantage in the certainty and rapidity with which the new generation is established. The seed habit has resulted in a plant type peculiarly adapted to life on land, as is shown by the extraordinary development of seed plants at the present time.

All the primitive seed plants have their seeds exposed on open leaves or scales, and are known as gymnosperms to distinguish them from the higher flowering plants, the angiosperms. Like the terms bryophyte and pteridophyte, these are convenient, but do not imply a necessary close relationship among all the members of the class.

The earliest seed plants, whose remains are found as far back as the Devonian era, were very different from any of the existing ones. Some of them were evidently related to the ferns and have been called pteridosperms or seed ferns. Others were related to the club-mosses, and still others are not clearly related to any existing types. The evidence that seeds were developed in a number of unrelated plants makes it extremely probable that the living seed plants also represent several independent lines of development.

Of the older types of seed plants still existing, the conifers—pines, firs, redwood, etc.—are the most numerous and familiar. The flowers of these are composed of closely set scales upon which are borne respectively the macrosporangia and microsporangia. The structure of these may be readily compared to that of some of the heterosporous pteridophytes. In the megasporangium a single large megaspore is formed within which a gametophyte with several archegonia is developed, much as in Selaginella. The megaspore, however, is retained permanently within the sporangium, and this necessitates a quite different method of fertilization. The megasporangium in the seed plants is known as the ovule.

The microsporangia are much like those of the ferns, and the microspores are formed in tetrads, as in all typical archegoniates, and are called pollen-spores. A very rudimentary gametophyte with two sperms is formed within the spore. The ripe pollen spores fall upon the apex of the ovule (megasporangium) and send out a slender tube which penetrates the tissue overlying the archegonia and discharges the sperms into the archegonia. Unlike those of the ferns, the sperms have no cilia. The pollen tube does away with the necessity of water for effective fertilization, and the last trace of the aquatic origin of these plants disappears.

In a number of the most primitive seed-plants, especially the fern-like cycads, motile sperms have been discovered. In these the pollen tube becomes greatly distended by an accumulation of water, and finally bursts and discharges the water together with the large ciliated sperms into a chamber which lies above the archegonia. So we see that, even in the seed plants, the same aquatic type of fertilization may occur that obtains throughout the whole archegoniate series from which these plants are descended.

That the seed habit developed a number of times in quite unrelated groups of pteridophytes is amply shown by the fossil remains of seed-bearing plants in the Paleozoic, as far back as the Devonian. Some one, or perhaps more than one, of the seed ferns were probably the progenitors of the living cycads and the abundant cycad-like forms of the Mesozoic formations. The cycads at present are few in number or species, but widely dispersed, and seldom sufficiently abundant to make them important constituents of the vegetation.

The conifers are preeminently the predominant gymnosperms of the present. Although the number of species hardly exceeds four hundred, they nevertheless, owing to their gregarious habit, are among the most important forest trees in many parts of the world—especially here on the Pacific Coast. Incidentally, they include the largest known trees.

It is pretty clear that the existing seed plants do not form a homogeneous assemblage. The gymnosperms show evident relationships with the pteridophytes, but the different orders, *e.g.*, conifers, cycads, may very well have been derived from quite independent pteridophytic stocks. The predominant modern flowering plants or angiosperms differ so markedly from the gymnosperms that it is a question whether there is any real relationship between them, and their origin is very uncertain.

The production of the seed marks the final step in the complete adjustment of the plant organism to strictly terrestrial conditions, and while seeds arose independently in several widely separated classes, most of the primitive seed plants have disappeared completely, or have left only a few descendants which maintain a more or less precarious existence at the present time.

One type of seed plants, however, has proved itself eminently adapted to modern conditions and comprises an overwhelming majority of living plants. These are the familiar flowering plants, or angiosperms, to use the botanical term. In the angiosperms the plant organism reaches its most perfect expression, and they now dominate the land floras of the whole world.

Plastic to a degree unequaled by any other plants, they have adapted themselves to the most diverse conditions. From the burning deserts of the tropics to the utmost limits of vegetation in the polar regions and on mountain summits angiosperms have made themselves at home. A few have even invaded the sea, and many live in swamps or completely submersed in lakes or rivers. Others, like the mistletoe or dodder, have adopted a parasitic life, and still others live at the expense of dead organic matter—or as we say are saprophytes, like the snow-plant of our high mountains. The parasitic and saprophytic angiosperms recall the fungi, and as they have more or less completely lost their chlorophyll, must depend on other organisms for their organic food. While the ferns and gymnosperms have left abundant and well-preserved fossil remains whose nature is unmistakable, of the angiosperms, except in the later geological formations, only scanty traces have been found, and these are often of very doubtful nature.

It is not until the later Mesozoic formations are reached that certain evidences of angiosperms are encountered. From the Cretaceous upward, they rapidly increase in number and variety, and many existing types can be plainly recognized among the Cretaceous fossils.

The apparent sudden appearance of angiosperms in the lower Cretaceous rocks and the close resemblance of these early fossils to living types make it certain that there must have been a long line of more primitive forms preceding them; but of these "prot-angiosperms" we have no definite evidence, and at present there is much controversy as to what was the origin of the angiosperms.

The flowers of the angiosperms are much more highly developed than those of the gymnosperms, and it is difficult to compare them. The young seeds, or ovules, instead of being exposed on an open scale, as in the pine, are contained in a closed receptacle (ovary) usually composed of special leaves, or carpels, grown together. The development of the seed, however, is much the same as in the gymnosperms—except that the gametophyte is very much more reduced. The microsporangia, or pollen sacs, are borne on specially modified leaves, the stamens—and the stamens and carpels are the essential organs of the angiosperm flower.

The flower may consist of only stamens or carpels, and the two sorts of flowers may be on the same plant, as in the oak or corn, or they may be on different individuals, as in the poplars, willows and the date palm. As some of the oldest fossil angiosperms, like the poplars and sycamore, have such "diclinous" flowers, it is probable that this condition is more primitive than the much more common "perfect" flowers having both stamens and carpels. Many botanists, however, believe that the diclinous condition is the result of reduction from flowers having both stamens and carpels, but there are serious objections to this view.

Most of our common flowers are "perfect" or "hermaphrodite"—or to use a more accurate term, amphisporangiate. Moreover they usually possess a conspicuous floral envelop, which may be composed of nearly uniformly colored leaves, as in a lily, or there may be a double envelop—the green calyx and the highly colored corolla. As we have already noted, the ovules are borne in a closed ovary, which may be the base of a single carpel or may be formed by the junction of several carpels into a compound pistil.

The position of the ovules in the closed ovary requires special adaptations for insuring fertilization. In the gymnosperms the pollen spores fall directly upon the apex of the exposed ovule. In the angiosperms there is a special organ—the stigma at the tip of the pistil—which receives the pollen and facilitates its germination. The pollen tube grows downward through the tissues of the pistil until it reaches the ovule in the ovary, and fertilizes the egg-cell in much the same way as in the gymnosperms, and the subsequent development of the seed is very similar.

The effect of fertilization extends to the carpels, which are stimulated in growth and at maturity enclose the ripe seed in a fruit. This not only serves to protect the ripening seed, but is concerned also with its distribution. The development of the fruit has undoubtedly been an important factor in the success of the angiosperms in the struggle for existence.

The simple diclinous flowers of a poplar or oak might in a way be compared with the flowers of a pine, and as in the pine, there is a very large amount of light pollen formed, which must depend on the wind to carry it to the pistil. In the somewhat more specialized floral types, the stamens and carpels are close together, and there is a definite floral envelop. The number of parts is often indefinite, but with the increasing specialization the flower shows a constant number in its members, and the corolla becomes bright colored. Further specialization results in tubular flowers, sometimes of peculiar form. A study of these changes in form and color and the development in many flowers of characteristic scents shows very clearly that these are associated with the pollination of the flowers, mainly through insect agency.

Just when the association with insects as agents in pollination—entomophily as it is called—became established and thus started the extraordinary evolution of both insects and angiosperms is impossible to determine.

That the earliest angiosperms were entomophilous is exceedingly doubtful. The earliest known are allied to forms which at the present time have inconspicuous wind-pollinated flowers. Moreover, what is known of the insects of this period indicates that none of the specialized insects, like bees and butterflies, had yet come into existence; but later on, the rapid increase in the number and variety of the angiosperms indicates that entomophily had begun to exercise a marked influence on their evolution.

The development of a showy corolla, which has been thought might have arisen from a transformation of stamens such as we may still see in some double flowers, is associated with the entomophilous habit, and it is by no means unlikely that the development of a true corolla was preceded by a condition in which the stamens, otherwise unchanged, became colored, and thus attractive to insects visiting the flower for pollen or honey. Such a condition may still be found, for example, in *Eucalyptus* and *Acacia,* where a corolla is either quite wanting or is relatively inconspicuous.

There is no question that the extraordinary numbers and diversity of the angiosperms are in very large measure the result of their adaptation to cross-pollination through insect agency. The seeds of cross-fertilized flowers have been shown to be more numerous and the seedlings more vigorous than those from self-pollinated flowers. It is also a legitimate assumption that increased variability due to crossing is advantageous in tending to develop new characters which are subject to natural selection. While insects are the principal agents in cross fertilization, certain birds may also act in this capacity. In America the humming-birds are familiar examples. They seem to show a special preference for red flowers, like the scarlet sage, fuchsias and some of the pentstemons, *Zauschneria,* etc. In other parts of the world, *e.g.,* South Africa, the sun-birds play a similar rôle, and these, too, seem to have a penchant for bright red. The aloes and red-hot poker in our gardens are examples of old world ornithophilous flowers.

While we may hesitate to accept all the conclusions of the enthusiastic students who first realized the immense importance of entomophily, we have no reason to doubt that the course of evolution of the two largest groups of plants and animals, angiosperms and insects, has been powerfully influenced by the mutual adaptations that have arisen in the association of these two groups of organisms.

The great variety of fruits developed in the angiosperms and the correspondingly varied devices for the distribution of the seeds have also been important factors in their success.

The early history of the angiosperms is very obscure, and we have no satisfactory evidence of their existence prior to the Cretaceous. The general uniformity of their essential structures makes it pretty certain that they have all originated from some common stock—or at least from some assemblage of related forms from which a number of lines of true angiosperms diverged. The prevalent division into two coordinate subclasses, monocotyledons and dicotyledons, is probably a somewhat artificial one. It is more likely that from an undifferentiated widespread primitive stock, for which the name protangiosperms has been proposed, a number of lines of true angiosperms arose, some monocotyledons, others dicotyledons.

Once established, the angiospermous type showed itself to be remarkably adaptable, and it soon established itself as the dominant element in the land vegetation. Whence arose their extraordinary plasticity can only be conjectured. The type of fruit, with the complete protection of the seed until its maturity, may have been one of the important factors in establishing their superiority over the gymnosperms; but this will not explain the extremely plastic plant body which contrasts so strongly with the limitations of the gymnosperms.

It may be that cross-fertilization among angiosperms arose early in their history and that thus a greater degree of variability was induced, resulting in the appearance of many modifications which could be seized upon by natural selection and thus tend to develop new types. Whatever may have been the reasons, it is their extraordinary adaptability that is at the bottom of the remarkable success of the angiosperms. One important phase of this is the utilization of animals for the distribution of pollen and seeds. Nearly all plants whose organs have been modified with reference to animal structures are angiosperms, and the great variety of flowers and fruits is doubtless connected with such adaptations. However uncertain we may be as to their origin, the remarkable fitness of these plants to modern conditions is obvious, and they have largely monopolized the land areas of the whole world. Only under exceptionally favored conditions are the lower plant types able to hold their own in competition with the all-conquering angiosperms.

OBITUARY

RECENT DEATHS

DR. IRA NELSON HOLLIS, professor of engineering at Harvard University from 1913 to 1925 and president of the Worcester Polytechnic Institute from 1893 to 1913, died on August 15, at the age of seventy-four years.

DR. LOUIS MURBACH, for many years head of the department of biology in the Central High School,