

13
Thesis - 1864.

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Contributions to
Vegetable Physiology. Prof. Goodyer,
2

Including some remarks on the Development of
the Leaf, and Spiral Vessels, and History of the latter,
also on the Relation existing between the Phyllotaxis
and the form of the Pith and Stem; Development
of the Wood; and the Definiteness of Development of
the Shoots of Plants.

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Development of the Leaf.

To the eye, the earliest representative of the leaf looks like a more homogeneous papule. Composed as it is for the most part of cells, it might - and that even with microscopic aid - without more careful examination, be looked upon as possessing no other constituent. Such, however, is not the case. Under a power of 215 diameters, certain other structures become apparent - structures which appear of first importance as regards the well-being of this, the leaf-bud, as of every other organ in the vegetable body, for no organ is destitute of them. The structures to which I refer are the Spiral Tubes.

There is another point of interest in the histology of the early leaf-bud. The cells of which it consists are not, as I shall endeavour to point out, derived solely from one of those cellular structures forming part of the growing axis. They are not derived solely from the bark, nor solely from the pith, but one group of them is a bark-structure, the other a pith-structure. Investigations made by Dutrochet seem to strengthen this position - at all events, while they

go to show the analogy between pith and bark, they throw much light on the manner in which the former of these operates in the development of the cuticular part at least, of the leaf. —

This botanist found that over a cut surface of growing pith there became speedily developed a structure similar to cuticle. Over the surface of the group of cells in the leaf-bud derived from the pith, the development of such a structure takes place. This is destined subsequently to become the cuticle of the upper surface of the full-grown leaf. That of the under surface is already cuticle while yet it forms part of the embryo leaf, for it is nothing more or less than a prolongation upwards of the green cuticular layer of the bark of the stem.

The evident ^{fact} of this formation of the upper and under surfaces of the cuticle of the leaf from structures in many respects so dissimilar as are the Pith and Bark seems to account in great measure for their difference in structure and function. It is certainly strange that that aspect of the leaf developed from the very structure which, of all others seems, in seeking a position in the very central depths of the axis, to shun the light the most, should, in its

place on the leaf, be the very one which counts the light most safely—maintaining the position it thus assumes with an energy almost instinctive, and to the discomfort of the representative of a structure great part of whose province it is to shield the organs from the glare of mid-day. But perhaps the decision we see practically carried into effect by their representatives in the leaf, would be the one which might result from a trial on equal terms, of the primary structures.

On a consideration of the manner in which the young bud is developed cell by cell, it is not my intention to enter. I suffice it to say that its growth is similar to that of all other vegetable organs, each subsequent cell resulting from similar pre-existing structures. Of the reason of its development at a determinate point I shall subsequently have to speak.

But I have referred to the spirals of the young bud. To these I shall refer somewhat more in detail. I introduce the figure principally to explain their formation, and, secondarily that of the cellular constituents of the leaf-bud. It is from an Isoprenous twig of this species grown, longitudinal.

section involving the structures of the axis and embryo leaf.



Figures I. Section of young shoot. Showing two young buds deprived of their scales and their connection with the structures of the axis — highly magnified.

1. The Pith.
2. The medullary system of spirals.
3. Layer of wood.
4. The Bark.
5. Cuticle of the stem.
6. Scar of fallen leaf.
7. Under cells of leaf-bud papilla.
8. Upper cells of leaf-bud papilla.

In the figure those divisions of the leaf formed from the pith and bark respectively, are traced in the same colours as these structures, the upper part corresponding, as I have said to the pith, the under to the bark.

The spiral systems I have drawn in red colours. It will be observed that spirals pass from the main structure forming the Medullary sheath, to the leaf-sears, to the bud-scales and to the young leaves.

Those spirals supplied to the latter are seen entering the base of each papilla, to course along between the group of cells developed from the bark and that developed from the pith.

Before proceeding to a more minute consideration of the development of the spirals, I shall shortly trace the papule with the aid of two diagrams, to its appearance as the perfect leaf.

Fig. II. One of the papillae at a later period, seen on face. —

1. The pith.
2. The spiral sheath.
3. Green layer of bark.
4. Cuticle of the stem passing upwards along the axis of the bud to form the cuticle on the back

of the leaf.

5. The enlarged Papilla seen from the inner side. The cells in its interior are visible through the cuticle of that portion of the leaf developed from the pith. The spirals in its interior have enlarged and branched. The margins of the Papilla are as yet entire

6. The vessels going to the scales, one of which is left.

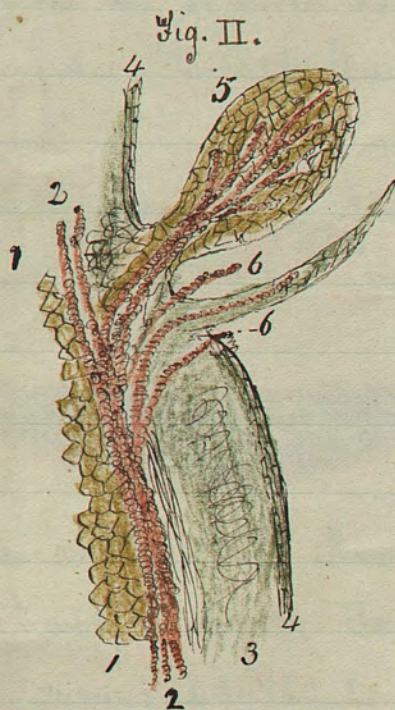


Figure III. (page 4) represents the transverse section of a mature leaf, showing its two divisions. The part coloured green - the anterior or superior part of the Parenchyma of the leaf is

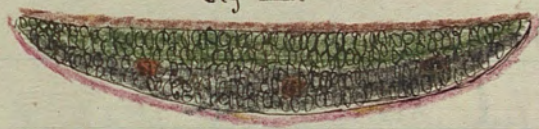
entirely cellular, no vessels being seen in it. This is the portion developed from the pith.

The posterior or inferior division of the Parenchyma, composed of cells and presenting a transverse section of the vessels (● ●) near its anterior part. — Coloured blue. This is the part of the leaf developed from the green layer of the bark.

— Cuticle on Superior aspect of the leaf and developed from the medullary portion of the Parenchyma.

— Cuticle on the inferior, posterior or dorsal surface, being a continuation of the cuticle of the stem.

Fig. III.



I have here represented three vascular bundles. This number, though most common in leaves, is not by any means constant. There may be only one or two, or, on the other hand five or seven. Sometimes they are innumerable.

But the vascular bundles in the leaf are not made up wholly of spirals to which alone I have hitherto referred in speaking of them.

There are two other structures associated with them; namely woody fibres and pith. The former occupy a position external or inferior to that of the spirals, from which they are anatomically separable according to some. I have not however been able to separate them distinctly. The other structure to which I refer is separated in the leaf by small rods of compact cellulose, one of these rods lying in the concavity formed by the vessels, and ramifying with them. Each bundle thus carries in its concavity a rod of pith, its position being external to that of the spirals. At the point at which the pith leaves that of the axis, the number of columns into which it is divided corresponds to that of the spirals. As they ascend into the petiole they coalesce into a rod surrounded by fibres, as in the stem. In the leaf they again diverge.

The relative position of the corresponding structures in the leaf and in the axis is strikingly similar. Beginning at the lower aspect of the leaf, we find the cuticle which corresponds to that of the stem. Then the cells representing the green layer of bark. Next, the woody fibres of the vascular bundles corresponding to a similar structure in the axis. Fourthly

we come upon the spirals and fifthly the fifth of the bundles and the upper cellular division of the leaf - corresponding respectively to the spiral sheath and the central fifth of the axis.

The same remarks apply also to the petiole. The analogy between this structure and the axis is strengthened to some extent by what we see take place in Umbelliferae. In these plants we see the fifth follow the same laws both in stem and petiole, absorption of it in the one structure taking place in a manner similar to that in the other.

I have next to say a few words with regard to the development of the spirals.

There has been some discussion as to whether these structures are to be looked on as ascending or descending structures. That their development at least is ascending, the examination of them in the young leaf as well as in certain other structures, leaves no room to doubt. Some of the circumstances which put the fact of this ~~down~~^{up}ward development beyond doubt I shall next proceed to examine.

In Figure I I have represented the spirals supplied to the young leaf. That such exist can easily be demonstrated in almost any species.

Here then we have, in a more vegetating functionless mass of cells, dependent for support on the cooperation of other structures, a formation which has been looked on as descending from the leaf, and developed in a downward direction, by the operation of the leaf itself. But this little cellular papule cannot be called a leaf.

The proper explanation of the mode of growth of the spirals must be one which looks upon them as developed in an ascending direction through the medium of previously existing cells of an organism similar to their own. They have a development in fact similar to that of the cellular constituents of the leaf. There is no doubt but that the other leaves of the growing plant have much to do in the elaboration of juices intended for the nutrition of the spirals in the bud, as well as for that of every other organ in the vegetable; and thus they may be said to develop as spirals. They may even on these grounds be said to develop their own spirals, but as I have said they do this only by elaborating the formative juice intended by the agency of similar previously existing structures, to be built

up into tube-wall and spiral filament.

This leads me today a few words concerning the non-peristaltic of thin downward or centripetal development as deduced from an examination of them in other organs. I shall confine myself to five examples:

Spirals exist in the following structures:

1. In the embryo.
2. In abortive branches.
3. In the flagellum.
4. In flowers.
5. In certain hairs.

Their existence in the embryo leaf we have already seen.

To examine these in detail: First, we have them in the embryo. An examination of the embryo, as it lies in the fleshy albumen and seed of the exhibits them to advantage. In that position which represents the axis of the plant we have small transparent rods of very equal size running along parallel to one another. Each is marked by lines that appear as transverse striae running across it at equal intervals. They are in reality however not transverse but spiral. These rods, or rather tubes

As the embryonic spirals. From the central group can be seen diverging in the axis of each cotyledon one or more of these spiral filaments.

Spirals can in a similar be seen in the abortive branch, as in the thorns of Crataegus. Here their position does not materially differ from that assumed by them in the young bud; they have a position central to that of the other structures. The same remarks apply to the flabellum. But here, instead of occupying the centre, they run along at some distance from it, surrounding the medullary sheath of the axes.

In flowers also spirals exist. A group of them or sometimes but one run along the central part of each sepal and petal. This can be demonstrated in any flowering plant. I take the example of the flower of Valerian (Fig. IV) in which a spiral vessel is supplied to each of the papillae which represent the limbs of the sepals. The spirals in this case, as in Compositae is only observable in these calyx-limbs while they



Fig. IV

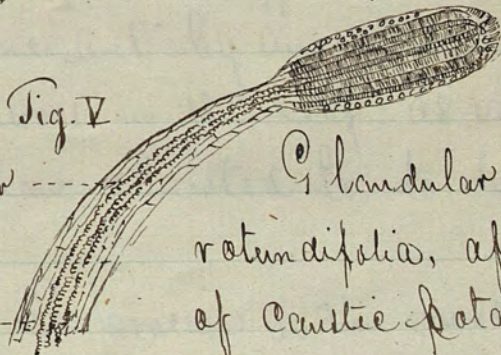
are in the state of papillae, and therefore cannot be seen in the

featuring Pappus.

Spirals are likewise seen in certain hairs especially in those called glandular hairs. They exist in the hairs of *Drosera*, in the youngest as well as in the oldest, not being confined to the stem of the hair alone, but abounding in the terminal bulb. In the latter structure they are of larger size than in the stalk or in the leaf itself, and are arranged closely together in a compact cylinder. I may mention however, that they have more the character of annular than of spiral vessels; and the existence of such structures in this secreting body, along with the obvious difference existing between them and the other spirals of the plant, seems to indicate that they have something to do with the function of the organ.

Fig. V

Spirals of hair
Elongated Cells
forming the hair



Glandular hair of *Drosera rotundifolia*, after the addition of Caustic Potass. Showing spirals.

The above-noted examples are enough to show that spirals are not necessarily leaf structures. But from their existence and development in these organs

Another conclusion is to be deduced, namely that the spirals are developed in an ascending direction, inasmuch as neither of the organs in which we have just observed them to exist, is endowed with power to produce de novo any of their component structures, dependent as they are for nutrition and growth on the general nutrient system of the plant.

Besides, apart from the main spiral formation of the axis, and unconnected with it by similar structure, there is no isolated spiral-forming nucleus to be seen. Admitting that no cell or fibre in the plant can be produced without the existence of similar previously existing cells or fibres, or their representatives, the circumstance I have alluded to would of itself be sufficient, if the fact were not borne out by an actual examination, to declare the spirals in the leaf, as well as in the other organs I have alluded to, to be ascending formations.

I proceed in the next place to examine the spirals in their mature condition.

Although a strictly physiological examination of these structures ought, for obvious reasons to value

their history in centrifugal sequence, that is in a direction from root to leaf. it will be more convenient to trace them from above downwards. I divide their course into three stages. 1st From their ultimate divisions in the leaf to their entrance into the phloem of the stem. 2nd As they lie in the wood, 3^d Their appearance as the medullary sheath.

1. It is in the numerous vascular ramifications and interlacements which intersect in all directions the cellular structure of the leaf, that we find the commencement of the spirals, the ultimate representatives of the sheath. Composed for the most part of spirals, with a few woody tubes, these bundles of vessels can be seen to form one or more midribs, running in petiolated leaves into the leafstalks, in the formation of which they are aided by cuticular cells; in non-petiolated leaves either at once entering the woody axis after having combined to form three or more bundles, or continuing into one bundle previously to diverging.

The vessels from the leaf, at their entrance into the axis, are usually collected in

three, five, or seven bundles. This can at once be seen on breaking off a leaf from whatever part of the stem or branch. The subsequent distribution of the bundles are however best observed in young shoots. Let us trace for example the course of the vessels in a this year's shoot of Alder. The number of bundles in the petiole of one of the leaves of this plant can easily be seen to be three. From the point of junction of each leaf with the axis, extend three elevated ridges. By dissecting away the bark we see the cause of this - three small rounded threads of vessels diverging downwards from the base of the petiole. The lateral two running down the axis obliquely, the middle one vertically. After they have passed for some distance down the axis, diverging more and more, they suddenly dip - and that without breaking up or intermingling in any way with the plexenchyma of the axis - into small oblique apertures channelled out in its substance for their reception. The Oak, Raspberry, Pear, Apple and a multitude of other plants afford examples of the same arrangement. But this number three is by no means invariable. It is only in alternate

leaved plants that we find ^{it} fairly constant. In the Horse Chestnut, not an alternate leaved plant the number of bundles is sometimes three, sometimes five or seven. The Alder is an opposite leaved plant. From each of its leaves proceeds three bundles of vessels, but at each side of these three there is a fourth bundle, smaller than the rest. This last bundle crosses over to combine with its fellow of the opposite side, the common trunk thus formed entering the wood in the same manner as the rest do. This arrangement I have not hitherto met with in any other plant. In Lamiate plants and some allied orders the most common number is two. In the Dead-nettle for example the petiole generally splits at the base into two divisions each of which contains a bundle. Sometimes the petiole is entire and contains a third middle bundle, which is however invariably insignificant. In all of these opposite leaved plants, the bundles, as regards their subsequent disposal are similar to those of Alder.

In some instances, the bundles, instead of entering the wood after having descended the axis for a short distance, are continued on separately a long way. The Mistletoe affords an example of this.

This parasite presents five bundles from each leaf. On peeling off its green plated bark, below a pair of its leaves we come on ten cords or bundles of vessels, not adjusting themselves so as to form a solid cylinder, but each separated from its neighbour by a narrow interval, into which the cellular bark dips, each remaining isolated as far as the next node. Here they no longer exist as external structures, but pass inwards and become the medullary sheath of the node below. If this be the disposition of the number of bundles of the ultimate node, what becomes of the bundles from the second one? These also pass down their own internode externally, then dip into the axis, forming the sheath of the internode below, and so on throughout the whole stem. On the very largest stem or branch of mistletoe can be seen these bundles - not shrivelled up, but green and vigorous, and much enlarged compared with those of a young node. At the oldest nodes where leaves have fallen off the ends of the bundles which had been thus exposed are embedded in a mass of cellular tissue, formed by a growth of the bark, which had grown over and concealed the scars of the leaves. These bundles

are probably connected with the wood above them. Thus, at whatever point in the axis of this plant we peel off the bark, we come on these bundles embracing the wood and standing out from it so as to give it a fluted appearance - an arrangement I have observed in no other plant.

The relative arrangement of the bundles of each successive year in woody exsurgens in general, will perhaps be best illustrated by reference to what we have seen take place in the ~~Mistle~~ Mistletoe. Here the bundles from the newly formed leaves assume a position internal to that occupied by the bundles of the leaves of the previous year. Thus their annual accession is endogenous. The same is seen though not to such advantage in other Exsurgens.

In the canal allotted to them in the wood, the bundles do not present much variety and thus their history will not detain us long. The point which it is of most importance to observe here is, that no structural communication takes place between them and the fibres of the primary wood. This of course applies to the fibres from nodes older than that newly formed which has not as yet

get any wood. This absence of all structural communication between the true wood and that from the leaves can hardly be reconciled with the theory put forth by Petit Thauvot and Pandichand representing the primary wood as the result of an aggregation of leaf-radicles. It can be easily and satisfactorily demonstrated, that, save the bundles of vessels sent down internal to the true or primary wood, there exists between the sheath and bark no woody structure deposited exogenously, connected with the leaf.

In this division of their course, the bundles are invariably accompanied by a process of pith proceeding to the axis of the leaf. To this process they form a guide, enclosing it like a palisade and assisting the bark in screening ^{it} from injury.

The total number of bundles supplied to one leaf bears the same relation to the pith of the young bud as the fibres of one of these bundles bear to a small rod of pith, derived from that of the axis, running up the channel formed by each bundle. The annexed figure is intended to represent the conditions to which I refer. It represents a transverse

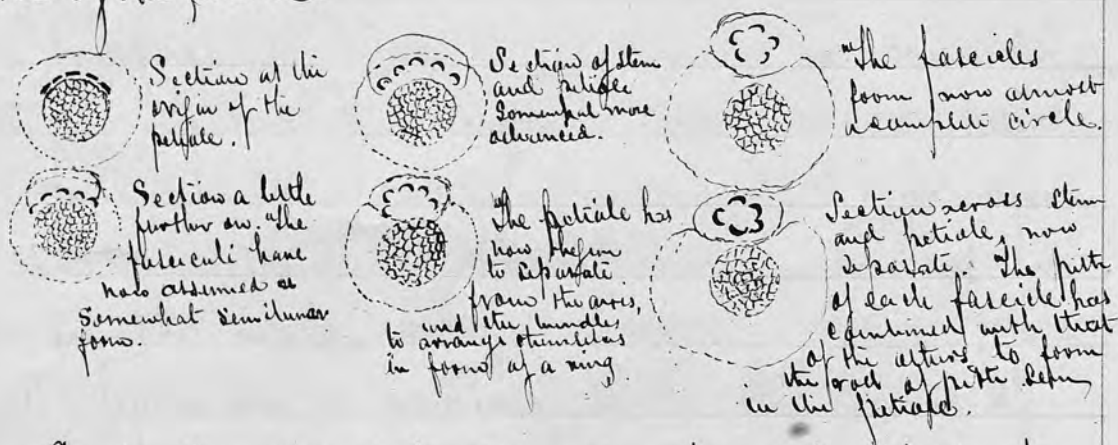
sections of the petiole of a leaf which three bundles of vessels are supplied. The small dotted spaces in the belly of each bundle of vessels represent the rad of pith.



As regards the function of these small columns of pith, there is no doubt but that they are intended for the conveyance of sap to the leaf itself, just as another portion of pith is devoted to the maintenance of the bud. It is probable that these branches of pith are principally of use during the young stage of the leaf. Otherwise we must suppose that one leaf acts with every other for the commonwealth of the Vegetables, its appropriate share of nourishment being meted out to it from the common store.

In many cases the rad of pith can be traced as far as the leaf-scar. In others it is easy to follow ^{them} for a considerable distance into the leaf. The phenomenon in question seems to reach its point of maximum development in Evergreen plants. The subjoined diagrammatic sections of the petiole of a leaf of Ivy are intended to illustrate the progressive history of the leaf-pith from the point of its derivation from

The central pith of the axis to that of its appearance in the rounded petiole. The first figure represents the fasciculi of the ~~spears~~ ^{petiole}, at the point where the five bundles begin to separate from the pith in order to proceed to the leaf. Their inner surfaces are in contact with the pith, around which they unite in a common curve, showing little of the semilunar form which they subsequently attain. The sections which follow approximate nearer and nearer to the leaf, and show how the fasciculi with their bundles of pith separate more and more from the main pith, as the petiole advances, assume a semilunar form, and then close so as to form a ring, the basal ends of the pith amalgamating into one cylinder occupying the curve of the petiole.



A section across the stem of a plant in which this arrangement exists, comprehending pith, wood and bundles would - especially if made at the base of the petioles

were included at this point. - disclose a view very similar to that afforded by a section across the skin of certain Malpighiaceous plants, wherein, in addition to the central pit, there are developed certain other cellular processes associated with woolly tubes enveloped in the woolly strama, and arranged around the centre in the form of a ring. But there exists this difference between these two secondary groups of cells and tubes, namely that whereas in the key spiral vessels are present, none such are seen in the Malpighiad.

The greater amount of development of the leaf-pit in Evergreens compared with that which takes place in plants which shed their leaves annually may be looked upon as in some measure accounting for the fact of their leaves remaining in connection with the parent trunk for a more extended period. The pit being looked upon as the active agent in the consequence of nourishment to the leaf we thus see the reason why, in deciduous leaved plants whose leaves are unprovided with this means of support, the leaves are not permanent, but die, shrivel up and are cast off at the end of their annual term.

But in addition to the development of these roots of pith being less marked than in evergreens those which are seen in other plants will be found to be interrupted, at the point which corresponds to the leaf, by a septum.

I now come to the third division in the course of the fasciculi, that, namely in which it appears as the medullary sheath.

In many instances the naked eye can easily single out the individual fasciculi composing the medullary sheath, especially in cases in which they are not numerous. Let us examine them first in those plants whose leaves are set on the angles of the stem. In the Alder which belongs to this group and in which the arrangement is easily traced, the fasciculi to each leaf are three in number. I made a transverse section across a this year's twig of this tree below the point at which a cycle of its tristichously-disposed leaves is completed. With the aid of a lens, or with the naked eye, we can count around the triangular pith nine distinct small dots of a lighter colour than the true wood. "These are the

fasciculi of the sheath or Corana derived from the leaves. Each of the three leaves of the cycle contributes, as can be demonstrated by dissection, towards the formation of the sheath, three fasciculi. Thus is formed the nine-fascicled medullary sheath. Had the number of bundles from each leaf been five then the sheath would have consisted of fifteen fasciculi, and so on. It is interesting to observe the relative disposition of these nine fasciculi. The bases are placed on the angles of the stem and each contributes three fasciculi as I have said. One of these processes down the angle on which the leaf is set, the other two to the sides of the other two angles as seen at Figure a, 1, 1, 1. Each of these last bundles leaves between it and the first a space which afterwards comes to be filled up by a fasciculus belonging to the second and third respectively. The appearance seen after the accession of the second leaf of the cycle is seen at b whence it will be seen the disposition is similar to that of the first, the numbers indicating the leaf to which the respective fasciculi belong. c shows the state of matters after the accession of the third leaf.



- a. Section of twig of Alder below the first leaf. 1, 1, 1. Fascicles of first leaf.
- b. Section of the twig below the second leaf. 2, 2, 2. Bundles of the second leaf.
- c. Section after completion of the cycle, showing the disposition of the bundles of the several leaves.

Let us take another example. In the Oak the phyllotaxis is $2/5$. Three bundles are contributed from each leaf. A section below the first leaf of a this year's shoot discloses the position of each of its three fascicles to be very similar to what we see in Alder, the number of bundles necessary to complete the sheath being fifteen. Each of the five subjoined diagrams represents a phase in the formation of the sheath where the



Phyllotaxis is $1/5$ - a condition however which I have never fallen in with, and hence the drawings must be looked on as purely hypothetical. This is very different from the arrangement which obtains in the Oak or any other plant whose arrangement is quincuncial.

The relative position of the bundles is that represented in VI. Here the middle bundle of the first leaf instead of being flanked on either side by a lateral bundle belonging to the second and ultimate leaf of the cycle respectively - the mode of arrangement seen in alternate-leaved plants the numerator of whose cycle of phyllotaxis is 1 - on the one side we have a lateral bundle of the third, on the other a lateral bundle of the fourth leaf. (VI).



In the instances which I have hitherto spoken of the number of fasciculi from each leaf is three. This is the number which prevails among all alternate-leaved plants whose leaves are set on the angles of the stem. In fact, as we shall subsequently see the angulation of the stem is due to the circumstance that the number is three, and to certain coexisting peculiarities of development.

When the bundles are more than three they may be looked upon as having undergone a process of lateral charisis. In complex phyllotaxis it is very difficult to allot the bundles their proper places, inasmuch as they come to lie so close to each other that they cannot be singled out.

In opposite-leaved plants the fasciculi are very differently disposed. Take for example a Liliaceae plant whose leaves are opposite and decussate. Two well developed bundles, and very frequently a third feebly developed bundle proceed from each leaf. The third bundle which occupies a central position as regards the other two, is of comparatively little importance. Each of these greater bands passes to an angle, spreading out in the form of a band to meet its fellow of the opposite side in the middle, their edges being separated a small space from each other by the diminutive central bundle. Thus we see that the system of vascular bundles provided to a single leaf is competent for the formation of one side of the quadrangular sheath. The sheath of the side opposite is furnished by the other leaf of the node. The completion of the sheath is effected by the bands from the leaves of the node above. There

are therefore eight bands of fibres necessary to complete the sheath, or, if we take into account the vascular bands, twelve. As four leaves are comprehended in a foliar cycle, so the eight bands of those four leaves are comprehended in a coracal cycle.

In most of the orders allied to the Gramineae a similar formation of the sheath prevails. The arrangement alluded to will be understood with the aid of the annexed diagram.

Bundles of the leaves of one of the nodes, viz. that immediately above the node which constitutes the lateral bundles.



Vascular bundles of one leaf spreading out and forming one side of the medullary cylinder. These, along with the two bands from the opposite leaf of the node form one half the sheath.

In the Potato, a plant whose leaves are set ~~not~~ on the angles of the triangular stem, but on the sides, there are three bands of vessels from each of the three alternate leaves. The central band is poorly developed, and this as we shall see is the reason why the place of the leaf on the stem does not coincide with an angle. Each of these primary bands goes to form that part of the sheath between the middle line and the angle nearest. There being three leaves in the foliar cycle, there are consequently six well-developed and three ill-developed bands in the

sheath. Here we have an alternate-leaved plant following the same mode of arrangement of fasciculi as we saw to hold good in the case of opposite leaved plants such as the Labiales.

The above examples will be enough to illustrate the formation of the medullary sheath, and from these considerations we may safely draw these conclusions:

1. In plants whose phyllotaxis is represented by one of the simpler fractions the number of fasciculi which enter into the formation of the medullary sheath is equal to the sum of the fascicles of one leaf multiplied by the denominator of the fraction.
2. In alternate-leaved plants, whose leaves are set on the angles of the stem, the typical number of fascicles contributed from any one leaf towards the formation of the sheath is three, the spaces left between the fasciculi of one leaf being occupied by bundles from other leaves of the cycle determined by numerator of the fraction of phyllotaxis.
3. In plants whose leaves are set on the sides of the stem the typical number of fascicles from leaf to sheath is two, the fascicles of a single leaf being competent

to form one side of the sheath.

A brief comparison of the manner of growth of the stem in *Endogens* and *Exogens* founded on the relation which the homologue of the medullary sheath in the former bears to that structure in the latter may not here be out of place.

The medullary sheath of *Exogens* is a structure which plays no mean part in the formation of the stem. If this structure cannot, in *Endogens*, be faintly put out as a vascular hollow cylinder enclosing the pith of the axis, we at all events know that its homologue takes a prominent part in the growth of the stem. Let us look at a section of Palm stem. It is a rod of pith traversed longitudinally by fasciculi of vessels connected with the bases of the leaves. It is by the annual addition of new bundles as well as by the growth of previously existing bundles the increase of the stem is in great measure effected. In the stem of *Mistletoe* we see a process take place very similar to this increase in the size of the previously existing bundles. An examination of the fibres from the leaves of an old mode of this parasite will disclose them to have attained a diameter many times greater than that of the bundles

from the leaves of a recent node. If the fasciculi of the leaves instead of plunging into the substance of the substance of the pith in Endogens quietly arrange themselves in a ring round its periphery (as in Grasses) and primary wood became deposited, then the process of growth however different the organization of the two classes, would be similar. For some Exogenous plants, again, as the *Serula* and *Marsil* of Peru pointed out by DeCandolle the fasciculi from the leaves pass into the substance of the pith, in this respect very much resembling Endogens. A somewhat similar condition is seen in the Water Lily.

I have next to offer a few remarks on the subject of the Pith and the influence it exerts on the stem. DeCandolle pointed out that the pith is the vehicle of nourishment to the young bud its function being the carrying round of the Pabulum intended for its maintenance. We have also seen that processes of pith are set aside for the support of the leaf also, but this does not concern us at present. A process of pith can be traced to each bud, and in its course gives rise to a ridge, the pith assuming in consequence a definite mathematical form. A remarkable coincidence is in general seen to exist between

the phyllotaxis and the form assumed by the structures of the stem. This circumstance has engaged the attention of many authorities among the most prominent of whom may be mentioned Peter Thunberg, Paliot de Beauvais, Decandolle and Louis Cagnat. The last named investigator especially, has wrought out the subject, his researches having been published in the *Annals de Sciences Naturelles*. He there states that 'the form of the constitutional parts of the stem and branches is determined, when it is not cylindrical by the Disposition of the Leaves.' But it rather ought to be stated that the form of the pith depends on the disposition of the buds in the axils of the leaves and the coordinate form of the other structures of the stem on that of the pith.

If we make a transverse section across a three-year's shoot of a plant whose phyllotaxis is represented by a simple fraction at a point a little below one of the buds we see an angle projecting towards it. The bud being in the axil of the leaf we find this repeated at every node. These projections are not however confined to a small space in the neighbourhood of the bud, but continue to influence

the form of the pith for a considerable distance below each node. This accounts for the angular character of the pith of plants whose phyllotaxis does not embrace a great number of leaves. So the form of the pith the wood, when it is not cylindrical owes its angular form, the bark in general taking the same form as the wood. Cespit observes that the pith retains its angular form after the other structures of the stem have become rounded. In very old trunks of Alder and Oak I have observed the angular form of the pith remaining very distinct. A transverse section below the last leaf of a complete cycle of Alder shows the angles of the various parts remarkably well - especially if a young shoot is taken. The pith will be observed to be triangular, the wood and bark forming round it a triangular encasement. The projection of pith belonging to one bud is separated from that of the next by an interval of one-third of a circumference. Each bud being placed in the axil of a leaf, the phyllotaxis is consequently tristichous. Again, make a section of a twig of Bramble. The pith is pentangular. The process of pith corresponding to the bud immediately above the point at which the section has been made will be

found to be the most prominent of the five. Look for the process second in prominence, which, we know shall correspond to second in order above the section. It will be found to the right of the first process but not in juxtaposition to it, for one projection intervenes. The second process is therefore separated from the first by two-fifths of a circumference, and consequently so are the first and second leaves separated by the same interval. The angle of phyllotaxis is therefore $\frac{2}{5}$. It is very unusual, however, to find the difference in the prominence of the processes so well-marked as to enable us to allot each its appropriate position in the scale, and in fact the Bramble is the only $\frac{2}{5}$ plant almost, of those which I have examined, in which the fraction of phyllotaxis could be arrived at by an examination of the pith, with any satisfaction. In the more complicated forms of phyllotaxis, the attempt to trace in the pith the relative arrangement of the leaves is futile. In the more simple arrangements however we are generally able to count the angles and in cases where the numerator of the cycle does not exceed one, we can with few exceptions determine the phyllotaxis.

It is only in those plants however, whose leaves are situated on the angles of the stem, that the coincidence

of the form of the pith with the fraction of phyllotaxis holds good, for we do not see it in those plants which have their leaves placed on the sides. This may in some degree be explained by a reference to the character of the fasciculi of the leaves. When the leaves are placed on the angles their vessels are generally arranged in three bundles, and of these the middle bundle is the one most highly developed. We have seen that these bundles arrange themselves in such a form as to facilitate the passage of the bud with the pith in its centre, into the axil of the leaf, the highly developed middle bundle coinciding with the middle line of both leaf and bud. Thus it is that the leaf comes to be situated on an angle of the pith, and therefore of the stem.

The influence exerted by the fasciculi on the angulation of the pith can be very well seen in some plants especially of the Rose tribe. No prominent mark are the processes of pith opposite not only the middle but also opposite the two lateral bundles as to cause the remaining angles to become so insignificant that they are apt to be overlooked. It is probably this pre-eminence of certain of the angles of pith as compared with the insignificant

character of the axis that leads Cagnat to aver that sometimes 'the number of angles is equal to the denominator of the cycle less the numerator ($a = d - n$).'

What I have myself observed has led me to think that this statement seldom holds good. In fact I have met with no single instance in corroboration of it, but in several cases to which I believed at first that the rule might apply. The fallacy was explained by the discovery of an arrangement similar to that prevailing among some genera of the Rosaceae interfering with the order of prominence of the processes of pith. In the familiar examples of the Apple and Pear the condition I have alluded to is remarkably well developed. In these plants the phyllotaxis is $\frac{2}{5}$.

A transverse section of a twig of either of these plants discloses what at first sight appears a triangular pith. But on looking somewhat more closely at the section we observe two other smaller angles at a point opposite the most prominent of the three. The pith therefore is not three but five-angled. Now then is the excessive development of these three angles accounted for? Each leaf has three fascicles. A fasciculus proceeds not only to the angle at which the leaf is set

but also to each of the other two adjacent angles.

These fasciculi draw out the pith at each of these points respectively, and the two remaining angles being here at a distance from their buds and therefore small, in this way arises the illusion of a triangular pith and consequently triangular wood. But what I mean principally to show from these abnormalities in the form of the pith is the influence exerted by the fasciculi on the creation of angles in it.

In those plants whose leaves are not placed on the angles the form of the pith is not determined by the same ^{cause} as in those whose leaves are so situated. We have seen that in these the central of the three fasciculi was either poorly developed or not developed at all, whereas the lateral ones are strongly so, exactly the reverse of what occurs in the other group. So defective indeed is the development of the vascular element between the two lateral bundles that, without the aid of some other contrivance the bud would fail to reach the soil. This contrivance consists in the development, immediately above each node of a cellular septum. Plants whose stems have three fascicles, the middle one strongly developed

could not have a better guide to the axil for their buds, and therefore in such, the interposition of a septum would be superfluous, looking on Decandolle's view of the manner of production and growth of buds as the correct one. This eminent physiologist traces the development of the bud at a determinate point to the stagnation of the juices. A cul de sac is probably formed in the channel resulting from the arrangement and development of the fasciculi in the one group of plants, and the line of this cul de sac being nearly parallel to that of the pith and ascending sap, a strong determination of the latter is set in operation towards the fundus of the sac, a dynamic development of the bud at that point being the result. In the other group however no such guide is developed. To supplement this deficiency the septum is thrown across the stem in such a manner as to cut off like a sluice the ascending current of sap and turn it towards the axil causing a cessation and stagnation of the nutrient fluid at this point and a development of pith and buds. Very similar to this is the provision to which Decandolle refers the development of buds into branches at certain determinate points of the stem of grasses.

Calamus and Equisetums, namely the knot supporting the leaves. But the position of this septum has no effect on the angulation of the pith lower down than at the point opposite the axil. On the contrary the very necessity for its existence as well as its position present this. The forces of pith thus comes to issue from the stem at a right angle almost, contrasting strongly with the obliquity of the corresponding process in angle-leaved plants and the consequent angulation of their stem for a good way below the axil.

But the stems of side-leaved plants are by no means devoid of angles, but have them on the contrary in many instances more strongly developed than those of angle-leaved plants. The manner of their development however is very different. The strong lateral bundles from the leaves on adjacent faces of the stem (one of them usually belongs to one node, the other to the node above) meeting at an angle, form together at that point a channel similar to that which we saw result from the arrangement of the fasciculi of a single leaf in angle-leaved plants. Along this channel the pith accordingly proceeds, filling it up, and thus results its angular form.

The number of angles thus resulting sometimes corresponds with the leaf arrangement, but more frequently it does not.

The following are a few examples of plants the form of whose petiole is symmetrical with the phyllotaxis:

Leaves Opposite

Pith four-angled. Pith six-angled Pith two-angled

Labiatae.	Stemulus bipulus.	Thuia.
Conocarpus ovatifolia.	Species of Clematis.	Ash.
Buxus.		Silac.
Same Rubiaceae.		Elder.
Didymopanax bipinnate.		Chestnut.
Cyperus.		Lonicera.
Same Bignonias.		

Leaves in whorls of Three.
Pith triangular.

Nerium Oleander.	Juniperus oxycedrus.
Rapialis parviflora.	Onica.
Juniperus.	Luchina.

Leaves alternate.

Pith two-angled.

Ono.	Leucispermum aestivum.
Vaccinium.	Mimosa scolopendroides.

Leaves distichous

Pith four-angled

Pith six-angled

Medicago, Melilotus	Befania sebina, Cornilla emersa
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Leaves twistish
Pith three-angled

Cyperaceae
Caulisculus arvensis
Alder

Beech
Potato
Beetroot
Ulex

Leaves linear
Pith five-angled

Apple.
Pear.
Mountain Ash.
Rhubarb.
Currant.

Poplar.
Chestnut.
Caulisculus.
Crucif.

Leaves $\frac{3}{8}$
Stem 8-ripped.

Berberis

Same Cruciferae.

The greater part of these are printed out by Cagnat in the *Annales de Sciences Naturelles*. A few I myself have added. The list by no means pretends to be exhaustive, I have merely named these examples as illustrative of my remarks.

I intend in the next place to make a few remarks on the Development of the Wood.

Most respectable Physiologists are now agreed that the Cambium layer, in conjunction with the

Aluminum is, in England the real agent in the production of New Wood. The Cambium in the young shoot is at first in immediate contact with the pith except at the points where the fasciculi of the sheath exist. The first secretion, if I may so call it, from the Cambium, is devoted to the formation, between these several fasciculi, of spiral tubes which almost completely fill up the interspaces except at the medullary rays.

The pith thus comes to be enveloped in a complete circle of tubes and fibres. The process which next takes place may be likened to the electrolysis, the Cambium representing the metallic part, its secretion the metallic solution, and the woody cylinder I have referred to, the conducting surface designed to receive the deposit.

The spirals thus, form the apices of the cones of wood subsequently deposited from the Cambium, the medullary cellular rays derived from the pith, dividing these from each other. The addition of wood then takes place by the annual deposit externally of successive layers.

The true wood was looked upon by Petit Thouars as derived from and forming the lobes of the leaves. The fallacy of this theory I have before alluded to. The medullary sheath is the only vascular or woody structure in the stem structurally connected

with the leaf.

In general there exists in the stem only one layer of tubes connected with the leaves. Occasionally, however, more than one layer forms part of the woody axis. This I have already referred to in my description of the medullary sheath in mistletoe, the various stages in the deposit of whose wood are seen in the subjoined diagrams.



A. represents a section made at a point where only one set of fasciculi are developed. The pith is seen internally surrounded by the young bundles, the bark externally.

B. Section at a point below the second node. The layers of fasciculi belonging to the node above, passing internally to form the sheath are now apparent. Wood is beginning to deposit between the two layers of fasciculi pushing outwards the more external layers.

C. The stem is now fully grown. The external layers of fasciculi have become much more developed, and still more pushed outwards by the accession of albumen.

I have already referred to a theory intended to explain the formation of wood in Exogens, representing the spiral system as the ascending, the wood the

descending or root structure of the leaf. Various arguments, some of which I have already referred, combine to disprove the practicability of the theory in question. Not adding in view the examples of the formation of wood apart from the leaves deduced by Green and others, I shall confine myself to two of these arguments: First: The accession of leaf bundles is endogenous, that of true wood exogenous.



Position of this year's wood (internal to that of last year) according to the descending theory.

This year's System.

Last year's System.

Supposing the theory named to be correct, then the annual deposit of wood, in other words, of the radicles of the leaves must have a position similar to that held by the arrows in the figure. In fact the wood should then be deposited endogenously. It is, however, deposited exogenously. Thus it is evident that the wood is not the descending system from the leaves, and the radicular theory of its formation must be fallacious. There are indeed a few connected fibres which accompany each fasciculus to the pith. These are of canal-like structure, endogenous structures and are derived from the woody layers in the immediate vicinity of the pith.

The second argument against the Phloem is, that since every leaf corresponds to a phloem, each must have a distinct part structurally connected with it, and hence must be traceable to an annual layer. Between the leaves of many shoots and the ring formed around the trunk no connection can be traced. It is clear that no one ever saw a plant growing and thriving, and yet separated by any distance from its root. At such a condition we should actually have more than this theory correct. In some shoots of Horse Chestnut, not larger than a foot, and only a third of an inch in thickness I have counted the leaf-stems of four decades. A section of such a shoot disclosed no trace of annual layering. Very diminutive indeed must the radicals of upwards of 200 leaves be, to be contained in so narrow a compass. A similar disparity between the annual production of leaves and the formation of corresponding annual layers is observable in the case of certain shoots of Beech. It is also remarkably well seen in the Larch. On a small tubercle no more than half an inch in length, and an eighth in diameter can sometimes be counted the marks of the leaves of ten years, sometimes more. It is plain that no ring is deposited here, any more than in the instances I have before alluded to, and yet in the trunk itself the annual deposit of wood is vigorous, but

no connection is apparent.

The effect of placing a firm ligature round a growing stem seems at first sight to support the Phytan theory. The result after a time of such an operation is a bulging above the point. Woody matter forms above in quantity. Below the point the development of the annual layer is very feeble. But this meagre development below the ligature is due, not to the roots of the leaves, or the annual wood being prevented from descending from the leaves, but to the cutting off of the Sap-Current, and the withdrawal of the formative juices. Whatever deposit of wood in such cases takes place is in accordance with the tightness of the strangulation.

In concluding these somewhat rambling, and, I feel assured, notwithstanding all my pains, very imperfect contributions, I beg to offer a few remarks on the Definiteness of Development of the shoots of plants.

In trees which shed their leaves in Autumn and have them restored in Spring, there is always an elongation of the axis for the purpose of bearing new leaves. This elongation is, in ordinary language termed a shoot. Now this shoot may be either a continuation of the chief, or main axis of the stem, or it may be an elongation of the secondary or branch axis, and its length varies accordingly. It now

been shown that the Sap in ascending passes first into the Central or primary axes, and afterwards into the branches, and it is probable that the Central axes continue to receive the greater supply of Sap not only in spring but all the year round.

From this it follows that the nourishment of the main axis is carried on more vigorously than that of the lateral axes, and consequently that the main axis increases more in every tree than do its branches. From a consideration of the rapid development of the Central axis and the greater development of the internodes in the terminal shoots, we may deduce the important conclusion that the main axis is the part of the tree destined to form the wood, and that the branches are merely the lateral axes which bear the twigs together with the leaves.