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THE PRESENT STATUS OF THE BIOGENETIC LAW[1]

The biogenetic law or the doctrine of recapitulation not long ago ranked as one of the most important principles of biology. In recent years it has been attacked repeatedly both from the botanical and zoological sides. Since the basal data upon which it is founded have not at any time been called in question and in fact have rather increased in number and importance, as a result of the more recent historical and developmental study both of plants and animals, it becomes a question of interest to discover why this change of attitude has taken place. One of the most important reasons for the momentary eclipse of the doctrine of recapitulation is doubtless the present vogue of the doctrine of mutation. It is distressing apparently to the mutational state of mind to grant that the past history of living beings is an important factor in their present organization. If it be generally true that new species can originate all at once by saltation or sudden change, the past history of such species becomes a matter of less importance and it naturally follows that the possibility of such a past being recorded in their developmental stages becomes highly problematical. As a consequence of this situation we have heard much destructive criticism of the biogenetic law on the part of zoologists of mutational tendencies, such as Montgomery, Morgan and others. It has been asserted, for example, that the gill arches of the mammalian embryo do not indicate, as was previously supposed, an aquatic habit on the part of ancestral forms from which on the basis of paleontological and developmental evidence, the warm-blooded animals have come. It is plausibly suggested that the undoubted presence of gill-arches in the mammalian embryo is an embryonic response to the early aquatic existence in the maternal amniotic fluid. In other words, it is asserted that what the morphologist and the paleontologist explain in terms of the biogenetic law as vestiges of a former state represent merely a larval adaptation, which is of no evolutionary significance. This is substantially the position assumed by Morgan in his "Critique of Evolution," which has recently enjoyed a great vogue.

There is another group of critics of the biogenetic law, whose objections are based too exclusively on a Paleozoic point of view. This group presents an interesting resemblance to those whose training makes

[1] Address delivered by invitation before Section K, British Association for the Advancement of Science, Toronto meeting, August, 1924.

them look at all modern life through the eyes of Greece and Rome. Very often they represent opinions, which, although long received, have by reason of later discoveries ceased to square with the known facts. Obviously it is impossible in a general statement to deal in detail with conscientious objectors of this type.

The higher plants, particularly the Conifers, supply an admirable basis for the examination of the fundamental basis of the biogenetic or recapitulationary law. Since the young of the seedplants is sheltered under uniform conditions throughout, in its embryonic or intraovularial phases, the complications of development known as larval stages in animals do not occur. In this respect, as in so many others, the higher plants show themselves superior to animals for the investigation of general biological principles on the basis of inductive reasoning. In the case of seedplants the process of events is accordingly not obscured or confused by any larval mask so that it is apparently easy, for the open mind at any rate, to interpret the facts of development and history. The situation in the case of plants is further favorable by reason of the many adaptations to actual environment which they have in the course of time been forced as it were to develop, by reason of their sedentary life, which contrasts so strikingly with the generally mobile existence of animals.

A very striking mode of adaptation in the case of plants is found in connection with the growth on a dry soil or one in which the water relations for one reason or another are unfavorable. An excellent illustration of this condition is supplied by the Cactus family. In the genus Peireskia, normal leaves are developed, but many of the other genera are quite leafless except in their early seedling stages, in which they usually develop more or less normal seed-leaves or cotyledons. The genus Cereus is interesting because in some of its species it does not even develop cotyledonary leaves. It is not improbable that related genera, such as Echinocactus, Melocactus, Anhalonium, etc., will prove to be equally without seedleaves or cotyledons. Preliminary investigations carried on in my laboratory show that in a number of these more highly specialized Cactus genera, even the vessels which so uniformly characterize the angiospermous seed-plants are likewise absent. The occurrence of cotyledons in genera of cacti, which are quite without leaves in the adult vegetative condition, can only be interpreted as the occurrence of an ancestral structure in the seedling, which has quite disappeared in the adult; in other words, as an example of the validity of the doctrine of recapitulation.

There are numerous parallel instances among species inhabiting dry or poisonous soil. For example, we have in North America many species of Veronica, in which the leaves have a quite normal development and a very characteristic form. In certain exotic Veronicas the leaves are very small and are confluent with the surface of the stem. In their young condition these xerophytic Veronicas have, however, leaves precisely like other Veronicas. The same condition is exemplified by the nearly leafless Rubus of the "Malle Scrub" of Australia, which in its seedling condition has leaves like other raspberries. Examples of this kind could be multiplied indefinitely and all show clearly that the young of desert plants show organization resembling that found in allied species growing under normal water supply. Since the young are absolutely under the same conditions of environment as the adults, the differences of nepionic or seedling organization are rationally explained as the persistence of a tendency to grow like the ancestral mesophytic forms, from which the xerophytic or desert-inhabiting modifications were originally derived.

The seedlings of plants which have become adapted to a dry or desert habitat accordingly supply an extremely good illustration of the doctrine of recapitulation, since in their first development they manifest peculiarities which are only explainable as the persistence of a tendency to grow like nearly related forms living under more normal conditions of water supply.

Similar conditions are supplied by plants provided with flattened stems or phylloclads or by that abnormal type of leaf known as the phyllode. In their seedlings these forms usually show the type of organization characteristic of the more normal nearly related species or genera. Innumerable similar examples could easily be supplied of angiosperms showing marked adaptations to special conditions of existence in the adult, which go through a normal development in the young state and thus supply evidence in favor of the validity of the doctrine of recapitulation.

We may now advantageously turn our attention to the conifers, a group of very special interest in the present connection on account of their great geological age. Although the group as a whole is evergreen and has obviously been so for many thousands of years, there are deciduous genera such as the larch (Larix) and the Chinese larch (Pseudolarix) which regularly shed their leaves in the autumn. Interestingly enough the seedling of our larches is for a few years evergreen. Since it grows under precisely the same conditions as the adult, this striking deviation in habit can only be explained as a persistence of an ancestral feature, namely, the typical coniferous evergreen habit, in the young individual and at the same time an exemplification of the validity of the biogenetic law. Another of our commonest and at the same time most interesting conifers is the pine. This is characterized by having its leaves attached to the stem in clustered fascicles, which in modern species are from two to five in number. In the first year's development the leaves occur singly and directly attached to the stem, which is obviously the harking back to an ancestral condition. In many of our higher conifers the leaves are small and more or less confluent with the surface of the stem. This condition, for example, is found in certain junipers, in the arbor vitae, the big tree, the incense cedar, etc. In the seedling all these forms have quite normal free leaves, the presence of which is explainable on the basis of the doctrine of recapitulation. The Japanese umbrella pine, Sciadopitys, which in the adult bears only needles comparable to those of a two-leaved pine, but fused together, in the seedling condition, for a short time, produces normal leaves. In certain conifers now confined to the southern hemisphere and belonging to the genus Phyllocladus, the branches are flattened to resemble leaves and the real foliar organs are rudimentary. In the seedling normal leaves and stems always are present for a time.

All the above illustrations of the exemplification of the doctrine of recapitulation by the conifers have reference to external organization and to living forms. We shall now turn our attention to the important internal structures and to fossil forms. I have devoted a large amount of time to the study of the anatomical organization of extinct conifers belonging to earlier geological times. It will be of interest in this connection to examine how certain well-known living conifers compare anatomically with their extinct ancestors and what basis they supply for the validity of the doctrine of recapitulation. Mention has already been made above of the pines. This genus, as some of you are aware, is a very ancient one, extending back in substantially its present form at least to the middle of the Mesozoic period (Jurassic). In its earliest occurrence Pinus was different in certain notable respects from its living representatives and, like the Cycads, was much more numerously represented by species than it is at the present time. The earliest pines, instead of the two to five needles in a cluster, which are a feature of our existing pines, had numerous leaves in a fascicle. Another interesting feature of these primeval pines was the fact that the wood in the leaf began its growth towards the upper surface of the leaf as is the case in the earliest known gymnosperms. In anatomical structure the wood was different from our living pines, in several respects, only one of which will be mentioned. In our existing species of Pinus, the rays of the wood are accompanied by horizontal tracheids or water-conducting elements. These structures were absent in the earliest pines. Even at the beginning of the Cenozoic, as exemplified by the pines of the Baltic amber deposits, the horizontal or ray tracheids only made their appearance after the branch had grown for a number of years. In the late Mesozoic (Cretaceous) marginal ray tracheids have been found in certain American species, investigated in my laboratory, but their appearance was deferred even later than in the pines of the Baltic amber deposits. In our living pines the tracheids are late in appearing in the seedling, and in the root, which is of all plant organs the most conservative, it is often many years before the ray tracheids make their appearance along the margins of the rays in the wood. In the cone or reproductive axis, which has from two to three annual rings, marginal or ray tracheids are usually quite absent. Dr. A. E. Longley has made some very interesting observations on the effect of injury on the wood of the pine. He has discovered that even in the old stem the wood formed after injury is for several years without the marginal ray tracheids. It will be obvious from the above statements that the oldest pines were entirely without ray tracheids in their wood and that after these structures made their appearance they were at first greatly delayed in the late Mesozoic and less so in the early Cenozoic of the Baltic amber pines. In the adult stem of living pines they appear at once in the first year's growth, but they are delayed in the seedling in accordance with the doctrine of recapitulation. Interesting subsidiary doctrines to that of recapitulation are exemplified by the old and interesting genus Pinus, unquestionably the most ancient surviving tree of our northern forests. In accordance with the doctrine of retention of ancestral conditions in conservative organs, we find a similar delay to that exemplified by the seedling of the pines in the root and cone in the appearance of the marginal tracheids. Further, as a result of injury the formation of marginal tracheids may be inhabited for several years and the structure of the wood thus reverts to the ancient condition of organization.

The doctrine of recapitulation is consequently admirably illustrated by our ancient but still living genus Pinus, as becomes clear from a comparison of its younger organization with that of the extinct species of earlier geological times. Further, the evidence derived from a detailed comparison of root and cone or reproductive axis shows that these two organs likewise present features of resemblance to the seedling stem. In other words, root and stem of the adult are conservative organs. These conditions I have described as illustrative of the doctrine of retention of ancestral structures by conservative organs and in the course of my anatomical investigations on other groups of plants from the Calamites upwards have found to be of wide validity. This doctrine so far as I am aware has not been developed in the case of animals. A very important general principle is that of reversion to extinct types as a result of injury. This condition exemplified by Pinus is of special importance because the reversionary reaction is often the most persistent indicator of former conditions, since it makes itself felt when all other indications of ancestral organization have become obliterated by time. The comparison of living pines with their extinct forbears of the Mesozoic and Cenozoic periods consequently supplies us with three useful working principles. These are, first, recapitulation, which is clearly and strongly supported by the data supplied by living and extinct pines. Second is the doctrine of retention or the doctrine of conservative organs. Finally, we have the doctrine of reversion as a result of injury.

Time-honored candidates for the position of the primitive surviving coniferous group are the Araucarian conifers, at the present time confined to the southern hemisphere but formerly flourishing side by side with the pine tribe or Abietineae in the northern latitudes. The view that the Araucarians are the most primitive living conifers is based on the comparison of the existing representatives of the stock with the Paleozoic gymnosperms. Such a point of view apparently presents the same disadvantages as does a purely classical training for the solution of the practical problems of modern existence. The Paleozoic is too far away to be compared directly with the Cenozoic, and many gross fallacies have been the result of this impossible comparison.

The Araucarian conifers as at present organized are distinguished by generally broad leaves comparable with the Paleozoic Cordaitales. Further the Araucarians have a type of wood superficially quite comparable with that of the Cordaitales, for, as in that group, the pits or valves of the tracheids alternate and the walls of the tracheids in the mature wood are quite without bars of Sanio. The Abietineae or pine subtribe by contrast has needle-like leaves and the tracheids have opposite pits, and bars of Sanio are present in the radial walls of the tracheids of the secondary wood.

Another ancient surviving group is that of the Ginkgoales with a single living representative, *Ginkgo biloba*. Although it is generally admitted that this is a very ancient group comparable with the most ancient of the conifers, it has the same type of tracheids as Pinus, namely, with opposite pits and bars of Sanio. Like Pinus it has also leaves borne on short shoots. Its reproductive anatomy also closely resembles that of Pinus, since the seeds and microsporangia are both borne in twos on the sporophylls and the megasporophyll has inverted fibrovascular bundles, as is the case with the Abietineae. Ginkgo is likewise provided with winged microspores which not only in this feature but also in their internal organizations are in detailed agreement with the Abietineae. A further interesting coincidence is presented by the mode of opening of the microsporangia, which is through the instrumentality of an internal mechanical layer in intimate connection with the fibrovascular system. This situation is all the more significant because the cycads and other lower gymnosperms as well as the ferns effect the dehiscence of their pollen sacs by the action of an epidermal mechanical layer, the annulus. A final interesting and striking point of resemblance between Ginkgo and the Conifers is the presence of "Rotholz." This reddish hued mechanical tissue is recognized as peculiar to the conifers. It is a most significant coincidence that the Ginkgo should be the only other lower gymnosperm to parallel this feature. It seems beyond question that Ginkgo and the Abietineae, particularly Pinus, their most ancient representative, are very closely related. As a consequence, if Ginkgo is an ancient type, as is universally conceded, the same must hold true for the genus Pinus, on the basis of a detailed anatomical agreement. It is expedient to emphasize the important evidence for the close relationship between the Ginkgoales as a preliminary to the further discussion of the Araucarian conifers and the doctrine of recapitulation.

We may now advantageously examine other characteristics of the surviving representatives of the Araucarian conifers. A very striking feature of the two surviving genera, Agathis and Araucaria, is the persistence of the conducting strands to the leaves long after the leaves themselves have fallen. In trunks a hundred or more years old, the foliar traces may still be found in the outer annual rings in regions corresponding to the fallen leaves, which they formerly supplied with water. No comparable feature is found in any other seedplant, and Professor Seward regards this peculiarity as strong evidence for the antiquity of the Araucarian stock. I am free to confess that I am unable to follow Professor Seward's logic in this conclusion, but I think that I am representing his point of view fairly.

An examination of the seedlings of the two genera Agathis and Araucaria in my laboratory has brought to light the interesting fact that although the leaf-traces persist in the old tree indefinitely they are of very short duration in the seedling, lasting only for a few years. This fact becomes of great importance in connection with the study of the fossil forms. Another interesting feature of the young Araucarian stem as well as of the root and cone-axis is the presence of wood parenchyma. In the Cordaitales no wood parenchyma ever occurs in the secondary wood, and this holds true for the wood of Paleozoic gymnosperms quite generally. Wood parenchyma is only certainly known to occur in Jurassic and later secondary woods. Perhaps the most interesting feature of the organization of the secondary wood in the Araucarian conifers is the occurrence of opposite pitting and bars of Sanio in its first-formed portion. This condition can not be harmonized with the theory of the cordaitean origin of the Araucarian stock, as is the view generally accepted in Great Britain and Germany. The neglect of comparative anatomy on the part of European paleobotanists seems deplorable because no permanently satisfactory conclusion can be reached without a thorough knowledge of the general anatomical structure of the conifers living and extinct, as well as the general principles of anatomical science as applied to all groups of plants.

A commonly emphasized argument for the Cordaitean origin of the Araucarian conifers is the occurrence of quantities of woods of the Araucarian type in earlier geological deposits. My students and myself have made very extensive examinations of the extremely abundant and varied material from the Mesozoic deposits of North America and have not been able to agree that the common European view in regard to the abundance of woods of the modern Araucarian type in Mesozoic deposits. In all our investigations, which cover material from Texas to Dakota and from Washington to Massachusetts, we have found only two specimens of woods of the type of Agathis and Araucaria. In these rare and isolated fossil woods as in the living genera the leaf-traces are persistent. An interesting difference between the mature stem wood of the true Araucarioxyla described by us and that of the living genera is the presence of abundant wood parenchyma. It has been stated above that on the basis of the anatomical structure of the whole organism in the case of Agathis and Araucaria, they must have come from ancestors with well-developed wood parenchyma, although this is lacking in the mature stem wood of the two living genera. We have accordingly pointed out that the term Araucarioxylon must be used in a restricted sense, in view of the general anatomical conditions in living Araucarians. Its use should be confined to woods with indefinitely persisting leaf-traces and well-developed wood parenchyma. If it be objected that comparative anatomical data are not of value, it may be replied that the zoological paleontologists attach great importance to comparative anatomy and it may further be suggested that much of the slight esteem in which botanical paleobotany is at present held is due to the perhaps unnecessarily wooden manner in which it has been developed. It can not be too strongly emphasized that it is impossible to work out the evolutionary position of extinct plants on the basis of the structure of secondary wood alone. If my European paleobotanical colleagues were to moderate by the light of reason their suspicion of what have recently been called "Phylogenetische Abwege," I feel that the results for the science would be happy. In this respect they might well take example from their zoological fellow-workers who have gained much by profitable excursions along phylogenetical byways.

It has become obvious as the result of the investigations of the past decade and a half that most of the woods that have been described as Araucarioxyla are not woods of forms comparable in any strict sense with our two modern genera, Agathis and Araucaria. By far the greater number of woods of the Cretaceous and Jurassic, which a few years ago were universally included under the form genus Araucarioxylon, do not belong there at all.

Nearly twenty years ago, I described for the first time, in collaboration with Dr. Arthur Hollick of Columbia University, the anatomical structure of the important Mesozoic genus Brachyphyllum, which was recognized at that time to be of Araucarian affinities, although not immediately related to Agathis or Araucaria. With the structurally preserved twigs of Brachyphyllum were fragments of wood which showed the same general organization as did the twigs of Brachyphyllum. Some of my European colleagues have at various times objected to the reference of these woods to affinity with the small twigs of Brachyphyllum. The diagnosis has been confirmed in the interval, however, by splitting out small branches from large fossil trunks. The result of the microscopic comparison of the small twigs with their parent axis have entirely justified the conclusions reached at that time on comparative anatomical grounds.

The wood at first referred to Brachyphyllum was three years later erected into a form genus under the generic appellation of Brachyoxylon. This wood presented a number of interesting features. With Araucarian pitting it united the absence of wood parenchyma, non-persistent foliar traces and the presence of traumatic resin canals. The last three features all marked it off very clearly from Araucarioxylon. I believe that this was the first instance in which it has been pointed out that experimental evidence is important in the case of fossil woods. The wound reactions of coniferous woods are often of great diagnostic importance and their significance is just beginning to be realized by my European colleagues.

It is quite obvious that by far the greater number of so-called Araucarioxyla previously described on this continent and in Europe in reality belong to the genus Brachyoxylon or allied genera and not to Araucarian conifers of the Agathis or Araucaria type. There is an interesting difference of opinion between American and European paleobotanists as to the interpretation of the results. For some unexplained reason my European colleagues have ignored the important genus Brachyoxylon and have invented other and often inappropriate names for other transitional woods described by my students and myself.

Brachyoxylon differs from Araucarioxylon by the absence of wood parenchyma and by its non-persistent foliar traces, as well as by the wound canals which can always be observed in adequate material. Obviously Agathis and Araucaria have come from ancestors which were without persistent leaf traces, since no wood with continuing traces has been described from the lower Mesozoic. This conclusion is likewise reinforced by the evanescent character of the foliar traces in the seedlings of Araucaria and Agathis. Professor Torrey, working up a large collection of Mesozoic and Cenozoic woods, discovered an interesting genus connecting Brachyoxylon and Araucarioxylon, to which he gave the name Telephragmoxylon. This shows the beginning of the formation of wood parenchyma but has the evanescent leaf-traces and the traumatic canals of Brachyoxylon.

The higher members of the Abietineae, such as for example Cedrus, Abies and Tsuga, are in general without normal ligneous resin canals except in the root. When any of these three genera has its wood injured, traumatic resin canals are formed, vertically only in Tsuga and Abies, but both horizontally and vertically in Cedrus. The rational as well as natural explanation of these conditions is that the three genera in question have come from Pinus by reduction and revert under conditions of injury.

Similarly, in the case of Brachyoxylon we have a reversion of an Araucarian type of wood as a result of injury to a condition, resembling, so far as the wound canals go, that found in Abies or Tsuga. Certainly, if we regard Abies or Tsuga as having come from Pinus, we must consider Brachyoxylon as also of Abietineous origin and derived from an ancestry allied to Pinus.

Both in Araucarioxylon and in the living representatives of the Araucarian conifers, we find opposite pits and bars of Sanio *at the beginning of the secondary wood,* a further feature justifying their derivation from Abietineous origin.

It is out of place at this time to go into the question of the evolution of the conifers further. It will be sufficient to point out in conclusion how completely the situation has changed in the past ten years or more in regard to the relative status of the pine-like and Araucarian conifers. Formerly the Araucarian conifers were regarded as preponderant and the Abietineae of slight importance. In the most recent German treatment of the subject six Mesozoic genera of the "Protopinaceae" are described, including thirty or more species mostly transferred from types formerly considered as Araucarian. As a consequence of this procedure the Abietineae become the predominant conifers of the Mesozoic, and the true Araucarioxyla constitute an insignificant remnant. I personally regard the most of these so-called Protopinaceae as forms which have reached the araucarioid condition from abietineous ancestry. The German paleobotanists arrive at the opposite conclusion. It seems unfortunate from their standpoint that they have now to transfer the greater number of coniferous Mesozoic woods, formerly supposed to be Araucarian, to abietineous affinities.

In any case it is highly probable that the logical use of the biogenetic law will in the future clear up this condition of confusion. When the dust of conflict has settled, it will probably appear that Ginkgo and Pinus stand side by side as the prototypes of Mesozoic gymnosperms of cordaitean derivation. It will then be realized that Agathis and Araucaria are aberrant extremes, which merely simulate Cordaites on the basis of extremes meeting but have no near affinity with them. In any case the thesis of the predominance of the Araucarians, in the Mesozoic, must be abandoned, because, by a *reductio ad absurdum,* the German and some other paleobotanists, by their very zeal to save the time-honored Araucarian thesis, are led to refer most of what were formerly regarded as undoubted Araucarian forms to the Abietineae.

The progress of biology along historical lines lends accordingly new support to the already well-documented doctrine of recapitulation. When the doctrine of mutation is relegated to its relatively unimportant position among biological working hypotheses, the great general significance of the biogenetic law or the doctrine of recapitulation will be clearly recognized.

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AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE COMMITTEE ON THE PLACE OF THE SCIENCES IN EDUCATION

The following persons have been appointed on this committee, and others are to be added:

Dr. Edna M. Bailey, supervisor of the teaching of science, University High School, Oakland, California. Representative of high schools.