

between them, the whole being surrounded by a very thin membrane which is only visible at the two ends. This is the structure which we may call a nucleus. It is surrounded by a space containing a substance which is only slightly stainable, and this again is surrounded by a deeply stained membrane, outside which is the slightly stained gelatinous envelope. Previously to its division the cell elongates; the nucleus also elongates and contracts slightly about the middle of its length. A dumb-bell shaped structure is thus obtained. The two nuclear rods divide completely to form two groups containing two rods each, which remain connected together for some time by the less deeply stained portion of the nucleus. The constriction becomes more and more pronounced until finally the two halves of the nucleus are completely separated. The outer capsule or cell-wall has meanwhile been also contracting towards the middle; the contraction keeping pace with the division of the central mass. This contraction goes on until, at a certain stage, a delicate transverse partition appears dividing it into two, each half contains one of the halves of the original nucleus. Ultimately the two halves become completely separated and two new cells are formed.

In the majority of cases the cells are completely separated before the division of the nucleus again begins, but in many instances the nuclear rods were seen to be dividing in cells which were still connected with each other.

After a time the division of the cells takes place less rapidly and finally ceases altogether. The division of the nucleus becomes very irregular, and at the time when cell-division has ceased the nucleus has become broken up into granules which are distributed irregularly in the contents of the cell.

This breaking up of the nucleus appears to be preliminary to the formation of spores, although the formation of these has not been satisfactorily observed.

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**ORIGIN OF POLYSTELY IN DICOTYLEDONS.**—Nearly all flowering plants have a monostelic structure in stem and root; that is to say, their conducting system forms a single central cylinder (stele), which consists of the xylem- and phloëm-strands, and of the conjunctive parenchyma by which they are united and surrounded, the whole being enclosed by a general endodermis belonging to the cortical



tissue. This central cylinder is common to stem and root, though the two organs differ in the distribution of its constituent tissues.

In spite of the almost infinite anatomical diversity which is met with among Phanerogams, this monostelic structure is scarcely ever departed from. Whatever may be the arrangement of the wood and bast, however much the differentiation of the conjunctive tissue may vary, whether there be indefinite cambial increase or not, or whatever form this increase may take, still the presence of a single central cylinder is an almost constant character.

In the Vascular Cryptogams this is not the case. Although in many Equisetums, in *Lycopodium*, *Isoëtes*, some species of *Selaginella*, and some of the simpler Ferns, the axis is monostelic, in the great majority of the Ferns, and in many *Selaginellas* a different type prevails. In these the central cylinder no longer remains simple; it bifurcates repeatedly, and the mature stem is traversed by a number of distinct, but anastomosing, vascular cylinders (the "concentric bundles" of De Bary's Anatomy), each of which is homologous with the single cylinder of a monostelic stem. It is, however, a fact of essential importance that in all vascular plants whatsoever the *embryonic* structure is monostelic, the stem, like the root, primarily containing a single cylinder of small diameter and simple organization. In the flowering plants progress takes the direction of increase in the size and complexity of the one cylinder; in the Cryptogams above cited a complex conducting system is attained in another way; the original cylinder branches and the stem becomes *polystelic*, in all the later-developed internodes<sup>1</sup>.

Van Tieghem, the originator of the anatomical conceptions which have just been indicated, well says that polystely is the most important modification which the structure of the stem can undergo<sup>2</sup>. According to our present knowledge there are only two genera of flowering plants in which polystely occurs, namely *Auricula*<sup>3</sup> and *Gunnera*. Though systematically so remote from each other, these genera agree, so far as most of their species are concerned, in posses-

<sup>1</sup> *Leclerc du Sablon*, Recherches anatomiques sur la formation de la tige des Fougères. Annales des Sci. Nat., Bot., Sér. VII, t. xi, 1890.

<sup>2</sup> Traité de Botanique, 2<sup>me</sup> éd. 1891. Pt. I, p. 767. See also *Van Tieghem et Douliot*, Sur la polystélie. Ann. des Sci. Nat., Bot., Sér. VII, t. iii, 1886.

<sup>3</sup> *Auricula* is usually regarded as a section of *Primula*. Van Tieghem makes it a separate genus, and his nomenclature is provisionally adopted here, though I express no opinion on the systematic question.



sing a number of distinct vascular cylinders in the main stem. Both genera indeed include monostelic species, such as *Auricula reptans*, and *Gunnera monoica* etc., but the majority are polystelic, the number of cylinders varying in different species from two to eighty. In the monostelic species of each genera the single cylinder has precisely the same structure as each of the many cylinders of the polystelic forms. In every case each 'stele' is almost destitute of pith, has its vascular bundles crowded together, and shows little or no secondary growth in thickness.

Now it is remarkable that both *Auricula* and *Gunnera* have near relations which are aquatic in habit, and which have the reduced vascular structure characteristic of aquatic plants. Among the Primulaceae there is *Hottonia*, in which the submerged stem has a central cylinder of simple structure, with little pith, confused vascular bundles, and little or no secondary thickening, just as is found in *Auricula reptans*, or in a single 'stele' of any of its allies. Van Tieghem, after pointing out this identity of structure, adds: 'Mais l'*Hottonie* doit sans doute l'étroitesse de son cylindre central à sa végétation submergée, de sorte que sa structure n'est pas rigoureusement comparable à celle des *Auricules*'<sup>1</sup>.

*Gunnera* also, as a member of the Order Haloragaceae, has a number of aquatic relations, the central cylinder of which (at least in *Myriophyllum* and *Hippuris*) perfectly agrees with that of the monostelic *Gunneras*, or with the several cylinders of the polystelic species. In drawing this comparison, Van Tieghem repeats the remark just quoted as to *Hottonia* and *Auricula*.

In the polystelic *Auriculas* the flower-stalks and the leaves have normal structure. In the *Gunneras* on the other hand polystely extends both to the pedicels and to the petioles and larger veins of the leaf.

It is a striking fact that the two Dicotyledonous genera, in which alone, so far as we know, polystely prevails, belong to families remote from each other, but agreeing in the fact that they include aquatic representatives of reduced monostelic structure.

The suggestion which I wish to bring forward is this: is it not possible that these polystelic Dicotyledons may owe their exceptional structure to descent from aquatic ancestors? When a plant becomes adapted to submerged aquatic life, we find as a rule that its vascular

<sup>1</sup> Sur la polystélie, l. c., p. 295.



cylinder becomes narrowed and reduced; the pith tends to disappear, the bundles are confused together, and the power of secondary growth in thickness, in the case of Dicotyledons, is nearly or wholly lost. Where the plants are entirely submerged this reduction may affect the whole axis; where however the flowering stem rises above the surface of the water it may retain a typical vascular cylinder, as is conspicuously the case in *Hottonia*.

Now supposing the descendants of a reduced aquatic Phanerogam to return to a terrestrial mode of life, they will evidently once more need that higher development of the vascular system which is proper to land-plants. The favourable variations bringing about this change may indeed take the direction of a renewed dilation and differentiation of the single cylinder, and if a Dicotyledon is in question, secondary thickening may again make its appearance. But it is also possible that the available variations may take a different line. Instead of the one vascular cylinder again becoming more complex, the necessary amount of conducting tissue may be provided in the form of many distinct cylinders, arising from the bifurcation of the original one. This is what undoubtedly happened in the case of most Ferns, which, when they originally adapted themselves to life on land, became as a rule polystelic<sup>1</sup>. It may well have happened also in the case of certain Dicotyledons, which, in having become aquatic, had sunk to the anatomical level of the simplest Pteridophyta.

On this view then the polystely of *Auricula* and *Gunnera* may be regarded as the anatomical expression of the return of plants of aquatic habit to a terrestrial mode of life.

We may conjecture that the Auriculas, which always retain a normal structure in their pedicels and leaves, may be descended from only partially submerged ancestors. *Gunnera*, which belongs to a more distinctly aquatic family, may well have had ancestors which had more completely lost the typical monostelic differentiation, and hence the renewed adoption of terrestrial habit may have been accompanied by polystelic modifications extending to all the subaerial organs.

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<sup>1</sup> Anatomical complexity in Ferns nearly always takes the form of polystely. But in *Botrychium* we have an indication of the other alternative—indefinite development of the single stele. If *Lyginodendron* and its allies really had Filicine affinities, this monostelic differentiation must have gone much further in the Palaeozoic representatives of the class.





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