

On the Secondary Tissues in Certain Monocotyledons.

BY

D. H. SCOTT, M.A., Ph.D., F.L.S.,

*Honorary Keeper of the Jodrell Laboratory, Royal Gardens, Kew, and late
Assistant Professor in Botany, Royal College of Science, London,*

AND

GEORGE BREBNER,

late Marshall Scholar in Biological Research, Royal College of Science, London.

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With Plates III, IV, and V.
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THE present paper treats of three distinct questions, relating to the general subject indicated by the title:—

1. The development of the secondary tracheides in *Yucca* and *Dracaena*.
2. The secondary growth in thickness of the roots of *Dracaena*.
3. The secondary growth in thickness of *Aristea corymbosa*, Benth. (N. O. Irideae).

No prefatory remarks to the whole paper are necessary, as a general knowledge of the monocotyledonous type of cambial growth is assumed.

I. THE DEVELOPMENT OF THE SECONDARY TRACHEIDES IN YUCCA AND DRACAENA.

For the last seven years a controversy has been carried on as to the nature of the water-conducting elements in the secondary wood of *Dracaena*, and other Monocotyledons with a similar mode of growth. Up to 1886 it had been generally

[Annals of Botany, Vol. VII. No. XXV. March, 1893.]

assumed that these structures are tracheides, each arising by the growth of a single cell, without any fusion of cells taking place¹. But the first who endeavoured to establish this opinion on a firm basis was Krabbe, in his remarkable work on sliding-growth². Although he states that he directly observed the young tracheides in process of elongation, he relies chiefly on the comparison of transverse sections, and on careful counting of the various elements of the secondary bundle at different stages of development. He established accurately the exact amount of growth in length of each cell which must take place; in *Dracaena Draco*, for example, he showed that the mature tracheide is, on the average, no less than thirty-eight times as long as the 'procambial'³ cell from which it develops. As, in this case, the average number of tracheides in the transverse section of a mature bundle happens to be also thirty-eight, the striking conclusion follows, that as a rule the entire system of tracheides of each bundle arises from a single series of cells, so far as this species is concerned. The predominant share taken by sliding-growth in all such cases of tissue-development, is obvious.

A totally different account of the development was however given, almost simultaneously with Krabbe's work, by Kny⁴.

¹ See, for example, De Bary, *Vergleichende Anatomie der Phanerogamen u. Farne*, 1877, p. 638, English Edition, p. 620: Strasburger, *Das botanische Practicum*, 1st edit. 1884, p. 127.

² Krabbe, *Das gleitende Wachsthum bei der Gewebebildung der Gefässpflanzen*, Berlin, 1886. Reviewed in *Annals of Botany*, vol. ii. p. 127.

³ The word *procambium*, introduced by Sachs (see his Text-book, 2nd English ed. p. 110), means the strand of *primary* meristem from which a vascular bundle arises. Its name implies that it is a structure prior to the cambium, in cases where the latter is present. Hence procambium appears a very inappropriate name for a tissue which is itself produced from a *secondary* meristem, as is the case with the young bundles formed from the cambium in *Dracaena*, &c. The term *desmogen*, however (used by Russow as synonymous with procambium, see his *Vergl. Untersuchungen*, 1872, p. 178) may we think well be applied here. We propose to speak then of *secondary desmogen* to indicate the strand of young tissue from which a secondary bundle develops, in the Monocotyledons under consideration.

⁴ *Botanische Wandtafeln*, Text, VII, 1886, and *Beitrag z. Entwicklungsgeschichte der 'Tracheiden'*, *Berichte d. deutsch. bot. Gesellschaft*, Bd. IV. p. 267, 1886. The former appeared just before, the latter just after, Krabbe's publication.

He endeavoured to show that the so-called tracheides are no tracheides at all, but short vessels produced by the fusion of longitudinal series of cells. A certain amount of sliding-growth at the ends of the vessels was however recognized. The stages of cell-fusion were not only described, but figured, by Kny. One of us (D. H. Scott) made some observations, which appeared at the time to confirm Kny's conclusions¹, which were further accepted by Strasburger, in the second edition of his *Botanisches Practicum*². Independent evidence for the origin of these elements by cell-fusion was next brought forward in a paper by Mdlle. Hedwig Lovén³. This observer also claims to have followed the stages of cell-fusion. Stress is further laid on the number of cells found in the transverse section of the bundle while in the merismatic condition. The number was found to be higher than that required by Krabbe's theory. Occasional, though very rare, traces of transverse walls in mature tracheides were also described.

So far there appeared to be a balance of evidence in favour of the origin of these tracheae by cell-fusion. In 1889, however, an elaborate paper appeared, by Röseler⁴, containing the most complete account of the subject hitherto published, and bringing forward weighty arguments in proof of the development of these elements by the growth in length of single cells. Röseler attacked the question from every side, but his most convincing evidence was obtained by means of maceration. In a species of *Yucca* which he investigated, the average length of the mature tracheide is 3 mm.; and that of a cell of the secondary desmogen is 0.1 mm. Hence, on the average each desmogen-cell which becomes a tracheide must grow to thirty times its original length if no cell-fusion takes place.

¹ *Annals of Botany*, iv. p. 157, 1889.

² *l. c.* p. 125, 1887.

³ Om Utvecklingen af de sekundäre Kärlnippena hos *Dracaena* och *Yucca*; Bihang till Kongl. Svenska Vetenskaps-Akad. Handlingar, vol. xiii. 1887. For a translation of parts of the Swedish text we are indebted to the kindness of Mr. L. A. Boodle, F.L.S.

⁴ P. Röseler, Das Dickenwachsthum u. die Entwicklungsgeschichte der secundären Gefässbündel bei den baumartigen Lilien; Pringsheim's Jahrbuch., Bd. XX, 1889, p. 292.

If this be true, we ought to find, on macerating a young bundle, tracheides at all stages of elongation, and each of them would probably contain a single nucleus only. Röseler succeeded in demonstrating that these conditions are realized. He figures young thin-walled tracheides, isolated by maceration, measuring 0.4 mm., 0.84 mm., and 1.8 mm. in length, i. e. about four times, eight times, and eighteen times respectively, the length of the original desmogen-cell. Each contained a single conspicuous nucleus¹. These observations were in reality decisive, but the effect of Röseler's work was somewhat enfeebled by the weakness of some of his other arguments. Thus his elaborate countings of the elements in transverse sections led to no definite result, but might seem rather to favour a mixed origin, by cell-fusion with subsequent elongation². He also failed to obtain any satisfactory evidence from longitudinal sections, in consequence of manipulative difficulties³. In spite, therefore, of the great merits of his paper, we cannot wonder that it failed to settle the question. Röseler's work was reviewed by Wieler, in the *Botanische Zeitung*⁴, with great and indeed unjustifiable severity. Wieler, however, contributed nothing himself to the decision of the points in dispute.

In 1891 Strasburger published his great work on the vascular tissues, and in this he withdraws his former view, and declares in favour of the origin of the tracheides by direct elongation of the short cells derived from the cambium⁵. He directly observed the young tracheides in sections, and confirms Röseler's statement that they are uninucleate. The observations of Röseler and Strasburger established a strong presumption that the view of Krabbe was, after all, the right one. A re-investigation, however, seemed to us desirable, especially as the observations previously made by one of us had seemed to favour the opposite conclusion. We attached

¹ l. c. p. 339.

² l. c. p. 333.

³ l. c. p. 334-338.

⁴ Bd. 47, 1889, p. 701.

⁵ Strasburger, *Üb. den Bau u. die Verrichtungen der Leitungsbahnen in den Pflanzen*; *Histologische Beiträge*, III, 1891, p. 400.

special importance to the direct examination of the stages of development as seen in longitudinal sections, in which alone the nascent tracheae can be observed in relation to the other elements of the bundle and of the ground-tissue. We found that the use of the microtome was of essential service. We obtained the best results by making continuous series of tangential sections through the region of secondary growth. In this way we were enabled to examine all the elements in each developing bundle, and to compare the various bundles at all stages of differentiation. The instrument chiefly used was the Cambridge rocking-microtome. The thickness of the sections in some series was $\frac{1}{8000}$ in. (.005 mm.), in others $\frac{1}{3333}$ in. (.0075 mm.). The usual paraffin-method was employed, and various stains were used, saffranin being on the whole the most successful. The result was of course checked by the constant comparison of transverse and radial sections, and also by means of maceration. Our work extended to several species both of *Yucca* and *Dracaena*, but our best results were obtained in an unnamed species of *Yucca*, in which we had abundant material of an old stem, reaching at least 3 in. in diameter. This stem had been in very active growth when preserved, and possessed a wide zone of thickening, with secondary bundles in all stages.

In this species the secondary bundles have the same structure as in the *Yucca* described by Röseler¹; they are collateral, with the small phloëm-group on the outer side, lying in a depression of the much larger xylem-mass. The latter consists mainly of tracheides, with lignified parenchymatous cells scattered among them, and lying between the tracheides and the phloëm. The whole bundle is surrounded by a sheath of flattened, partially lignified cells, easily distinguishable from the comparatively thin-walled ground-tissue. We found that the average number of elements in the transverse section of a secondary bundle, taking the mean of twelve countings, is—tracheides 36, xylem-parenchyma 13, phloëm-elements 17.

The elements of the sheath average about fifteen in number.

¹ l. c. p. 297.

If we include them in the xylem-parenchyma, as Röseler appears to have done, we obtain figures which are not very different from his¹. We shall return to these numbers later on; it is sufficient now to point out that, leaving the sheath out of consideration, more than half the elements in the mature bundle as seen in transverse section, are tracheides, while in the xylem they form about three-quarters of the whole number. In a tangential section passing through the middle region of a bundle the average number of tracheides cut through is about six. In such a section not more than two parenchymatous cells are likely to be met with at any one level. The tracheides in this species attain an average length of 2.78 mm. (mean of twelve measurements). The mean length of a cell of the secondary desmogen is .075 mm. If therefore the entire tracheide is formed by cell-fusion, a series of thirty-seven desmogen-cells must, on the average, fuse to form each tracheide. If, on the other hand, the tracheides are formed by longitudinal growth alone, then each desmogen-cell which forms a tracheide must, on the average, grow to thirty-seven times its original length. The whole of this elongation would be by 'sliding-growth,' as we are speaking of a region in which the stem as a whole has long ceased to grow in length. On the hypothesis of cell-fusion we should find, in the developing bundle, as many rows of fusing desmogen-cells as there are tracheides at maturity, i.e. about thirty-six rows in the entire strand, or about six in any tangential section passing near the middle of the bundle. If, however, the development is by sliding-growth, we should find only *one* cell, on the average, at each level, in the whole strand, elongating in order to become a tracheide. A thin tangential section could of course only occasionally pass through one of these cells at the commencement of its elongation.

Now let us consider what we actually find on observing a continuous series of tangential sections through the zone of secondary increase.

Proceeding from without inwards, we first come, immediately

¹ l. c. p. 298.

on passing the cambium, to the earliest condition of the desmogen-strands. We can trace the first longitudinal divisions of the mother-cells from which these strands are formed. As is well known, it is usually a single longitudinal row of mother-cells, derived from the cambium, from which the entire strand is developed¹, though sometimes two adjacent rows may contribute to its formation. As we advance inwards the young desmogen continues to show a beautifully clear and simple structure. The outlines of every daughter-cell are clear and sharp, and the limits of their mother-cells can still be traced. All the desmogen-cells at this stage are alike; they are prismatic in form, with wedge-shaped ends fitting closely together. Each cell has a single nucleus, and all the nuclei are similar to one another. As we now proceed to examine sections rather further inwards, we find that the somewhat more advanced strands show a differentiation in two respects. (1) We notice every here and there an exceptionally large nucleus, often much elongated, and sharply distinguished from the small nuclei of other desmogen-cells. (2) We find that the regularity of structure of the desmogen is now at some places interrupted. Most of the regular prismatic cells remain unaltered, but occasionally we find among them a cell with more pointed ends projecting beyond those of neighbouring cells. Sometimes the ends of these elongated cells cannot be traced at all as they dip out of the plane of section. *These exceptional elements are invariably those with the specially large nuclei.* At first they are very rare, but as we advance to older bundles they are found more and more frequently. But now they are hardly ever found complete in a single section. Their length, and somewhat curved course, renders this impossible, and it is only by the comparison of successive sections that we are able to build up the entire element. As we proceed to yet older bundles we find that the greater part of them is now formed of these long, irregularly curved cells. Ultimately we recognise the latter in a changed condition; their walls are thicker, bordered pits

¹ Cf. Röseler, l. c. p. 322.

appear, and the cell-contents gradually vanish. As long, however, as the living body of the element persists, it possesses the single large nucleus by which it was at first distinguished.

While the young tracheides are going through these changes the other elements of the bundle undergo at first little modification. In fact, the strand of desmogen remains, but becomes gradually enveloped (except at the extreme outer edge) and partly permeated by the hypha-like tracheides. The latter grow in diameter as well as in length, and so come eventually to form much the greater part of the mass of the bundle,—a part altogether out of proportion to their number.

The developing tracheides have at first a denser protoplasm than the neighbouring cells, a fact which often helps greatly in recognizing them. In the later stages the denser protoplasm is found to be limited to their pointed ends, which we must suppose to be the seat of active growth.

In order to observe the stages of development satisfactorily it is essential to have very thin sections. This has the disadvantage that the complete tracheide is hardly ever contained in a single section. Hence the necessity for serial sections from which the form of the whole element can be reconstructed. It remains difficult to find suitable preparations for drawing. Fig. 1 is fairly satisfactory, but even here there is reason to believe that the extreme upper end of the tracheide is incomplete.

The developing tracheides often have a somewhat crooked course, as seen in tangential section. This would in itself agree well with their origin by cell-fusion, as the desmogen-cells of successive tiers do not lie in the same straight line, but roughly alternate with each other. It is evident, however, that the same course must also result from sliding-growth, for the growing tracheides must undergo a bend whenever they pass the points of junction of neighbouring cells, which are not in the same straight line. After the development of the tracheides has made some progress, the phloëm becomes differentiated at the outer side of each bundle. The sieve-

tubes become recognizable by their denser contents, and the perforation of the sieve-plates can be traced. It is important to recognize the phloëm at the earliest stage possible, as otherwise the young sieve-tubes might easily be taken for tracheides developing by cell-fusion, a mistake which we suspect has actually been made.

The careful study of serial tangential sections appears to us decisive against the hypothesis of cell-fusion, and in favour of that of sliding-growth. As regards the former point, the negative evidence is in itself very strong. More than half the bundle consists of tracheides. If they arose by cell-fusion therefore, this must take place on a great scale. In tangential sections through the middle of young bundles we should find most of the cells in various stages of fusion. Even supposing the fusion to take place so rapidly as to have been always missed by us (a very improbable supposition considering that the whole thickness of the growing zone was examined in many different series of sections), still at one stage we should find the xylem consisting of separate merismatic cells in rows, and at the next stage we should find it chiefly made up of continuous tubes, which must correspond exactly to the previous rows of cells. Either the nuclei must disappear or fuse, or they must be found in large numbers (thirty-seven on the average) in each tracheide. They certainly do not disappear till very late; for a long time we find a single large nucleus in each tracheide, which is even more conspicuous than those of the other cells. Nor will fusion explain this. The fusion of more than thirty nuclei in a vessel more than thirty times the length of its constituent cells could not possibly be a quick process, and its stages certainly could not escape observation. Nothing of the kind was ever seen.

The stages we actually find are: (1) the regular rows of desmogen-cells; (2) the same arrangement, but slightly disturbed here and there by the presence of a longer element among the shorter ones; (3) more disturbances of the primitive regularity, more elongated elements, the shorter cells more and more enveloped by them, until ultimately all the

inner part of the bundle is mainly formed of the long elements, with the short cells scattered among them.

So far the view that cell-fusion is the main factor in the development has been, as it seems to us, disproved; that a very large amount of sliding-growth must take part in the development of the tracheides, is certain. It remains to consider the possibility that a relatively short syncytium, i.e. the product of the fusion of a few cells, might grow out to form a tracheide. This view might seem to present fewer difficulties; the cell-fusions would be comparatively rare, and so much the easier to miss; there would be fewer nuclei to fuse in each element, and thus the apparent absence of fusion-stages might be explained away. So far as the evidence from transverse sections is concerned, Röseler admitted the possibility that the facts might be accounted for if about five cells fused to form each tracheide, and the resulting syncytium grew out to six or seven times its original length. If this happened in the species of *Yucca* we investigated there would be about six parallel rows of fusing cells in each young bundle.

This view is in reality as untenable as the hypothesis of entire development by cell-fusion. The single nucleus of the future tracheide is conspicuous throughout, until it is absorbed with the rest of the contents. If this nucleus arose by the union of several nuclei, some indications of this fusion must be found. Some of the growing tracheides observed were little longer than the desmogen-cells, so that there was no possibility of cell-fusion here. The idea of the outgrowing syncytium, though tempting in so far as it might seem to reconcile conflicting observations, must be rejected, from the entire absence of evidence in its support.

The development of the tracheides was investigated by the same method of serial sections in *Dracaena fragrans*, Gawl. and *D. angustifolia*, Roxb. In these the secondary bundles are concentric, the xylem completely surrounding the phloëm. The results entirely agree with those obtained in the *Yucca*. The material however was less favourable, as the zone of developing secondary tissues was narrower, and consequently

fewer stages of development were met with in each series. But so many young tracheides were observed at various stages of elongation, and always with a single nucleus, that there could be no doubt of their development by growth alone.

The results obtained from sections were confirmed by the method of maceration. The ordinary Schulze's mixture (nitric acid and potassium chlorate) was used. Thick tangential sections through the zone of secondary growth were treated with the reagent, and it was then found possible, in many cases, to isolate the elements of the developing bundle. In Fig. 2 a young tracheide of *Yucca* *sp.* is shown, which had only reached about a quarter of its mature length (.725 mm.). The single large nucleus is conspicuous. Some desmogen-cells of the same strand are shown for comparison. Fig. 3 represents a young macerated tracheide of *Dracaena fragrans*. Here the average length of the mature tracheide is 3.15 mm.; that of the young element shown is .95 mm. It is obviously uninucleate. Here again desmogen-cells are shown for comparison. These results require no long description, as they simply repeat those obtained by Röseler.

Krabbe, Kny, Mdle Lovén, and Röseler, all lay great stress on the results obtained by counting the elements of the bundle, as seen in transverse section, at various stages. If the tracheides were formed entirely by cell-fusion it is obvious that the number of elements in the transverse section of the desmogen-strand, after the completion of its divisions, would be the same as in the mature bundle. If however the tracheides arise by elongation of single cells, the desmogen-strand must contain less than half as many elements as the mature bundle, in transverse section. Thus in our species of *Yucca* the average number of elements seen in mature bundles is sixty-six (neglecting the sheath). Of these, thirty-six are tracheides. The strand of desmogen when its divisions are completed must therefore show an average number of sixty-six elements on Kny's view. As, however, on the opposite supposition, only one cell at each level grows out to form a

tracheide, the desmogen-strand, after completed division, but before elongation of the tracheides, should show in transverse section an average number of thirty-one elements only.

Now this method seems at the first glance very promising; as a matter of fact it has led, in the hands of different observers, to absolutely contradictory results. Röseler, the last author who employed it, obtained, as we have seen, results seeming to point to a considerable amount of cell-fusion¹, a conclusion which is quite inconsistent with direct observations on serial sections or on macerated material. He found, in fact, too many elements in his supposed unaltered desmogen-strands; in the light of other observations we can easily explain this by supposing that a certain amount of sliding-growth of the tracheides had already taken place. This, however, is assuming the point to be proved, and the inefficiency of the counting-method by itself is manifest. Apart from the obvious difficulty arising from the great variability of the number of elements in different bundles (ranging from forty-four to ninety-four in the examples counted by us), there is the further difficulty that sliding-growth certainly begins before all the divisions have taken place, so that we have no fixed point at which to begin our numeration.

Although the counting method does not help us in detail, yet the comparison of transverse sections of developing bundles is very instructive. We find at a certain stage a small strand, with active cell-division in all parts. At a later stage the strand is larger, the external portion (in *Yucca*) remains unchanged, or may show some additional divisions. The more internal part, although the seat of the chief growth, shows no fresh cell-division whatever. Its increase is due to the intruding ends of young tracheides, growing in from other levels. Tracing the changes in older bundles we continue to find an enormous increase in the number of elements of the xylem of the bundle, as seen in transverse section, without any cell-divisions to account for it. This is only to be explained by sliding-growth, and in fact affords by itself, a

¹ Röseler, l. c. p. 333.

decisive proof of its occurrence as the chief factor in the development of the bundle.

Our final conclusions then as to the development of these tracheides are as follows:—

(1) The tracheides are formed by longitudinal growth only, each tracheide arising from a single cell, which may grow to 30—40 times its original length, but remains uninucleate throughout its whole development.

(2) As the secondary tracheides are formed in a region which has ceased to grow in length, their development is entirely by *sliding-growth*, and consequently the number of initial desmogen-cells from which they arise is very small. In the *Yucca* investigated, for example, only a single cell in each tier of the desmogen-strand can become a tracheide.

There can be no doubt that the development of the tracheides in the primary bundles is similar, but as the latter are formed in a region which is still lengthening as a whole, a proportionately smaller amount of sliding-growth is involved.

The process in the case of the secondary bundles is a highly remarkable one and vividly recalls the invasion of a tissue by the hyphae of a luxuriant parasitic fungus. The initial cells from which the tracheides develop, might be compared to the spores of the fungus. We tried in vain to determine the position in the desmogen-strand of the initial cells for the tracheides. They certainly do not form a continuous longitudinal row. We believe that they may occur in any part of the strand, with the obvious exception of that group which is destined to form the phloëm¹.

As our investigation has completely confirmed the views of Krabbe and Röseler, and the later view of Strasburger, it may be thought our duty to offer some explanation of the contradictory result obtained by Kny and Mdlle Lovén, a result which one of us formerly accepted. From our own experience we think the chief sources of error are the following: The course of the tracheide as it passes between the overlapping and bevelled ends of the other elements of

¹ Cf. Krabbe, l. c. p. 64.

the strand often gives it just the same shape as if it had arisen by cell-fusion. When it bends aside to pass from one tier of cells to the next it is often constricted, and an oblique wall lying over it at such a point may easily simulate a perforated septum. Confusion of the very young sieve-tubes with developing tracheides is also possible, and would of course suggest cell-fusion. Accidental tearing of the delicate end-walls of the desmogen-cells may also give rise to deceptive appearances. The idea that the tracheides are multinucleate may have arisen partly from the confusion of coincident elements in different planes, partly from the presence in the tracheides of coagulated masses of protoplasm, which might be easily mistaken for nuclei. We know from our own experience that all these cases are possible sources of error; but we cannot undertake to explain how other observers may have been misled. In Kny's Fig. 2, Pl. XIV,¹ the long element to the right may probably be a developing tracheide, though not recognised as such by the author.

Appearances suggestive of cell-fusion are rare, and are most frequent in the least satisfactory preparations. We are convinced that such appearances are in all cases illusory.

We hope that the question may now be regarded as definitely settled, and that one of the most striking cases of sliding-growth in the development of vegetable tissues has thus been firmly established.

II. SECONDARY GROWTH IN THICKNESS OF THE ROOTS OF DRACAENA.

Until the year 1884 our knowledge of the development of secondary tissues in the roots of Monocotyledons was very meagre. The earliest account known to us is that given by Caspary in 1858². He examined several species of *Dracaena*, and states that the cambial layer of the root lies between the 'Schuttscheide' (endodermis) and the central mass of vascular bundles; in modern terminology the cambium observed by

¹ l. c., Berichte d. deutsch. bot. Gesellsch. IV.

² Die Hydrilleen; Pringsheim's Jahrbüch., Bd. I. p. 446.

him was pericyclic. He describes the bursting of the endodermis in consequence of the secondary growth. The short account given by De Bary is practically identical with this ¹.

In 1884 Strasburger published an investigation of the roots of *Dracaena reflexa*, and showed that the cambium is first formed in the pericycle, and continues for a time to produce secondary tissues inside the endodermis, which thus becomes ruptured, but that sooner or later this activity ceases, while the cortical cells immediately outside the endodermis take up the division, and carry it on indefinitely ². The structure of the secondary tissues in the root is identical with that in the stem.

In 1885 Morot published his important paper on the pericycle. He examined the secondary thickening in the roots of various *Dracaenas*. He found that it usually takes place in the pericycle, but may exceptionally arise in the cortex. This may happen when there has been very little activity in the pericycle, and while the endodermis is still continuous ³.

In his book on the vascular tissues Strasburger confirms his former statements, and adds several interesting details. He finds that the xylem of the first-formed secondary bundles abuts in each case on two xylem-groups of the primary cylinder, thus enclosing one of the primary phloëm-groups. The strand of secondary phloëm is connected at its lower end (i.e. towards the root-apex) with a primary group. At the places where the endodermis is ruptured the internal and external tissues become perfectly continuous, and secondary bundles extend from the pericyclic into the cortical zone. The roots are epinastic as regards their secondary thickening, which begins on the upper side, and continues to be more vigorous there. The cambium is pericyclic near the

¹ Comparative Anatomy, English edition, p. 622.

² Das Bot. Practicum, 1st edition, 1884, p. 202. This account is omitted from the second edition.

³ Morot, Recherches sur le péricycle, Ann. des Sci. Nat., Bot. Sér. 6. t. xx. p. 247.

apex of the root, and cortical in its older portion. These statements apply especially to *D. reflexa*¹.

Our own observations were made on the roots of *Dracaena fragrans*, Gawl., *D. Draco*, L., and *D. angustifolia*, Roxb. The last-named species was first examined, and in those roots which showed secondary thickening at all, we were surprised to find that it took place, from the first, entirely outside the endodermis, starting with the division of the first or second cortical layer. The pericycle was thick-walled, and neither had undergone any divisions, nor could do so at a later stage. So far as we saw there was no connection between the cylinder and the external vascular tissues. Our material, however, was limited, and it is probable that if we had been able to trace the tissues for some distance longitudinally, continuity through the endodermis would have been established.

These observations, however, showed that the accounts in the literature are not complete. It was evident that the cortical thickening might start on its own account, without any previous pericyclic divisions, at any rate in the same region of the root. Hence we were led to investigate the relation between pericyclic and cortical thickening more thoroughly than had previously been done.

Our best material was of *D. fragrans*, Gawl., of which we had a number of adventitious roots, up to almost an inch (2.3 cm.) in thickness, and showing secondary growth in all stages. Our most complete observations then were on this species.

As a rule, the cambium only appears in large adventitious roots, and in them only at a late stage. In a fully formed adventitious root about 1 cm. thick we may expect to find secondary growth beginning. This, however, is very variable, and in one case we found a complete zone of secondary tissue in a root only 4 mm. thick. The primary cylinder of the roots varies very much in structure. In the small root just mentioned, for example, it showed an ordinary polyarch

¹ Strasburger, *Histologische Beiträge*, III, 1891, pp. 403 and 508.

arrangement, such as is general in Monocotyledons, with a normal pith. In all the larger roots, however, the primary structure is much more complex, the pith being traversed by a variable number of xylem- and phloëm-strands, generally associated together, and imbedded in groups of sclerenchyma. These peculiarities have been described so often that we need not dwell on them here. Strasburger has shown that the medullary strands of the root are directly continuous with vascular bundles of the stem¹. Transverse sections through roots in which secondary growth has begun may show three different conditions:—

(1) The cambium may have appeared in the pericycle, and the entire zone of thickening may be limited to the inside of the endodermis. This may still be the case in quite advanced stages, where there is a mass of secondary tissue, containing several concentric rows of bundles.

(2) There may have been no pericyclic divisions at all. In these cases the primary structure of the cylinder is unaltered; the secondary zone has been entirely superadded by the activity of a purely cortical cambium (see Fig. 5).

(3) We may find a mixed condition, the secondary growth having begun in the pericycle, and then having been taken up by a cambium formed in the cortex. This is the case described and figured by Strasburger². The two processes are mixed up in the most irregular way. In one radial row of cells the pericyclic divisions will have gone on for a long time before the cortical activity supervenes; in the next row the pericyclic cambium ceases to act almost immediately, and nearly the whole growth is cortical. Hence we find fragments of the endodermis carried out into the secondary zone to a most variable distance (see Fig. 6).

The same transverse section may show only one condition, or may include two, or all three, in different parts of the periphery of the cylinder. Thus in Fig. 4 conditions (2) and (3) are shown; in Fig. 7, conditions (1) and (2), between which the

¹ Hist. Beiträge, III. p. 403.

² l. c., III, p. 404, Pl. V. Fig. 45.

transition happens to be a sharp one. In the mixed case (3) it is remarkable how thoroughly homogeneous the secondary tissues are, whether they are of pericyclic or cortical origin. The same bundle may pass out from the one zone into the other, one part being formed by the cortical, and the other by the pericyclic cambium. Some of the endodermal cells are still thin-walled when the secondary growth begins, and consequently are not easily recognisable when the displacements due to thickening have taken place. Hence the endodermis may appear to be ruptured at more points than is really the case. It is very probable that the thin-walled endodermal cells may themselves take part in the cambial divisions, as was noticed by Morot¹. We did not find a clear case of this however. At the base of the adventitious root, near its insertion in the stem, it appears that the whole endodermis is thin-walled, and in advanced stages it is here impossible to make out the limit between pericyclic and cortical formations.

This peculiar mode of growth is really only a special case of the type of secondary thickening prevailing in Monocotyledons. There is not as a rule a single initial layer here, as there is in typical Dicotyledons and Gymnosperms². The same cambial cell only continues active for a limited time, and then the divisions are taken up by an adjacent cell towards the exterior³. An extreme illustration of this process is afforded by Fig. 8, which shows an early stage of purely cortical growth in thickness in the root of *D. Draco*. Here three or even four distinct rows of cortical cells have already taken up the cell-division. It is essentially the same phenomenon when pericyclic is succeeded by cortical divisions, only here there is usually a thick-walled endodermis to be overleapt. If this physiological barrier were really continuous it would probably be an effectual obstacle to any such mode of growth. We know, however, that it is not absolutely

¹ l. c. p. 248.

² Some doubt has been recently cast on the constancy of the initial layer even in these classes; see Raatz, Stabbildungen im secundären Holzkörper und die Initialentheorie, Pringsheim's Jahrbuch., XXIII. 1892.

³ Cf. Strasburger, Hist. Beiträge, III, p. 396. Röseler, l. c. p. 309.

continuous, though it may be so for long distances. That the divisions should pay no respect to the morphological distinction between stele and cortex cannot surprise us¹.

The case where the cambium at once appears outside the endodermis is more puzzling. Here both pericycle and endodermis may be very thick-walled, and, so far as the transverse section shows, there may be no interruption to their continuity. The secondary tissues therefore are from the first cut off from any direct communication with the primary cylinder at the same level. In this case it is by no means always the *first* cortical layer which divides; sometimes it is even the fourth layer from the endodermis in which the first divisions appear.

It is impossible to understand this type of secondary growth unless we trace the course of the cambium and its products in the longitudinal direction. The statements in the literature appear to show that the secondary tissues taper off regularly towards the root-apex, their maximum thickness being at the base of the root, where the process presumably started in the first instance. It has also been noticed that the thickening is almost always highly excentric, the upper side of the approximately horizontal root, according to Strasburger, receiving the first and greatest increment. The thickening near the apex is said to be always pericyclic, cortical cambium first appearing in a more advanced region.

Although this account of the process is no doubt applicable to certain cases, or it may be to certain species, we have not found it confirmed by our observations on *Dracaena fragrans* and *D. Draco*.

We only found one instance in which the secondary growth appeared to have started from the base only of the adventitious root and advanced regularly towards its apex. This was in *D. fragrans*, and in this case the thickening remained pericyclic throughout. In all other thickened roots of these two species which we investigated (and in *D. fragrans* they were fairly numerous) the maximum thickness of the secondary

¹ Cf. Scott and Brebner, On Internal Phloëm, Annals of Botany, vol. v. p. 287.

zone was attained, not at the base of the main adventitious root itself, but at the insertion upon it of a branch-root. From this point the secondary tissues thinned out both in the upward and downward direction, and also peripherally. Near the insertion of the lateral root we constantly found pericyclic thickening; at a distance from it, in whatever direction, the secondary zone was invariably formed in the cortex. The transition was in some cases a sudden one; more usually it was gradual, and in the intermediate region both pericyclic and cortical thickening had taken place.

Further, we found that in these cases the thickness of the secondary zone bore no relation to the upper or lower side of the root, but was always greatest near the insertion of a branch root, wherever the latter might arise.

We will describe a particular case more in detail. In a root of *D. fragrans*, 2.3 cm. in diameter, we examined radial sections passing through the base of a branch-root. At the insertion of the latter there had been abundant secondary development. There are numerous zones of secondary bundles, the inner of which slope obliquely outwards, forming a connection with the tissues of the branch-root. The outer secondary bundles have an approximately longitudinal course. A normal zone of thickening has in fact been built up upon the secondary network of bundles belonging to the base of the branch. The whole of this secondary mass has been formed by a pericyclic cambium; the endodermis lies entirely outside the secondary tissues. As we recede from the insertion of the rootlet in either direction, the thickness of the secondary zone gradually diminishes. The endodermis curves rapidly inwards, passing obliquely through the secondary tissues, which in this region have been formed partly within it and partly to the outside. Further on still the endodermis takes a straight course, and borders directly on the primary cylinder. Here the thickening has been exclusively cortical. In the transitional region the endodermis is often interrupted, and sometimes we could trace a secondary bundle through it from the inner into the outer zone. As regards the actual dimen-

sions, in one case measured, the thickening had become purely cortical at a distance of 1.3 cm. from the nearest part of the base of the branch-root. The length of the region of transition renders it inconvenient to figure on an adequate scale; consequently we have contented ourselves with reproducing a corresponding transverse section (Fig. 7), to which we shall return.

If a transverse section be taken at some distance from a lateral root (say 1-1.5 cm. above or below), only cortical secondary tissues are shown. They may extend all round the cylinder or be limited to the side on which the lateral root is situated; that depends on the amount of progress which the thickening has made. In any case, however, the zone is thicker on the side corresponding to the branch-root. If the transverse section be made nearer the latter, we find both pericyclic and cortical secondary growth at one side, which as it thins out to the right and left becomes purely cortical (see Fig. 4). Lastly, if the section pass through, or close to the insertion of the lateral root, we find pericyclic thickening next the insertion, and cortical at a distance from it, with a more or less gradual transition between them. There are many variations in detail, of which Fig. 4 and Fig. 7 will give some idea; Fig. 5 is from a region of purely cortical thickening, at a distance from a lateral root, while Fig. 6 is from the transitional region. In Fig. 7 the transition is unusually sudden, causing a sharp break in the endodermis, reminding one of a geological 'fault.'

If our sections be cut from comparatively young roots, we find only the pericyclic thickening near the base of the lateral roots. It thins out altogether at a distance from them, and the cortical thickening has not yet begun.

It may be worth while to mention that in one large root, 2.1 cm. in diameter, where the secondary tissues extended round the whole circumference, their maximum thickness, on the side towards the lateral root, was 3.5 mm., the minimum thickness, on the side opposite the lateral root, was .5 mm. In this case there was some pericyclic thickening all the way

round, but on the side remote from the branch-root it became very small in amount, and almost wholly parenchymatous. Nearly the whole of the secondary zone in this part was of cortical origin.

So far we have established a definite relation between the secondary thickening and the insertions of the branch-roots. The observations which we made on *D. Draco* confirmed those on *D. fragrans*. In one root of the former we found, on examining radial sections, that no sooner had the secondary tissues begun to thin out in receding from a lateral root, than they began to widen again as the next lateral root was approached. In this case the whole thickening was pericyclic, the cortical stage of growth never being reached between the two rootlets.

A strong presumption has been established that the secondary increase actually starts from the insertion of the rootlets. In fact, the younger stages in which we have pericyclic thickening only, limited to the immediate neighbourhood of the rootlet, raise this presumption almost to a certainty. The usual case appears to be that the cambium forms in the pericycle at the insertion of the rootlet, and that the divisions spread gradually in all directions, but at first are limited to the layer in which they started. As secondary tissue is formed the continuity of the endodermis is broken, and at the place where it is interrupted the divisions are taken up by the neighbouring cortical cells. By the time that the cambial activity has extended to the more remote parts of the root, the pericycle in those parts will have usually become thick-walled and incapable of division. Hence at a certain distance from the rootlet only cortical cambium can as a rule arise. In one case we were so fortunate as to observe, in radial section, the very first cambial divisions in the cortex. They took place immediately outside the place where the endodermis was ruptured, near the base of a rootlet. The dividing cells were thus in direct communication with the pericyclic cambium. When once started, the cortical divisions can spread up or down the

root independently of any further communication with the pericycle.

It is not probable that *all* lateral roots form the starting-points for secondary growth. In some cases they showed no secondary bundles at the base (though there was some radially arranged parenchyma) and no signs of cambium.

The connection between the internal and external tissues is established partly on a large scale, where the two zones are continuous, through large gaps in the endodermis of the transitional region; partly on a small scale by local connections. We have several times seen a single secondary bundle passing through the endodermis, and in one case we found a horizontal strand of tracheides connecting the primary xylem of the cylinder with the secondary tissues which had been formed in the cortex. We can confirm Strasburger's statement that vessels only occur in the *primary* xylem-groups of the roots. The secondary bundles are quite like those of the stem, and their water-conducting elements are invariably tracheides.

It appears, then, that in most of the roots investigated by us the formation of secondary tissues starts from the insertion of the rootlets, and at first serves to establish additional channels of conduction between the branch and its parent organ. Subsequently the process of new formation thus initiated extends to all parts of the root. An acropetal formation of secondary tissues, starting from the base of the adventitious root itself, also occurs, but does not extend far, and serves to establish the connecting link between the secondary tissues of the root and those of the stem.

It may be mentioned that the cambium in the root often forms several layers of secondary cortex on its outer face.

Periderm is regularly formed in these roots, sometimes from the layer next within the exodermis, sometimes from a deeper layer of the cortex.

Our results may be summed up as follows:—

(1) In the adventitious roots of *Dracaena fragrans* and *D. Draco*, the secondary growth in thickness starts from

a number of distinct points. One of these starting-points may be the base of the root itself. The chief formation of secondary tissues, however, begins at the bases of rootlets, and thence extends both up and down the root, and also peripherally.

(2) At the base of the rootlet the thickening takes place entirely by means of a pericyclic cambium. At a distance from it there is usually only cortical cambium, and consequently the whole of the secondary tissues are here external to the endodermis. In the transitional region there may be first a pericyclic, then a cortical cambium, and the secondary tissues are here formed on both sides of the endodermis.

(3) The connection between the vascular tissues inside and outside the endodermis is not only maintained through the transitional region, but also by means of special bundles which traverse the endodermis at various points.

(4) The important part played by the cortex in the formation of secondary vascular tissues in these roots, shows that the morphological distinction between central cylinder and cortex is not necessarily correlated with a permanent difference of function.

III. THE SECONDARY GROWTH IN THICKNESS OF *ARISTEA CORYMBOSA*, BENTH. (N.O. IRIDEAE).

Within the natural order Irideae, which now includes between 900 and 1000 known species, there is a little group of shrubby forms. Only four such species are at present known to science; all belong to the tribe Sisyrinchieae, subtribe Aristeae, and all are natives of the south-western provinces of the Cape Colony. The plants in question are *Aristea fruticosa*, Pers., *A. corymbosa*, Benth., *Witsenia maura*, Thunb., and *Klattia partita*, Baker. The two first-named species now form the subgenus *Nivenia* of the genus *Aristea*, of which twenty-seven species are known in all. *Witsenia*, Thunb., as at present limited, and *Klattia*, Baker, are both monotypic genera¹.

¹ See Baker, Handbook of the Irideae, 1892, pp. 145 and 146, where the

We are not aware that the anatomy of the stem in any of these species has so far been described. Professor F. O. Bower, F.R.S., first called our attention to the occurrence of secondary growth in thickness in *Aristea corymbosa*, and to him we are also indebted for the supply of abundant fresh material from the Glasgow Botanic Garden.

Aristea corymbosa is a low shrub; the stems are elongated, much branched, and cylindrical; the younger branches are flattened in the plane of the distichous leaves, which are equitant, linear, rigid, and erecto-patent, attaining a length of from 4 to 6 inches¹.

It may be mentioned at once that the external characters of the other three shrubby Irideae are very similar to that of our species. *Aristea fruticosa*, Pers., is a dwarf under-shrub, much smaller in all its parts than *A. corymbosa*. *Witsenia maura*, Thunb., on the other hand, is a tall plant, with woody erect stems 2-4 feet long; *Klattia partita*, Baker, is perhaps the most like *Aristea corymbosa* in appearance; its woody, branched stems are 1-2 feet in length. All four species agree in their distichous equitant leaves, and flattened branches which become cylindrical with advancing age. It is highly probable that the account of the anatomical structure and development which we are about to give in the case of *A. corymbosa* will be found to hold good in essentials for all these shrubby forms.

1. *Primary Structure*.—We will begin with a short description of the primary structure.

The equitant leaves are in their upper ensiform portion typically centric in structure, with assimilating tissue and stomata on both sides. The collateral vascular bundles form a flattened ring, the xylem in each facing towards the interior,

synonyms will be found; also Baker, *Systema Iridacearum*, Linn. Soc. Journal, Bot., vol. xvi. 1878, pp. 108-110; Bentham and Hooker, *Genera Plantarum*, vol. iii. 1883, pp. 701, 702.

¹ The above is a slight extension of Baker's description, *Handbook of Irideae*, p. 145.

the phloëm towards the nearest surface of the leaf. Occasionally concentric (amphivasal) bundles are found in the middle of the mesophyll. The bundles forming the ring each have a stout strand of sclerenchyma outside the phloëm. Isolated strands or plates of sclerenchyma are also present in the leaf, especially at its edges. The central part of the mesophyll is colourless.

The leaf-base, which completely embraces the stem, has of course a different structure, and is in fact bifacial. We only found stomata on the outer (morphologically lower) surface, to which also the assimilating tissue is limited. The xylem of the bundles is here directed towards the upper surface. The sclerenchyma is mainly towards the upper surface, where it forms a continuous hypodermal layer.

The leaf-base has about twenty bundles altogether. The two largest are both median, lying one behind the other in the same radial plane. The other bundles are mostly of fairly uniform size, but become gradually smaller in the posterior direction. There are a few much smaller scattered bundles, usually placed further to the exterior than the main ones.

The leaf-traces on entering the stem curve in towards the middle of the cylinder, and then very gradually pass outward again, fusion between the bundles taking place towards their lower ends. In other words, the course of the bundles belongs to the familiar Palm-type. The larger bundles penetrate most deeply into the cylinder. The upper median bundle on entering the stem turns sharply upwards, and then as sharply down again, to take the usual course into the cylinder. We found that the number of vascular bundles in the transverse section of the primary cylinder of the stem averages about seven times the number of bundles in a leaf-base. Hence we may infer that on the average the bundles pursue a separate course through about seven internodes. It is probable, however, that this varies greatly, even among the bundles from the same leaf.

If we examine a transverse section of the flat stem, in a region where living leaves are still present, we find the

following structure (see Fig. 9). The middle part of the stem is occupied by a well-marked central cylinder, of lenticular section, which presents the ordinary characters of monocotyledonous structure. The scattered vascular bundles (which number 140 or more) are of extremely unequal size. The ground-tissue of the cylinder is thin-walled in its inner part, but becomes sclerotic towards the exterior. The cortex is conspicuously thicker at the ends than at the sides of the section, so that the stem as a whole is more strongly flattened than is the stele. The cortex is traversed by leaf-trace bundles. They are collateral here, as they are in the leaf, the xylem only partly embracing the phloëm. As soon as the bundle enters the cylinder, however, it becomes concentric.

If we now consider the structure of the primary cylinder rather more in detail, the first point to be noticed is that the vascular bundles differ among themselves in structure as well as in dimensions. Only a few of the larger bundles have any definite group of protoxylem. Of all the bundles in the cylinder perhaps one-eighth possess protoxylem (see Fig. 12, *px*). When present it occupies the usual position on the proximal¹ side of the strand. The large and small bundles are scattered irregularly throughout the cylinder; the larger, however, are more frequent towards the middle, the smaller towards the outside, to which part the smallest of all are limited. Several large bundles are always grouped near the centre, sometimes forming a ring around a central point of the ground-tissue which might be called pith. Of these inner bundles some, but not all, have protoxylem.

The bundles with protoxylem are those which are differentiated earliest, namely the upper parts of the principal traces. The lower portions of the latter and the finer

¹ The terms *inner* and *outer* are confusing in this connection as it is often doubtful whether they refer to the individual vascular bundle, or to the stem as a whole. We therefore propose to use the word *proximal* for that side of the bundle (or other structure) which is turned towards the centre of the axis, *distal* for that side which is remote from the centre.

bundles in their whole length are differentiated later, and have no protoxylem-elements¹.

The protoxylem has the usual spiral structure; we did not determine whether its elements are vessels or tracheides. The later-formed xylem (which is alone present in most of the bundles) contains tracheides only, with reticulated or pitted walls. A certain amount of xylem-parenchyma is present among the tracheides. The phloëm calls for no special description; the elements bordering on the xylem are parenchymatous; the central group consists of sieve-tubes and companion-cells.

The ground-tissue of the cylinder consists of rather elongated parenchymatous cells. Those surrounding the bundles are thicker walled and often prosenchymatous. Towards the outside of the cylinder the whole ground-tissue assumes the latter character.

The cortex is thin-walled throughout; many of its cells contain tannin.

2. *Secondary Tissues*.—If we next examine a transverse section through an older part of the stem, which has already assumed a cylindrical form, we find a very different structure (see Fig. 10). In the middle part of the section we recognize the lenticular outline of the primary cylinder, which is unaltered. But superadded on this we find an entirely new zone of tissue. Its maximum radius is at right angles to the major axis of the primary cylinder. Hence the effect of the addition of the secondary zone has been to give a circular section to the entire vascular system. At the same time the transverse section of the stem as a whole also becomes circular; this is assisted by the formation of periderm, which has been produced near the surface of the flat sides of the stem, but in a more internal position opposite its prominent edges. At the stage figured in Fig. 10 the cortex outside the periderm still remains; later on it is thrown off altogether.

¹ Cf. Strasburger, *Hist. Beiträge*, III, p. 398; also Röseler, l. c. p. 295.

The secondary tissues form two distinct regions of conspicuously different structure. The outer zone is characterized by scattered, sharply defined secondary bundles imbedded in comparatively thin-walled, radially arranged parenchyma. The inner secondary zone has the bundles densely crowded, so as not to be readily distinguishable, with but little parenchyma between them (see Fig. 10). Here there is no obvious radial arrangement. We will first describe in detail the structure of the outer zone.

On its exterior side it is surrounded by a regular cambial layer which is manifestly the seat of formation of the secondary tissues (see Fig. 14). The details of development will be considered later. On its outside the cambium produces secondary cortex, which eventually grows to a great thickness (see longitudinal section, Fig. 15).

The secondary vascular bundles, like all other bundles in the stele, are concentric. The ring of xylem consists chiefly of long tracheides, with a very tortuous course. Their walls have corresponding bordered pits with slit-like openings; among the tracheides a few parenchymatous elements are scattered, some of which border on the phloëm. The latter presents no peculiarities; as the constituent elements of the sieve-tubes are short, their sieve-plates, which are horizontal, are often met with in transverse sections. It is very common to find two groups of phloëm in the same bundle; they may be placed either tangentially or radially. This is due to the fact that the secondary bundles often anastomose in both planes, as is easily seen in the corresponding longitudinal sections. The system of secondary bundles thus forms a continuous network.

The tracheides form much the greater part of the bundle. We found the average numbers to be for each bundle, as seen in transverse section, forty tracheides, nine cells of the xylem-parenchyma, and eight phloëm-elements. The rectangular pitted cells of the secondary ground-tissue have a very regular radial arrangement, which is only disturbed where the vascular bundles occur. The latter are arranged generally in concentric series.

It will be seen that this outer secondary zone shows a general agreement with the corresponding tissues of a *Dracaena*.

The inner zone has a more remarkable structure. The phloëm-groups stand out plainly enough, but the outer limits of the bundles are often impossible to trace. The whole appearance rather suggests some anomalous Dicotyledon with 'phloëm-islands' imbedded in a continuous mass of wood. The bundles are in fact to a great extent confluent, and are only here and there separated by a radial or tangential row of parenchymatous cells. The great bulk of the tissue in this zone consists of the tracheides of the crowded bundles. Consequently it is not surprising to find that no regular radial arrangement is evident. This is also partly accounted for by the mode of development, which will be explained below. The whole structure is the expression of a network of bundles, with thick strands and nodes, and very small meshes (occupied by parenchyma) between them.

The limit between the outer and inner secondary zones is a fairly sharp one. So also is the boundary of the primary cylinder, which is easily distinguished by its scattered bundles, circular in transverse section, imbedded in sclerotic ground-tissue.

This will perhaps be the best place to say a few words as to the periderm and the secondary cortex.

The first periderm forms at about the time when secondary thickening begins. The seat of its formation at the sides of the flattened stem is the hypodermal layer. Towards the narrow edges of the stem the next inner layer of the cortex takes up the division, then a more internal layer, and so on. Thus opposite the prominent edges of the stem the phellogen is deep-seated, and gives rise from the first to internal periderm. The thickness of the cortical layer within the periderm is consequently about the same all round the stem.

The phellogen usually forms two layers of phelloderm on

its inner side, and many layers of cork towards the exterior. The cells cut off by the phellogen often undergo further division by oblique walls, which may cause some disturbance of the normal radial arrangement.

As the stem grows older, successive internal periderms are formed, until the whole of the primary cortex is cut off. This does not happen however until the outer zone of thickening has made good progress. Thus at the stage shown in Fig. 14, some primary cortex is still left.

The formation of secondary cortex from the cambium does not begin until after the inner zone of wood¹ has been completed. During the development of the outer zone of wood, secondary cortex is formed with increasing rapidity (cf. Figs. 14 and 15; the latter was from the oldest part of the stem at our disposal). It may attain a thickness of about twenty layers before the primary cortex is lost. Ultimately the latter is cut off by periderm, and henceforth the entire cortex is secondary. The formation of internal periderms does not stop here however. The periderm shown in Fig. 15 has evidently been formed in the secondary cortex itself. As new cortex is formed from the cambium, the older layers are constantly removed by more internal periderms.

The periderm is provided with lenticels, but we did not follow their development. We may mention here that we found distinct indications of an abscission-layer at the base of the leaves. This subject also requires further investigation.

3. Development of the Primary and Secondary Tissues.—

It is clearly of importance to determine whether the formation of the secondary tissues is a mere continuation of the primary development (Sanio's 'Thickening Ring' having an unlimited activity), or whether the cambium is an entirely secondary meristem, arising by the division of cells

¹ We use the term *wood* here for all the secondary tissue formed centrifugally on the inner side of the cambium. This is sanctioned by the authority of De Bary (*Comparative Anatomy*, Eng. ed. p. 591), but a better terminology is much needed.

which have already assumed the character of permanent tissue.

With this object in view we traced the development of the stem as shown in a number of transverse sections, made at measured distances from the apex. Several such series were examined, and the results checked by comparison with longitudinal sections. We will base our description in the first instance on a vigorous stem, in which we traced the differentiation of tissues from the apex downwards for a distance of 5.2 cm. Of course it will be understood that the absolute distances from the apex have no general value, and would come out very much smaller in less vigorous branches.

At about 1 mm. from the apex¹, nearly all the bundles of the cylinder are very oblique, the internodes not having lengthened much as yet. The leaf-trace bundles entering through the cortex are the most developed; the larger of them have their protophloëm and protoxylem already differentiated. The smaller leaf-trace bundles, however, even in the cortex, are still quite in the procambial² condition. In the cylinder too only the largest bundles (obviously belonging to the upper portions of the principal leaf-traces) show a differentiation of the first xylem- and phloëm-elements; all the rest are procambial. There is no regular centrifugal order in the development of the different bundles in the cylinder. As however the smaller leaf-traces, and the lower ends of the principal ones, are limited to the outer part of the cylinder, it is here that we find the largest proportion of procambial strands, some of the outermost of which are in the very earliest stages of formation. In the outer zone of the cylinder active cell-division is in progress, especially towards the edges of the flat stem, and new bundles are being originated.

¹ We did not concern ourselves with the actual growing-point, the investigation of which has no bearing on our main question.

² We use *procambium* and *primary desmogen* as synonymous terms. Our use of the term *secondary desmogen* has been already explained (p. 22).

The cortex and epidermis are already nearly fully formed, and in the former the tannin-sacs have acquired their characteristic contents. The stage shown in Fig. 11 is at about 2 mm. from the apex. At this distance the bundles of the cylinder have become more straightened, owing to the elongation of the internodes, and so better sections can be obtained. Otherwise there is not much change. The divisions at the periphery of the cylinder (Sanio's 'Thickening Ring') take place irregularly in all directions.

At 5 mm. from the apex considerable progress has been made. The primary development of the cylinder as a whole has almost ceased. Scarcely any fresh divisions are now found in the 'Thickening Ring.'

Many of the outermost bundles of the cylinder, however, are still in an early procambial stage. The principal bundles appear to have their phloëm fully formed. The proximal part of their xylem has been completed in the usual centrifugal order. A few of the elements of the distal half of the xylem-ring are also becoming lignified. In this part of the bundle the differentiation of the xylem-elements follows no definite order. We may speak of this later-formed, non-centrifugal part of the xylem as *metaxylem*¹. In the large bundles the phloëm follows the normal centripetal order of differentiation. In all the other bundles (forming the great majority) the whole of the xylem is metaxylem. There are no spiral elements, and there is no centrifugal development. Differentiation begins indiscriminately at any points of the xylem-ring, and no preference whatever is shown for its proximal side. So too with the phloëm; in these later-developed bundles the phloëm does not develop centripetally; so far as any regular order can be traced, the phloëm-elements in the middle of the bundle appear to be completed first.

¹ The term was introduced by Van Tieghem for that part of the primary xylem in the root which is differentiated after the normal centripetal development is completed; see his *Traité de Botanique*, 2nd ed. p. 684. *Mutatis mutandis* the same term may well be applied to late-formed *non-centrifugal* xylem in a bundle belonging to the stem.

Fig. 12 is drawn from a section at 5 mm. from the apex. The differentiation of the bundles with metaxylem only, takes place rather later, and was studied in other series of sections.

Returning to our first stem, we find at 23 mm. from the apex that the primary development of tissues is completed, and we have the normal structure of the central cylinder in its fully differentiated condition. This is the stage at which development would cease, if we were dealing with an ordinary Monocotyledon. Two points, however, must be noticed. Near the periphery of the cylinder, bordering directly on the pericycle, we still find a few unfinished bundles; some are quite procambial, in others about the proximal half of both xylem and phloëm is differentiated. Secondly, in the pericycle itself we find here and there a very few scattered cells in which a recent tangential division has taken place. These two points indicate that a further process of development is still to follow. Otherwise the structure has been sufficiently described at p. 47. At 31 mm. from the apex we found the tangential divisions in the pericycle more frequent, and on one side of the cylinder the dividing cells formed a continuous tangential band, which already suggested a cambium.

At 41 mm. the cambium was well established in the pericycle, on both sides of the cylinder, but not at its ends (as seen in transverse section). At this stage we determined a fact which was confirmed by many other observations; the tangential divisions are not limited to a single layer of pericyclic cells, but two such layers may begin to divide simultaneously. Hence, from the very first, there is no single initial layer present. It will be remembered that a perfectly similar fact was noticed in the roots of *Dracaena* (cf. Fig. 8).

At 47 mm. from the apex we found that the development had reached a very instructive stage. The formation of secondary tissues had just been started. In one place a few tracheides had been added to complete one of the unfinished primary bundles; at another a new, altogether secondary bundle had been started. In fact, after the long pause, tissue-

formation has again fairly commenced, and the secondary period of growth is entered upon.

A stage similar to this (from another series) is shown in Fig. 13. At least two of the original pericyclic cells may contribute by their divisions to form one secondary bundle.

At the end of our series, at 52 mm. from the apex, the secondary zone is slightly more advanced.

The whole series is most instructive, showing that there is a long interval between the cessation of the primary development and the commencement of secondary increase. At 5 mm. from the apex the primary merismatic divisions had almost ceased; only at 31 mm. had anything approaching to a continuous cambium arisen by fresh divisions, and the first formation of secondary tissues did not begin until a distance of 47 mm. from the apex was reached. There is thus a perfectly definite distinction between the primary and secondary tissues, though individual vascular bundles may be common to both, as indeed is necessary in order to keep up physiological continuity.

In feeble branches the interval between primary and secondary development is much less marked, and may even be almost obliterated. This is evidently due to a 'telescoping' of the developmental stages, and does not affect the conclusions drawn from vigorous shoots, to which we must look for the typical mode of growth.

We will now complete, from another series, our account of the secondary development.

The mode of formation of the inner zone of thickening is peculiar. No regular radial series can be traced, and in fact there is no single continuously active layer of cambium. A cell of the pericycle divides up a few times—say six—by tangential walls formed in centrifugal order; the daughter-cells subdivide to form the elements of a bundle, or may directly become cells of the secondary ground-tissue. Meanwhile another pericyclic cell, on the distal side of the first, has begun to divide; this contributes its share, and then in turn its activity ceases, and so on. Hence the fully formed

elements of the secondary 'wood' do not necessarily fit on, in any way, to the cambial cells bordering on them externally. From the irregular character of this inner secondary zone, and the marked absence of any definite initial layer, one might be tempted to doubt whether this tissue can properly be called secondary, and whether it may not simply form the completion of the primary cylinder. The long interval, in normal cases, before the formation of the zone in question begins, an interval during which the primary cylinder has become fully differentiated, negatives any such idea, which is also inconsistent with the fact that the bundles of this zone are cauline, and only indirectly connected with the leaf-traces.

The development of the inner secondary zone appears to go on slowly. In a piece of stem 10 cm. long it was just commencing at the top, and just completed at the bottom. Hence the completion of this zone must have taken place at a distance of about 15 cm. from the apex. (Cf. p. 55.) It is possible that this may correspond to one year's growth, but of this we could obtain no evidence.

Not till the inner zone of thickening is nearly completed does the cambium extend round the ends of the cylinder (in transverse section); consequently there is never more than a thin layer of tissue belonging to this zone at these points. Its maximum thickness is at the middle of the broader sides of the stem (see Fig. 10).

When the transition to the outer secondary zone takes place the cambial divisions become more regular, and we find longer continuous radial series of cells. Henceforward the development goes on quite normally, and so far as we could tell the same cambium is active throughout. The normal process of secondary thickening is now established, and continues year after year. It is not, however, until after several series of the distinct secondary bundles have been formed, that any appreciable amount of secondary cortex begins to be developed.

As regards the details of development of the secondary

bundles of the outer zone, it is rare for the whole bundle to be formed from a single radial series. Usually two such series take part in its formation, sometimes one row forms the median part of the bundle, while the two adjacent rows cut off cells which contribute to form its flanks; sometimes all three rows contribute equally, but this perhaps only happens when an anastomosis is to be formed. The phloëm of each bundle is formed very early. A cell cut off on the inner side of the cambium divides up by two or three inclined longitudinal walls. Thus a little group of small cells is formed, which represents the future phloëm. Almost simultaneously an inner cell of the same radial row divides up to form the proximal part of the xylem. Next, cells situated at the sides, and either derived from the same radial series or from adjacent ones, take up the divisions, and form the lateral portions of the future ring of xylem. Lastly, fresh cells are added by the cambium to the distal side of the strand, and these ultimately complete the xylem towards the exterior. Of course all the stages run into one another, but it appears to be the rule for the phloëm to take the lead.

We had the same question to face here as in *Dracaena* and *Yucca*; how do the tracheides of the secondary bundles develop? The answer is here also a perfectly definite one; they develop by sliding-growth alone. The comparison of transverse sections is never conclusive by itself, but it affords valuable indications. We can say at any rate this much; not more than about twenty elements, as seen in transverse section, are, on the average, formed in the desmogen-strand by division. We know that the average number of elements in the transverse sections of a mature bundle is fifty-seven, of which forty are tracheides. The extraordinarily tortuous course of the tracheides, which form a sort of twisted skein in which the isolated cells of the xylem-parenchyma are entangled, and by which the phloëm is enveloped, also strongly suggests an origin by longitudinal growth in a confined space (see Fig. 15).

But direct evidence is not wanting. In longitudinal sections isolated desmogen-cells are sometimes found which have grown

to a much greater length than their neighbours. They remain uninucleate. Several stages were observed between the ordinary desmogen-cell and the fully formed tracheide. The course of the tracheides, however, renders it impossible to trace them far in sections. Hence recourse was had to maceration, and Fig. 16 represents a couple of very young tracheides, one isolated, the other still in connection with some desmogen-cells, which were obtained by this method. The process of development is undoubtedly the same here as in *Yucca* and *Dracaena*. In Fig. 17, the whole length of a mature tracheide is shown, in two halves. It can be compared with the desmogen-cells and young tracheides in Fig. 16, which are shown on double the scale of Fig. 17.

The sliding-growth begins very early, and has already made considerable progress in the proximal half of the xylem, while cell-divisions are still going on in its distal portion.

4. *The Roots*.—We found no secondary thickening in the adventitious roots at our disposal. From our experience in *Dracaena*, we paid special attention to the points of insertion of rootlets, but here also no signs of cambium were present. In fact, we may say for certain that the roots examined by us never could have formed a secondary zone. The whole of the cortex was already dying away, and the wide pericycle (8–10 layers in thickness) was too sclerotic ever to become the seat of a secondary meristem. The roots are of polyarch structure, and call for no detailed description. It may be mentioned, however, that they contain true vessels of large size, whereas vessels, with the possible exception of protoxylem-elements, are altogether absent from the other organs of the plant. The larger vessels of the root may be either reticulated or have bordered pits. They have inclined scalariform terminal walls; we demonstrated their perforation by injection with French Blue under pressure.

This occurrence of large vessels in the root only is also characteristic of *Dracaena*.

5. *Summary*.—Our chief results respecting *Aristea* are the following :—

(1) *Aristea corymbosa*, Benth., in common no doubt with the few other shrubby species of Irideae, forms an indefinite amount of secondary tissue by means of cambium, which continues active during the whole life of the plant.

(2) The tissues formed centrifugally, on the inner side of the cambium, consist of secondary concentric bundles, imbedded in ground-tissue; on the outer side of the cambium a large amount of secondary cortex is formed. The latter is wholly parenchymatous.

(3) The xylem of the secondary bundles consists chiefly of tracheides, each of which arises, as in *Yucca* and *Dracaena*, by the enormous elongation of a single cell.

(4) The cambium arises in the pericycle, and is a new formation; the cambial divisions do not begin until some time after the development of the primary vascular cylinder is completed.

(5) The inner zone of secondary tissues is characterized by its very crowded bundles. The cambium which forms this zone has no definite initial layer; each cambial cell undergoes a few centrifugal tangential divisions, then its activity ceases, and the divisions are taken up by an adjacent cell to the exterior. Consequently the elements of the inner zone do not show a regular radial arrangement.

(6) After a time (possibly, under normal circumstances in the second year) the divisions become more regular, a cambium with a definite initial layer is established, and the formation of the outer zone of thickening begins, and continues without limit. This zone is characterized by its scattered bundles imbedded in comparatively thin-walled ground-tissue. After this zone has begun to develop the formation of secondary cortex commences.

(7) Successive layers of periderm are formed, by which the whole of the primary cortex is eventually removed, the subsequent periderms arising in the outer part of the secondary cortex.

The occurrence of secondary thickening in this little group of Irideae, a group which is so narrowly limited both systematically and geographically, appears to us to be a fact of

considerable interest. It is impossible to doubt that secondary growth in the Irideae has originated *de novo*, and probably at a comparatively recent period, after the Order had attained something like its present development and geographical distribution.

In spite of this there is a remarkable general agreement between the process in Irideae, and that in the arborescent Liliaceae and in the Dioscoreae. But in these two groups also secondary growth must have started independently. We arrive then at the conclusion that a closely similar mode of anatomical development must have been separately evolved in at least three distinct groups of Monocotyledons—probably more. We thus find that the phenomena which we have considered in this paper offer a striking example of homoplastic modification, i. e. of the origination of similar, and apparently homologous structures in groups of organisms which are phylogenetically distinct.

It is very probable that the first origin of secondary growth may be taking place in some of the Monocotyledons at the present day, just as we find medullary bundles appearing in certain Dicotyledons as an individual peculiarity. From this point of view it would be very interesting to examine some of those species of *Aristea* which are not shrubby, and to see whether their short stems show any indications of secondary increase.

For our material we are indebted to the Director of the Royal Gardens, Kew; to Prof. F. O. Bower, F.R.S., Regius Professor of Botany in the University of Glasgow; and to Mr. F. W. Burbidge, F.L.S., of the Trinity College Botanic Gardens, Dublin, to all of whom we tender our warm thanks.

The investigation was chiefly carried on in the Huxley Laboratory for Biological Research, at the Royal College of Science, London; it was completed in the Jodrell Laboratory of the Royal Gardens, Kew.