

THE ONTOGENY OF VASCULAR PLANTS
and
THE THEORY OF RECAPITULATION.

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In the year 1866 Haeckel (*Gen. Morph. d. Organismen*) propounded the famous doctrine that during their individual development organisms tend to recapitulate their racial history. This great generalisation gradually emerged from a mass of observed facts in the fields of animal embryology and palaeontology, during the time when the theory of evolution was still fighting its own struggle for recognition, and it helped to a great extent in the acceptance of evolution itself as a guiding principle in biology. Although formulated in general terms, so as to cover both the animal and the plant kingdoms, the theory of recapitulation not only owed its origin to the facts of animal life, but for a long time depended for support almost entirely upon zoological evidence. It would be expected, however, that a biological principle of such a fundamental nature, if it holds good in the case of animals, should apply also to the plant kingdom. But while among zoologists recapitulation has long exercised a profound influence, and is still embraced by many almost as an article of faith, it has never been received by botanists with anything like the same enthusiasm.

My object in choosing this subject for to-day's address is to see if after all the case for recapitulation in plants is not better than it has been made out to be. For it seems to me obvious, from the nature of the case, that it must either stand or fall as a whole, and the strength of the doctrine on the zoological side should encourage one to seek botanical support for it with more confidence than one would otherwise do.

It is of course well-known that even at the hands of some zoologists the doctrine has recently had to face severe opposition*. But this is the common lot of all great generalisations which owing to their very attractiveness lend themselves to unguarded use and ex-

* See Garstang, *Journ. Linn. Soc. (Zoology)*, vol. 35, 1922, and the works of Sedgwick, Morgan, O. Hertwig and others, cited therein.

aggeration, inevitably bringing some undeserved criticism in their train. (See Bather, *Rep. Brit. Ass. Cardiff, 1920*, and J. A. Thomson, *The Science of Life*). Too much was expected of a theory which was put forward not as a "contribution to the physiology of development" but rather as a deduction from the facts of comparative anatomy and embryology.

The animal kingdom appears to afford many more instances of probable linear genetic series than we find among plants, but even the most convincing of them would be a miserably incomplete picture of the racial history. The most that the comparative morphologist can ever hope to lay bare is the general evolutionary tendencies, and the most that we can reasonably claim for ontogeny is a recapitulation of those tendencies. It would be idle to seek, among the developmental stages of a plant or an animal, the specific characters of an actual series of ancestors. The potter moulds his lump of clay successively into shapes less and less generalised till the desired specific type of vessel appears. He may, of course, stop at any stage of the process, to produce a vessel of a simpler, more generalised type. But to give it a specific character he must put in the finishing touches (colour, ornamentation and glaze) which characterise it as distinct from a mere stage in the creation of a more elaborate form.

This would, of course, mean that recapitulation is a much more vague and uncertain phenomenon than some have supposed it to be. So it is. But even so it remains a grand conception. In many cases it may be a mere recapitulation of the grades of differentiation, but then what is evolution itself in its fundamental aspect, but progression through successive grades of differentiation?

In this, its fundamental point, then, as expressed in the familiar words "ontogeny tends to recapitulate phylogeny" the doctrine of recapitulation appears to stand on unassailable ground.

Prof. Bower and others have indicated some of the reasons for the relative indifference of botanists towards a doctrine which supplied such a powerful stimulus to the study of animal embryology and palaeontology. In an illuminating historical account of the early attempts to extend the theory to plants Prof. Bower (*Land Flora* 1908 p. 173) draws attention to certain important differences which most higher plants show in their mode of development from that seen in the majority of animals.

For instance, the power of continued apical development, which is retained throughout the active life of so many plants, finds no counterpart in animals, in which all the essential organs are laid down once for all early in the embryogeny, and development proceeds by transformation of the entire embryo. In the plant, on the contrary,

the process is largely one of successive intercalations behind the apical meristem, and the newly formed parts ordinarily become fixed both in position and structure once they have been laid down. Now, the apical meristem of a plant is obviously not an embryo in the same sense as the embryo of an animal. It is therefore not surprising that the intensive study of the growing tips of plants, characteristic of the works of Hanstein, Naegeli, Leitgeb and others, however useful in other ways, did not yield anything in the nature of recapitulative stages.

Nor does the early embryogeny of the sporophyte, the initial segmentation of the zygote, appear to throw much light upon its ancestry, beyond the vague indication that it arose, as Prof. Lang has suggested, by the elaboration of a filament, which itself originated in a single cell.

The prevalence, among plants, of the sessile habit, and especially the fact that the tissues consist of walled cells, has involved important peculiarities in the mode of growth and development which are rarely met with in the animal kingdom. Dr. Ruggles Gates (*New Phyt.* Vol. 19, 1920, p. 230) has recently suggested that a greater frequency of mutations among plants may be a factor that has contributed to this difference. The botanist has no fine array of larval or embryonic types to put up as the ancestral forms of his sporophytes, as the zoologist has for his crustaceans and echinoderms, and molluscs and even his vertebrates. As already stated, the development of the animal is usually a process of transformation, the earlier stages in the life-history being *replaced* by the later. Only in exceptional cases, such as in the growth of foraminiferan and molluscan shells, does the adult animal preserve any trace of its juvenile conditions. In the higher plants, on the contrary, this is the general rule. Each organ, as it is laid down, retains its position, and in due course becomes a permanent feature of the anatomy, so that in an adult specimen we have a more or less complete record of the life-history. The primary development of the plant may thus be compared, although in a crude way, to the erection of an edifice. Looking at the development alone, as apart from growth, we may say in a general way that while the majority of animals unfold their life-history only in Time, most plants do so in both Space and Time.

Incidentally, this difference brings a certain advantage to the botanist, for in favourable cases the examination of a single specimen may reveal the whole developmental sequence—a fact which has been utilized with remarkable success by Chandler (*Ann. of Bot.* 1905 p. 365) in his study of fern "seedlings" and by Gwynne-Vaughan (*Ann. of Bot.* Vol. 17, 1903) in working out the ontogeny of *Alsophila excelsa* and other ferns.

(Perhaps nowhere in the plant kingdom does the theory of recapitulation find such clear illustrations as it does in the Filicales.) Since about the beginning of the present century the developmental study of vascular plants has received a fresh impetus, and a renewed attempt has been made towards a phyletic interpretation of ontogeny.) A feature of this recent attempt is the special attention given to the vascular structures. Beginning with the critical researches of Jeffrey and of Leclerc du Sablon, which gave birth to the new stelar theory, a mass of facts concerning the ontogeny of vascular cryptogams, and especially of the ferns, has accumulated through the labours of Boodle, Brebner, Gwynne-Vaughan, Tansley, Bower, Chandler, McL. Thompson and others. At the same time the study of the seedling anatomy of flowering plants has been vigorously pursued—a line of research in which one welcomes the striking share taken by members of the fair sex.

Let us take first the Filicales. The facts of ontogeny are now so well known that they will hardly bear repetition, but as the basis of discussion a brief summary of the salient points must be given.

On the basis of stelar anatomy, ferns may broadly be classified into three groups: the protostelic, solenostelic and dictyostelic. These terms have reference to the type of stele traversing the main axis of the plant in its adult condition, no matter what the juvenile conditions may be. But it is a well established fact, based on the developmental study of numerous cases, that (taking a generalized instance) even in a dictyostelic fern the vascular system is initially a protostele, giving off simple traces to the juvenile leaves. As the plant grows, the protostele expands like a funnel, soon acquiring a pith and giving off traces in a typical solenostelic manner. Presently, the final or adult phase supervenes, with its more crowded and fully developed leaves, and a telescoping of the solenostele into a dictyostele.

Similarly, the solenostelic ferns are not solenostelic to start with, but pass through a transient protostelic phase.

Only in the protostelic forms does the juvenile type of structure persist throughout life.

Intermediate in structure between the proto and the solenostelic types, is a fourth type deserving of special mention, the well known "*Lindsaya*-type", characterised by a core of internal phloem but devoid of a true pith. Here also the juvenile condition is protostelic.

How are these familiar facts to be viewed? From independent evidence, evidence that has nothing to do with the facts of ontogeny, we may safely conclude that protostele, solenostele and dictyostele are progressive stages in an evolutionary sequence. It is therefore not unnatural that the ontogenetic sequence, which normally runs

parallel to this, should have been regarded as in a general way recapitulative of the ancestral history.) It is necessary to emphasize that it is only in a general way recapitulative, for as we know from experience of individual life-histories, the recapitulation is neither complete nor specific. It would obviously be a hopeless task to reconstruct, from however complete a knowledge of the ontogeny, the actual pedigree of, say, *Alsophila excelsa*, which, since Gwynne-Vaughan worked out the anatomy, has become one of the clearest instances of recapitulation in plants. Similarly, no one could seriously maintain that the genus *Lindsaya* is on the direct line of descent of all ferns whose stelar anatomy passes through the so-called *Lindsaya*-phase. But the *Lindsaya*-phase does represent a tendency, further pronounced in the solenostelic ferns, which has probably been a potent factor in the evolution of the flicinean vascular system.

More than this one cannot say. All we can do is dimly to visualize some of the broad features of the ancestral organisation.

There is, however, another way of looking at the same facts. In an able address delivered before Section K of the British Association (*Manchester* 1915 p. 6), where Professor Lang advocates a change of attitude in the study of plant morphology, he views the developing embryo from what he calls the causal standpoint. The gradual progression from the simple to the elaborate vascular system may be looked upon, not necessarily as a case of phyletic recapitulation, but as an expression of the increasing resources of the young sporophyte in the way of constructive materials. As these materials accumulate the stem gradually increases in diameter and is able to support larger and larger leaves. This increase in the diameter of the axis is closely followed by an expansion of the solid into a medullate stele, and may in a sense be regarded as causally related to it.

The same point of view has been adopted by Tansley (*New Phyt.* 1907 p. 150) and Bower (*Proc. R. S. Edinb.* Vol. 41, 1920 p. 9), who trace the origin of the medullate condition directly to the influence of peripherally inserted leaves on a stem of increasing thickness. Unless the diameter of the stele is below a certain (variable) minimum the leaf-traces would make a direct water-demand only on the peripheral xylem. The ultimate result would be that the central tracheides, in which the water would tend to stagnate, would be reduced to the condition of a water-storing tissue. This is no doubt a most plausible explanation of the phenomenon but as Professor Lang himself says, there is no antagonism between the phyletic and the causal points of view. The one reveals to us certain facts, namely in this case a parallelism between the ontogeny and phylogeny, the other seeks a physiological explanation of those facts. Both lines of

enquiry are bound to enrich our conception of the individual development, for they are merely aspects of the same thing. The case would have been very different if our phylogenetic schemes based upon comparative study were inconsistent with physiological reasoning.

(An apparent obstacle in the way of the recapitulation theory is the fact that under certain conditions the normal course of the ontogeny may be temporarily arrested, or even reversed. Thus Professor Lang's studies on *Helminthostachys* (*Ann. of Bot.* vol. 29, 1915 p. 33) have brought to light cases in which a rhizome, after having once attained its adult (medullate) stele in the normal way, reverts temporarily to the juvenile protostelic condition.) The occurrence of scattered xylem elements in the pith of *Osmunda regalis*, which Gwynne-Vaughan (*Ann. of Bot.* Vol. 28, 1914, p. 351) observed in a wounded specimen, is an essentially similar case; further instances of the kind have come to the notice of other workers.

The immediate cause in such cases may be anything. It may be wounding, or inefficient nutrition due to a variety of other factors which it would be most interesting to investigate. But the fact of such chance reversions to the juvenile condition is not inconsistent with the general recapitulative nature of ontogeny.

It is a truism that the structure of an organism at all stages of its life is a reflexion of its past and present experiences: a combination of characters acquired both in the wide sense (that is, from previous generations) and in the narrower sense, from its immediate environment. And it is significant that when the normal equilibrium is upset by adverse conditions, adjustment is often effected by a "fall-back" upon the surer basis of past experience. Herein lies the rationale of the interpretation of so-called "abnormalities" (as apart from obvious monstrosities) as being in the nature of reminiscences of the past, when they formed part of the normal and stable organization in some more or less remote ancestor.

We may liken such cases to the retreat of an army in the face of a strong adversary, a retreat along the old line of communication being naturally preferred to a doubtful escape by an unfamiliar path.

Another apparent difficulty in the way of a phyletic interpretation of ontogeny is parallel evolution, of which the vascular system of the Filicales offers striking illustrations. For example, polycyclic forms of dictyostely have almost certainly arisen independently several times in the history of the group, for they are observed in distinctive ways of affinity. These facts fit in eminently with a causal interpretation. But they are not inconsistent with the recapitulation theory of the ontogeny, so far as stele structure goes, is still a more diversified recapitulation of its particular phyletic line.

The same argument would apply to some other familiar facts of ontogeny, which may come under the general head of parallel developments. They are parallel developments within the limits of one and the same species or even individual. It is well known, for example, that plants produced by vegetative means, from adventitious buds, bulbils and so on, during their development repeat more or less closely the normal ontogeny of the parent plant, derived from an embryo. It would suffice to mention only a few out of numerous instances of the kind: *Psilotum*, *Tmesipteris*, species of *Asplenium* and *Adiantum*, *Woodwardia* and many other proliferating ferns.

We know further from the work of Stenzel, Gwynne-Vaughan, Mettenius and others (summarised in Sahni, *New Phyt.* Vol. 16, 1917) that even branches often behave similarly, especially when they develop from small-sized dormant buds. Some remarkably clear examples are seen among the ferns. *Alsophila excelsa*, *Aspidium speciosum*, *Struthiopteris germanica*, and the stoloniferous species of *Nephrolepis*.

The degree of faithfulness with which the branch follows the ontogeny of the parent axis naturally varies with the conditions of nutrition. This is very clearly shown in *Nephrolepis cordifolia* if we compare the development of a plant raised from a prothallus with one that has appeared as a branch from a stolon. In the one case the plant develops slowly from the small beginnings of a fertilized egg, elaborating its slender resources as it grows; in the other, being already connected by an efficient channel to the fully developed resources of the mother plant, it rapidly attains maturity by omitting some of the transitional stages which probably formed important landmarks in the phylogenetic history of the species (Sahni, *New Phyt.* Vol. 14, 1915, pp. 263, 271). It is significant that although there is this striking difference in the *rate of progress* in the life-cycle, there is no deviation from the normal track (Heilbronn, *Flora* Vol. 101 1910). We have here an interesting botanical parallel to the

Indian frog *Hylodes* which, developing from an egg specially rich in yolk, is enabled to hatch direct, that is, without the intervention of a free-living tadpole stage.

It would thus appear from a consideration of the vascular structure of the stem, that recapitulation is a phenomenon of wide occurrence in the Filicales. Some equally striking instances are seen in the development of the leaf-trace, which has followed an independent course of evolution on the whole somewhat different from that of the axial cylinder. In the first place, as is well known, the leaves successively formed during the ontogeny of the stem show an increasing elaboration in their vascular supply, an

elaboration that roughly keeps pace with the stelar advance in the stem. Secondly, the same kind of sequence is sometimes repeated, although in a more or less abbreviated form, even in the development of the individual leaf of the adult type. Thus the leaf-trace in *Dicksonia* (*Cibotium*) *Barometz* has the simple C-shaped form at its origin, but as we follow it distally it divides into a number of distinct strands arranged in the form of an arc (Gwynne-Vaughan, *Ann. of Bot.* Vol. 17, 1903).

Recent palaeobotanical work has done much to demonstrate the phylogenetic significance of the different stages through which the leaf-trace passes during its course through the cortex of the stem and through the petiole. This principle naturally finds its fullest expression in those cases where the leaf-trace assumes a number of different shapes before it finally arrives at its definitive form. *The successive transitory forms of the leaf-trace are regarded as resembling more or less closely (though never actually representing) the permanent form of the trace in a series of ancestors* (P. Bertrand, *Progressus* Vol. 4, 1911, pp. 213, 266-70). No one who has followed the growth of our knowledge of the anatomy of palaeozoic ferns, through the labours chiefly of Kidston and Gwynne-Vaughan, of Paul Bertrand and of Gordon, will deny that there is a sound basis of truth in this principle, however far we may be from a realization of the actual ancestors.

Yet if there is any justification for adopting this view it follows that we have here a striking instance of *ontogenetic* recapitulation. For, knowing that the growth of the fern leaf proceeds, as in the stem, by successive intercalations behind an apical growing point, even though the actual ontogeny of fossil ferns may be for ever lost to us, we are justified in assuming, by analogy, that the different parts of the mature leaf represent stages in its ontogeny. The simple mesarch leaf-trace of *Thamnopteris Schlechtendalii* (Kidston and Gwynne-Vaughan, *Trans. R. S. Edinb.* Vol. 46, 1909 p. 654) leaves the axial xylem in a protostelic manner, but in its upward course through the cortex an island of parenchyma appears adaxially to the protoxylem. This island enlarges and ultimately opens out to form an adaxial bay, the protoxylem at the same time dividing first into two and later into several bundles. The elliptic mesarch leaf-trace is thus converted first into a closed ring and finally into an open arc with a number of endarch protoxylem groups. This is the sequence of changes which the individual leaf-trace of an "adult" type of leaf undergoes as we follow it obliquely upwards through the cortex; this must also have been the sequence in its ontogeny. Since the mature leaves of *Thamnopteris* are crowded round an erect axis with

the leaf-traces ascending almost vertically through the cortex, a single cross-section through the stem supplies the entire leaf-trace sequence required for our purpose. According to Kidston and Gwynne-Vaughan these stages may be taken as "indicating the changes undergone in the ontogeny and phylogeny of the leaf-trace, and therefore they offer useful and reliable suggestions as to the origin and derivation of the adaxially curved leaf-trace so representative of the Filicales" (*Proc. R. S. Edinb.* Vol. 28, 1908, p. 435).

The fact discovered by Gwynne-Vaughan (*Ann. of Bot.* Vol. 25, 1911, p. 529) that in the genus *Osmunda* some of the juvenile leaves are supplied by a solid mesarch strand, although in the later leaves the trace is curved and endarch at its very origin, readily fits in with the view that the mesarch condition is an ancestral character.

From the Osmundaceæ let us pass to the allied group of the Zygopterideæ, a remarkable series of extinct ferns noted for the heterodox shapes of their petiolar bundles. The bundle as viewed in cross-section exhibits an extraordinary variety of form, quite distinct from anything seen elsewhere among ferns, whether recent or fossil.

Thus in the Clepsydroideæ, the definitive form of the trace may be compared, in different species, to such diverse objects as an hourglass (*Clepsydropsis antiqua*), a pair of spectacles (*C. australis*), a dumb-bell (*Asterochiaena laxa*, *Ankyropteris corrugata*), the letter H (*A. Grayi*) a double anchor (*A. vibractensis*) and a battle-axe with two blades (*A. Williamsi*). Yet, as Paul Bertrand has shown (*Études sur la fronde des Zygopteridées* 1909), these various types are all built upon a single fundamental plan, which binds together the whole series of forms, from the Devonian to the Permian. They are all variants of the simple form of trace found in *Clepsydropsis* which, being also geologically the oldest so far known, may be regarded as approximately ancestral for the Clepsydroideæ.

In the sister series, the Dineuroideæ, distinguished by the presence of quadriseriate "pinnae", we find an even greater variety of form in the foliar bundle, which here assumes some of the most complex and curious shapes imaginable for a filicinean petiolar trace. Slender and graceful X-shaped forms there are, with fine-pointed "antennae" looking like pincers or claws (*Diplolabis*, *Zygopteris*). A somewhat aberrant form, *Stauropteris*, has the four rays of the "star" mostly separated from each other in the middle. Several are variants upon the H-shape (*Etapteris*) with the vertical arms either slender and pointed (*E. diupsilon*), or thick and clumsy (*E. tubicaulis*), or, again, bent inwards and gradually swelling towards their free ends into four club-shaped processes (*E. Scottii*, *E. Lacattei*). At the

base of the whole series, in a position similar to that of *Clepsydropsis* in the Clepsydroidae, stands the simple elliptic trace of the Lower Carboniferous genus *Dineuron*.

We are still far from knowing the actual interrelationships of the Zygopterideae, and it remains to see how far petiolar anatomy is a reliable index of affinities in this family. But on the evidence so far available it seems pretty clear that the two series diverged from a common ancestor, and that each of them represents progressive differentiation along one or more highly specialized lines. Speaking generally, therefore, simplicity of form in the leaf-trace here means relative primitiveness. The common ancestor, the prototype of the Zygopterideae, probably had a simple elliptic foliar bundle with a protoxylem near each end, and this was presumably derived from a circular mesarch bundle, the commonly accepted *Urform* of the filicinean leaf-trace. The presence or absence of parenchyma in association with the protoxylem may be regarded as a comparatively unimportant detail.

Let us now see what the ontogeny of the leaf-trace, as revealed by serial sections in a few of the better known forms, has to tell.

Among the Clepsydroidae, the leaf-trace of *Asterochlena* arises as a circular strand with a single central protoxylem (primitive filicinean leaf-trace); as the strand ascends through the cortex the protoxylem divides into two, the bundle at the same time becoming flattened tangentially (primitive Zygopteridean type). This condition is, however, shortlived, for a median constriction and other changes soon transform the bundle into its definitive, somewhat clepsydroid, or rather dumbbell-like form. In *Clepsydropsis* itself, where the protoxylem is intermixed with parenchyma at the very beginning, we notice the same tangential flattening of an originally circular mesarch bundle, and then a median constriction resulting in the characteristic clepsydroid or spectacle-like shape. In the genus *Ankyropteris*, too, if we ignore the complications due to the so-called axillary branch, which is adnate to the petiole, the process is essentially the same: nipping off of a circular mesarch bundle with "mixed" protoxylem; tangential flattening; and subsequently a median constriction accompanied by a division of the protoxylem into two. But it is noteworthy that this clepsydroid or dumbbell-like condition is here only temporary, being superseded by an antero-posterior extension of the peripheral loops. This extension is more marked in some species than in others and, combined with other modifications, leads, in different species, to such shapes as a double hatchet (*Ank. Williamsoni*), the letter H (*Ank. Grayi*) and a double anchor (*Ank. bibractensis*).

Among the Clepsydroidae, then, the leaf-strand of all the genera passes through a stage which was presumably permanent in the prototype of the Zygopterideae, and that of *Ankyropteris* passes through a *Clepsydropsis* stage, considered primitive for the Clepsydroidae.

What happens in the Dineuroideae? Data are available only in the case of *Metaclepsydropsis* and *Diplolabis*, but their evidence is unmistakable. In *Metaclepsydropsis*, as we know from Gordon's work (*Trans. R. S. Edinb.* Vol. 48, 1911, p. 163), the leaf-trace originates as an elliptic strand with two protoxylems. Presently, at each end of the ellipse an island of parenchyma appears in connexion with the protoxylem, and the trace assumes a shape "precisely similar to the fully developed foliar bundle of *Dineuron*" (Scott). From this condition, as the bundle ascends through the petiole, the shape characteristic of the genus gradually moulded. In *Diplolabis*, too, Gordon (*Trans. R. S. Edinb.* Vol. 47, 1911, p. 711) has recognized, at successive levels, transient phases resembling (i) the elliptic trace with two protoxylems, ancestral for the whole family, (ii) the *Dineuron* type, primitive for the Dineuroideae, (iii) the *Metaclepsydropsis* type, simpler than *Diplolabis* in its thicker "waist" and shorter "antennae."

We thus see that in the Zygopterideae the leaf-trace of several genera passes successively through stages which are permanent in related form of simpler construction. What is the conclusion? I do not say that the series of forms from simple to complex represent actual phyletic lines; but on the existing evidence it seems highly probable that the leaf-traces of the Zygopterideae, considered comparatively, reveal certain evolutionary tendencies, and these tendencies, as we have seen, are recapitulated in the ontogeny.

Let us now pass on to some other vascular cryptogams. As Holloway (*Trans. N. Z. Inst.* Vol. 50, 1917, p. 33) has shown, the stem of a young sporophyte of *Tmesipteris* is traversed by a solid protostele instead of the ring of bundles seen in the mature stem.*

In the New Caledonian species *Tm. Vieillardii*, an erect terrestrial form, probably the most primitive member of the genus, the lower, that is the first-formed, part of the shoot, possesses a certain amount of cauline medullary xylem; in the later-formed (distal) parts of the same axis this undoubtedly primitive tissue is absent (Sahni, *Nature*, Vol. 111, 1923, p. 84).

* The two conditions have not, however, been so far observed in different parts of the same shoot. It appears that the protostelic shoots generally retain their juvenile anatomy throughout life, and that they are succeeded by new shoots (developed from other branches of the rhizome) which alone are destined to develop the siphonostelic structure.

We are all familiar with Treub's work on the embryogeny of lycopods, and with his ingenious theory of the protocorm (*Ann. du jard. bot. de Buit.* Vol. 8, 1890, p. 30). Treub regarded the protocorm of *Lycopodium cernuum* as a vestigial organ of great antiquity, the precursor of the leafy shoot in ancestral Pteridophytes. Usually a small transient organ of obscure function, it is important as a means of perennation in *Phylloglossum*, while in some species of *Lycopodium* it serves for a whole season as a rhizome (Holloway, *Trans. N. Z. Inst.* Vol. 49, 1916, p. 90), branching and even reproducing itself through bulbils.* As to its phylogenetic significance opinion differed a good deal until recently, when Treub's theoretical assumptions materialised in the discovery of an actual group of archaic Pteridophytes, the Psilophytales, in which a closely comparable organ persisted to the adult stage, as it also does in the modern Psilotaceæ (Kidston and Lang, *Trans. R. S. Edinb.* Vol. 52, pp. 619, 846).

In the genus *Lycopodium* the radially arranged stele, found in the *Setago* section, is generally regarded as more primitive than that in which the xylem and phloem alternate in horizontal plates, as in species belonging to the *Clavata* and *Cernua* sections. The fact discovered by Holloway (*Trans. N. Z. Inst.* Vol. 48, 1915, p. 299) that the "seedlings" of these species have steles of the radial type, may be of some phylogenetic significance, although the same kind of structure may reappear in the ultimate branches.

Heterophylly is clearly a specialized condition, derived from one in which the leaves are all of one kind. From the ontogeny of heterophyllous species of *Lycopodium* Holloway (*Trans. N. Z. Inst.* Vol. 48, 1915, p. 295) has shown that the "seedlings" at first bear leaves of one kind only, the heterophyllous condition arising subsequently in development.

In many other vascular plants, both cryptogams and those higher in the scale, in which the leaves or shoots characteristic of the adult plant exhibit special modifications, some clue to the primitive condition is often given by the young plant (Goebel, *Org. d. Pfl.* 2. Aufl. (i) 1913 p. 356 ff.) This does not, of course, mean that all juvenile structures are to be interpreted in the same light, and this caution is specially necessary in the case of seed-enclosed cotyledonary leaves:

* If Treub's view is correct *Phylloglossum* would be an interesting parallel to the famous Axolotl among animals: a sort of "adult seedling" comparable to *Welwitschia* and many ephemeral angiosperms which, growing under adverse circumstances, are obliged to flower at the seedling stage. Whether *Phylloglossum* and *Welwitschia* can ever be induced to come out in their true colours, like the Axolotl did at Paris, must be left for those to decide, who are in a position to observe these rare plants under varied artificial conditions. (See Goebel, *Org. d. Pfl.* 2. Aufl. (i) 1913, p. 363 ff.)

Instances of the kind under consideration are so numerous, and their interpretation so commonly accepted, that it is superfluous to mention more than a few: *Ulex*, species of *Phyllanthus* and *Acacia*, most Cactaceae and many cactoid Euphorbias; among Gymnosperms, the genus *Phyllocladus*, whose seedlings have normal cylindrical shoots with spirally placed needle-leaves; several Cupressineae, as well as species of *Dacrydium* and *Podocarpus* with cupressoid "adult" leaves. Similarly, the short-shoots of *Pinus*, *Cedrus*, *Larix* and *Ginkgo* are an adult characteristic only gradually developed by the seedling as it grows up. The deciduous habit, involving as it does the formation of a special absciss layer, is clearly a derived condition, and the persistence of leaves on the seedling is a well known feature of *Larix*. It is seen also in *Quercus* and no doubt occurs in many other genera.

Professor Jeffrey (*Anat. of Woody Plants* 1917, p. 237) believes that the first ring of the secondary wood in living Araucarineae shows a feature (the abundance of parenchyma) which recalls a condition persisting throughout the secondary wood in Mesozoic representatives of the family, and he adds: "The situation here indicated is of great value and wide validity not only for the gymnosperms but also for the dicotyledons".

The development of the young ovule of *Torreya* into the mature seed affords an instructive example of recapitulation. It is well known through the work of Professor Oliver (*Ann. of Bot.* Vol. 17, 1903, p. 451) that the supply bundles of the seed pass through two foramina which pierce the stony layer of the integument at a level much nearer to the micropyle than to the chalaza. Yet it stands to reason that the vascular supply must primitively have entered at the basal end and not near the micropyle. And there is strong evidence for the view that the family to which *Torreya* belongs is descended from ancestors, probably Cordaitan, in which the main vascular supply entered the sclerotesta through a single chalazal foramen (Oliver, *loc. cit.* and Sahni, *Ann. of Bot.* Vol. 34, 1920, p. 117). The two foramina of *Torreya*, although entering much nearer the micropyle, would therefore represent as Prof. Oliver says the "ancestral chalaza", and the two vascular bundles passing through them must have originated in the course of evolution by the splitting of a single basal strand. If this view is correct the portion of the seed lying between the two supply bundles in *Torreya* (the hyposperm of Professor Oliver) is in a phylogenetic sense of recent origin compared to the upper portion, called the archisperm. Now it is interesting to see that even in the ontogeny the hyposperm is a later formation. In the young ovule (where the nucellus is superior) the points of

entry of the two supply bundles are actually at the chalazal end. As growth proceeds the ovular base expands in the region between the bundles. The bundles are thus taken apart, right and left, while through the widening seed base the newly formed tissue, which is destined to become the hyposperm, bulges downwards in the form of a pouch.

On the authority of Coulter and Chamberlain who have made a wide study of the original literature, "almost without exception" the Sympetalae, the highest-evolved division of Dicotyledons, possess anatropous ovules (*Morph. of Angiosperms* 1912, p. 57). Such ovules would on comparative grounds alone be regarded as derived from orthotropous ones, and this conclusion is confirmed by the study of their development, for anatropous ovules are at first erect or nearly so, early developing a curvature near the chalazal end.

The arrangement of floral parts known as epigyny is obviously a condition derived from hypogyny. Hypogyny is not only the prevalent state of things in all the more primitive angiosperm families at the present day but probably dates back to mesozoic times when it was inaugurated among their ancestors. The study of a developing epigynous flower shows that the floral primordia are arranged in a hypogynous manner. The fact that both hypogynous and epigynous flowers sometimes occur in one and the same family does not materially affect the position.

It must be admitted that the results so far obtained from the study of seedling anatomy in the higher plants, when viewed as a whole, are not encouraging to the recapitulationist. This is specially so in angiosperm seedlings. Here palingenetic characters appear to be so little in evidence that Dr. de Fraine (*Ann. of Bot.* Vol. 24, 1910, p. 172) was led to remark: "it is not justifiable to use the seedling structure as an indicator of phylogenetic connexions." The constant presence of paired strands in the cotyledons of many of the primitive dicotyledons (Ranales and Rhoecadales) appears to be about the only archaic feature of importance. It is probably safe to regard this as a relic of the double leaf-trace so frequently met with in the older gymnosperms, which in turn appears to be a manifestation of the primitive dichotomous branching of the leaf (Thomas, *New Phyt.* Vol. 6, 1907, p. 90).

Among gymnosperms, cycad seedlings are specially interesting as passing through a short-lived protostelic phase, and it is significant that at least in some cases the earlier leaf-traces are straight, not girdled. In *Ginkgo* and the Conifers perhaps the most notable feature from our point of view is the frequent presence of centripetal xylem, the relic of an ancestry possibly filicinean.

Developmental phenomena which are probably to be classed under recapitulation are also to be met with among the Thallophyta and Bryophyta, for example, in the ontogeny of the Volvocineae, of *Batrachospermum* and *Cutleria*, and of some Liverworts and Mosses (Goebel, *Org. d. Pfl.* 2. Aufl. (i) 1913, p. 374 ff.)

I must content myself here with this very cursory treatment of a difficult because controversial subject, which requires a more detailed treatment than is appropriate to the occasion. Nor is it possible to do full justice to the wide range of facts and arguments in the brief course of an address.

But even from this inadequate survey of the facts of ontogeny it appears that the phenomenon of recapitulation is of wide occurrence among plants—of wider occurrence, perhaps, than many botanists have assumed. This much at least is certain that most, if not all, of these facts, like numerous others found scattered in the literature, have individually been either understood or interpreted in this light, at one time or another. Indeed, botanists have often tacitly accepted the principle, though, curiously enough, few have cared to avow it. One reason for this hesitation may be the fact that much of the evidence is derived, not from the embryo or “seedling” as ordinarily understood, but from the development of individual organs produced at intervals during the adult life of the plant. This circumstance should not, however, affect, as I venture to think it has affected, our attitude towards the general question. For, however paradoxical it may seem, the embryogeny of vascular plants does not end with the embryo or “seedling”, but extends into the adult life, being as a rule co-extensive with life itself.