

On the Anatomy and Histogeny of Strychnos.

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With Plates XVIII and XIX.

THE dominant position which the Dicotyledons unquestionably hold among existing forms of vegetation is probably due in a greater degree to their method of secondary growth in stem and root, than to any other single character. The ability to increase indefinitely the amount of mechanical, conducting and storing tissues in the axial organs, in proportion to the increasing development of the foliage, has more or less generally existed in all the most successful classes of plants; but it is in the Dicotyledons that the highest differentiation of the secondary tissues is attained. The ascendancy of the Dicotyledons is most marked among those forms in which the duration of life renders a considerable secondary growth possible. The study of the modifications in the secondary formation of tissue in this class is therefore an important branch of biological inquiry. Though the process in its typical form is so well known, the recent work of Robert Hartig and others shows that there is still

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much to be learnt, even from the best investigated cases. The state of our knowledge regarding those very numerous modes of secondary growth which are usually classed as 'anomalous' is much less satisfactory. Here as elsewhere the rule holds good that structure cannot be understood without development, and we still know but little of the development in a large proportion of these cases. It is the object of the present paper to clear up, as regards one anomalous genus, some of the points which previous investigations have left obscure.

LITERATURE OF THE SUBJECT.

The original literature relating to the anatomy of *Strychnos* is very meagre, and so far as we are aware, is the work of three investigators only. The peculiar structure of the stem appears to have been first noticed by Fritz Müller¹. He found that the wood is traversed by a number of isolated strands of soft tissue, but he was not in a position to make any microscopic observations, and so the exact nature of this tissue could not be ascertained. The first to make any detailed investigation of the subject was de Bary², and his account is still the one generally accepted. His work is so familiar to English readers that it is unnecessary to do more than give the briefest possible summary. De Bary found that in the stem there is at first a normal ring of bicollateral leaf-trace bundles. The external primary phloëm consists of small groups of cells, among which sieve-tubes could not be demonstrated with certainty. The cambium appears in the normal position, but forms no sieve-tubes in the secondary bast. Its activity is for a time almost entirely centrifugal, producing secondary wood only. At a later stage considerable additions are made to the external bast, but only in the form of phloëm parenchyma, and, in some species, of short-celled sclerenchyma. The secondary sieve-tubes are situated

¹ Über das Holz einiger um Desterro wachsenden Kletterpflanzen, in Bot. Zeitung, 1866, p. 68, Fig. 10.

² Vergleichende Anatomie d. Vegetationsorgane, 1877. Eng. ed. 1884, pp. 578-580.

in the wood. They form, together with thin-walled parenchyma, isolated strands surrounded on all sides by the tissues of the xylem. According to de Bary 'suitable developmental stages easily show that these phloëm-strands in the wood are given off by the cambial zone towards the inside¹.' It should be noted that de Bary had no fresh material of the stem more than 1 mm. in thickness. All his observations relating to the anomalous secondary growth were made on dry material. His Fig. 229, the only one given, is a diagrammatic, slightly magnified transverse section, and throws no real light on the development. A similar structure is described in the malpighiaceae genus *Dicella*, which was also one of the plants observed by Fritz Müller.

In another passage² de Bary draws a comparison between the structure of *Strychnos* and that of certain Chenopodiaceae, and formulates a general rule, applicable to all such cases, that all secondary tissue formed centrifugally inside the cambium is to be regarded as wood, while all that is formed centripetally on its outer side belongs to the bast. On this principle the secondary phloëm-strands of *Strychnos* come under the category of wood. With one exception, to be mentioned immediately, all later writers on the subject seem to have simply adopted de Bary's statements as to this genus³. We shall see later on that the anatomical peculiarity consisting in the presence of phloëm groups imbedded in the xylem is now known to occur in many genera besides the two mentioned by Fritz Müller and de Bary.

Hérail's *Recherches sur l'anatomie comparée de la tige des Dicotylédones*⁴ contain a valuable series of observations on the development of anomalous stems, and *Strychnos* is among the genera investigated. His account of the development is much the most satisfactory which we possess. His chief results are as follows: he finds, in agreement with de Bary,

¹ l. c. p. 579.

² l. c. p. 591.

³ See for example Van Tieghem, *Traité de Botanique*, p. 796; and Solereder, *Über den systematischen Werth d. Holzstruktur b. d. Dicotyledonen*, 1885, p. 178.

⁴ *Annales des Sciences Naturelles*, sér. vii, T. ii, 1885.

that the production of external secondary bast is at first very slight. When the stem is two years old the outer boundary of the wood becomes uneven, and its depressions are filled by little groups of phloëm, which subsequently become the 'phloëm-islands¹.' The cambium remains in contact with the wood during their development, and hence the phloëm-islands must be produced on its exterior side. The intercepted portions of the wood are reunited by means of divisions in the cells of the pericycle lying outside the newly formed phloëm group, and thus the latter becomes imbedded. Hérail compares this process with that in *Bignonia*, in which the phloëm-plates are also formed by increased centripetal and diminished centrifugal activity of the cambium at certain points, though in *Bignonia* the phloëm does not become enclosed in the wood. The fact that regular radial rows of cells, continuous with those of the wood, can only be traced in the *inner* part of the phloëm-islands, is used by Hérail as an argument in favour of their centripetal development. He concludes by pointing out that *Strychnos* conforms to the 'general law' that a cambium only forms one kind of tissue, wood or bast, on each of its faces. He gives two figures, one of which (Fig. 24) accurately represents a developing phloëm-island, showing clearly the continuity of the radial series of cells inwards, but not outwards. The other figure will have to be referred to again later on. The main point is, that Hérail's account directly contradicts that of de Bary. According to the former the phloëm-islands are formed centripetally, and thus belong, like other phloëm, to the bast tissues, while, as we have seen, de Bary believed that they are formed centrifugally, and are thus a constituent of the wood.

We will now proceed to describe our own observations, deferring all comparative consideration of parallel cases to the end of the paper. It may be mentioned that the essential part of our work, in so far as it relates to the development of

¹ This name is so appropriate for the isolated phloëm-groups imbedded in the xylem, as they appear in transverse sections, that it will be adopted throughout this paper.

the phloëm-islands, had already been done before we became acquainted with Hérail's paper, so that our points of agreement with him afford an independent confirmation of his statements.

GENERAL STRUCTURE OF STEM.

Before tracing the development in detail, it will be useful to give a short description of the structure of a well-developed stem. If a transverse section of an internode of *Strychnos nux vomica*, L., not less than 5 mm. in diameter¹, be examined, the following structure is observed. On the outside is an external periderm, consisting of several layers of cork, with scanty phelloderm. Within this is the parenchymatous cortex, of no great thickness, and then a dense two-layered ring of very sclerotic cells. This immediately surrounds the radially arranged bast-parenchyma. In its outer region the small groups of primary phloëm may still be recognized here and there. Next comes the cambium, and within this the broad zone of wood, occupying much the greater part of the whole area. Scattered about in the wood, and arranged irregularly in three or four concentric rings, we find the phloëm-islands, roundish groups of soft bast separated from one another by broad tracts of the continuous mass of wood. At the inner boundary of the wood lies the ring of medullary phloëm-groups, intruding into the pith. They are usually about twelve in number, and are of almost the same size as the phloëm-islands in the wood. The pith itself is rather thick-walled, and in our specimens is of uniform structure throughout, containing abundant starch. One very conspicuous point is, that all the medullary phloëm-groups, and all the more deeply-seated islands show great masses of crushed and obliterated tissue, and it is at once seen that in the phloëm-islands of the wood the obliterated tissue invariably lies on the outer side, while in the medullary groups it is as constantly

¹ The stem in question was at least five years old, probably more. We were not able, in hot-house grown plants, to distinguish the annual rings with certainty beyond the second year.

situated on their inner side, towards the pith (compare Figs. 5 and 11). Conversely, the living, functional tissue always occupies the inner part of the phloëm-islands, and the outer part of the medullary groups. This fact of the obliteration of effete portions of the phloëm in both regions does not appear to have been noticed by any previous observers, probably because their material was either too young, or if older was herbarium material, in which the soft tissue is all so disorganized that it is impossible to distinguish between its active and its obliterated portions. The facts just mentioned afford a most valuable clue to the direction of development in both cases. Another point which is easily observed is, that in the phloëm-islands the radial rows of cells can always be readily traced inwards into the wood, while no such continuity exists in the opposite direction. It was the observation of these two classes of facts which first led us to question the accuracy of de Bary's account of the development, and to infer that the medullary phloëm-groups are developed centrifugally, but those in the xylem centripetally¹.

DEVELOPMENT OF THE STEM.

The earliest stage of development observed was in *S. spinosa*, Harv., in a stem about 0.6 mm. in thickness. Within the epidermis is a cortex consisting of about three layers of short parenchymatous cells. Next to this comes the pericycle, which is three to four layers thick; the outer layers are formed of rather elongated parenchyma (not readily distinguishable from the external cortex in transverse section), and the innermost layer consists of multinucleate prosenchymatous elements, often radially elongated as seen in transverse section. In the ring of leaf-trace bundles the protoxylem elements already have spirally thickened walls. The xylem

¹ As confusion has occasionally arisen from the use of these words, it may be well to state expressly that development is said to be *centrifugal* when each new element cut off from the cambium lies further from the centre of the axis than the next older element, while the converse order of development is termed *centripetal*.

is arranged in regular radial rows (only two elements in each row usually having thickened walls). This points to the occurrence of regular cambial divisions even at this early stage. The interfascicular tissue also shows a radial, though less regular arrangement of its cells. The small external phloëm-groups, evidently produced by cell-divisions in all directions equally, are in immediate contact with the pericycle. There are usually two of these groups to each bundle, but they also occur opposite the interfascicular tissue. The internal (medullary) phloëm groups are much larger than the external ones, though only about half as numerous. It may be estimated that they already contain collectively twice as many cells as there are in the external phloëm. The cells of the medullary phloëm show some signs of a radial arrangement (cf. Fig. 1). The pith is thin-walled throughout. It is clear then that the medullary phloëm is a primary formation developed simultaneously with the protoxylem and the external phloëm, and that thus the bundles are bicollateral from the first. The internal phloëm accompanies the bundles on their exit into the leaf. The transverse section of a petiole shows five bundles, arranged in a curved row, concave towards the upper surface. All these bundles are bicollateral, the superior phloëm-groups being often more developed than the inferior. In the main bundles of the lamina, the bicollateral structure is still preserved, both phloëm-groups having about the same extent; the smaller bundles, however, are of the normal collateral type with inferior phloëm only. The medullary phloëm of *Strychnos* thus possesses the characters which Petersen¹ and Weiss² have found to be general in other bicollateral bundles. It forms an integral part of the leaf-trace bundle to which it belongs.

De Bary did not decide whether the normal external

¹ Ueber das Auftreten bicollateraler Gefässbündel, u. s. w., in Engler's Jahrbuch für Systematik, Bd. iii, 1882, p. 391.

² Markständiges Gefässbündelsystem und Blattspuren, in Bot. Centralblatt, Bd. xv, 1883, pp. 396, 401.

phloëm of *Strychnos* contains sieve-tubes or not. This question can be best investigated at a stage slightly later than that just described. In transverse sections the horizontal sieve-plates can be recognized as dotted areas, while the longitudinal section shows that these plates are perforated. Normal companion cells accompany the sieve-tubes. The latter, however, sometimes contain nuclei, which in most sieve-tubes disappear at an earlier stage, and this fact may point to the rudimentary character of the normal phloëm here (see Figs. 2 and 3).

Later stages of development from the same plant show that the cambial divisions go on in those cells which are in immediate contact with the external phloëm. Even when the wood has increased to a thickness of sixteen to eighteen cells, no considerable addition has taken place on the outside of the cambium. The outer layers of the pericycle undergo sclerosis, while its prosenchyma first becomes thick-walled, and is then obliterated. The structure of the pericycle is a character which differs very much among the different species of the genus. Other material, probably of the same species, but from a different source, showed the formation of a hypodermal phellogen producing cork centripetally, and abundant phelloderm centrifugally. The phelloderm contains many sclerotic cells. The normal cambium increases its activity, and produces large quantities of bast parenchyma and short-celled sclerenchyma. At this stage the stem has no less than four distinct consecutive zones of mechanical tissue in its cortical region. Towards the exterior are the sclerotic cells of the phelloderm, then those of the pericycle, next the fibres of the pericycle (soon becoming obliterated), and lastly the secondary sclerenchyma of the bast. Cambial increase of the medullary phloëm groups soon begins, by means of divisions in the cells situated towards the protoxylem, and a certain amount of obliteration on the inner side of the group is the result.

Petersen¹ found that in a large proportion of the plants

¹ l. c. p. 395.

with medullary phloëm the periderm is internal, so that the normal phloëm comes to lie dangerously near the surface. This is not the case in *Strychnos*. In the species examined the periderm was always external (hypodermal in some, epidermal in others, e.g. *S. Grayi*, Griseb.), and though the primary cortex is often thin the external phloëm is very well protected by sclerotic tissue, and is exposed to no greater risks than in most normal plants.

It may be noticed that in the older specimens referred to *S. spinosa*, groups of very beautiful stone-sclerenchyma occur in the pith.

More advanced stages of development were chiefly observed in *S. nux vomica*, L. The anatomy of the stem differs in some points from that of *S. spinosa*. The primary cortex is thicker, consisting of about seven layers of cells. The pericycle is limited externally by a single layer of very long fibres with thick cellulose walls. These elements are multinucleate when young. Within the fibres there are one or two layers of parenchyma, and then comes a sclerotic ring, usually two layers thick, of very thick-walled lignified cells, which are parenchymatous in form, but of very variable length¹. The minute groups of external phloëm either abut directly on the sclerotic ring, or in some cases are separated from it by a single parenchymatous cell. These phloëm-groups are even more rudimentary than in *S. spinosa*. The centripetal activity of the cambium is for a time very slight. When the xylem is from ten to fourteen cells in thickness, its outer margin is often separated from the sclerotic ring by three cells only, including the cambial layer. The wood itself shows no special peculiarities. Besides the spiral vessels of the primary xylem, it consists of vessels with bordered pits, very abundant and thick-walled libriform fibres, woody parenchyma, and medullary rays one to three cells in thickness. The groups of medullary phloëm are of large size. At the stage we are describing the larger groups are about fourteen cells and the smallest about

¹ The pericycle of this species was described by Morot, *Recherches sur le péricycle*, in *Ann. des Sci. Nat. sér. 6*, T. xx, 1885, p. 264.

nine cells in radial thickness. They are separated from the inner margin of the wood by two or three layers of somewhat flattened parenchyma resembling that of the pith. The earlier stages, however, prove that these cells form part of the original procambial strand, and so do not properly belong to the pith¹. Cambial divisions of the cells at the outer edge of these phloëm-groups go on more actively than in *S. spinosa*, and the increase of their tissue soon leads to the obliteration of the elements lying towards the pith. It is not necessarily the case that this obliteration advances regularly from within outwards. Often a row of obliterated cells is seen at the extreme inner margin; next we find a row of still normal cells, and then another obliterated layer. The older sieve-tubes are evidently the first elements to yield to obliteration, while the turgid parenchymatous cells offer a longer resistance. As regards the primary structure of the medullary phloëm, it consists of sieve-tubes with somewhat inclined transverse sieve-plates, companion cells, and phloëm parenchyma, the cells of which are about eight diameters in length. The pith itself is of uniform structure throughout, consisting of parenchymatous cells of variable length, full of starch, with thickened, pitted, and somewhat lignified walls. It forms an unyielding matrix in which the phloëm-groups have no room to expand (see Fig. 4).

We will complete the history of the medullary phloëm before going on to the other tissues of the stem. The centrifugal activity of the special cambium² goes on until a large part of each group (sometimes its entire inner half) becomes obliterated, forming a stratified mass of 'Hornbast,' with no cavities left in it beyond mere cracks. The cambial cells can still be recognized in Fig. 5, but their activity has evidently slackened. There is no centripetal formation of tissue worth mentioning;

¹ Cf. Petersen, l. c. p. 391.

² Vesque calls meristem in this position 'false cambium,' chiefly because its productiveness is only unilateral. This is not a constant character, and 'special' or 'local' cambium is a less objectionable term. Cf. Vesque, *Anatomie comparée de l'écorce*, in *Ann. des Sci. Nat. sér. 6*, T. ii, 1875, p. 138.

only one cell is usually cut off on the side towards the wood. The secondary sieve-tubes formed by the local cambium have inclined walls, each of which sometimes bears three sieve-plates. The cambial cells are perhaps best studied in a radial section, in which they are easily recognized by their abundant protoplasm and conspicuous nuclei. The sieve-tubes appear to lose their contents before obliteration, and sometimes show a little callus on their plates.

In *S. nux vomica*, as in *S. spinosa*, a hypodermal periderm is formed, but in the former species there is little phelloderm. The fibres of the pericycle become obliterated, while the sclerotic cells increase in number, probably by sclerosis of some of the outer cells of the bast parenchyma. The latter eventually receives considerable additions from the cambium, and at the stage now to be considered is about six cells in radial thickness. The external groups of soft-bast become almost wholly obliterated by the pressure of the newly formed cells.

DEVELOPMENT AND STRUCTURE OF THE PHLOËM-ISLANDS.

The formation of the phloëm-islands begins late in the second year of growth, at least this was certainly the case in those stems where the annual rings could be distinguished with certainty. At this period the wood is from thirty-five to forty-five cells in radial thickness. As regards the position of the phloëm-islands relative to the primary bundles we have found no general law. The position is best determined with reference to the medullary phloëm-groups which always lie immediately inside the primary xylem-strands. Sometimes the first formed phloëm-islands lie opposite every alternate medullary group, and later on a second ring of islands is formed alternating with the first, so that every medullary group now has a phloëm-island corresponding to it. But this does not always hold good, for sometimes even the first formed islands lie in

the interfascicular tissue, and not opposite a primary bundle at all, and after the first two rings are formed all regularity of arrangement ceases.

We will now trace the development of a phloëm-island (see Fig. 6). The first sign of its appearance is the increased activity of cell-division in a portion of the normal cambium. Otherwise the cambial divisions go on very slowly (at least in hot-house specimens), and wherever a number of fresh tangential cell-walls are apparent we may infer that an island is about to be formed. The cambium is at all stages of the development in contact with lignified cells on its inner side, so the formation of centrifugal phloëm, as described by de Bary, is out of the question (Figs. 6, 7, 8, 9, and 10). The development of the island is due to increased centripetal activity. There is not at first any corresponding diminution in the wood-forming productiveness of this portion of the cambium, and so the outer margin of the secondary wood may remain for a time unbroken. Thus the depressions ('anfractuosités') in the wood on which Hérail¹ lays stress are not a necessary concomitant of the origination of the phloëm-islands. They are in fact very misleading as a clue to the earliest stages, for irregularities in the outline of the wood are frequent, independently of the islands, and we have already seen that the converse is also the case. After a careful comparison of Hérail's Fig. 23 with our own preparations we cannot feel convinced that this figure really represents the origin of a phloëm-island at all. The groups marked *l* are certainly *primary* phloëm, which may or may not happen to lie opposite the place of development of an island, and which in any case take no part in its formation. The phloëm of the islands is, as we shall see, the direct product of cambial divisions, and bears no resemblance at any stage to the small-celled groups shown in Hérail's figure. His statement therefore that these groups 'become' the phloëm-islands cannot be accepted, though in other respects his account agrees with our observations.

As additional phloëm-elements are formed on the outside of

¹ l. c. p. 258.

the centripetally active cambium, the growing tissue has to find room among the pre-existing bast-parenchyma, which consequently becomes locally compressed. At this stage the transverse section of the developing island has the form of a segment of a circle (the cambium forming the chord), which projects into, and displaces the bast-parenchyma. Among the crushed elements bordering the new tissue one of the primary phloëm-groups may occur, but this is not constantly the case. The cells cut off by the cambium rapidly pass over into permanent tissue. Each sieve-tube is formed directly from a cambial cell, the only divisions which it undergoes being those by which its companion cells are formed (see Figs. 6 and 8).

The space required by the developing phloëm-island is however only partly provided by displacement of the external tissue. The cambium forming the island soon ceases, or nearly ceases to produce wood, and its activity in phloëm-formation now just balances the activity of the normally wood-forming cambium on either side. Hence the new phloëm comes to be flanked on the right and left by newly formed secondary xylem, and thus lies in a depression of the woody mass (see Fig. 7). That this process must be accompanied by 'sliding growth' between the phloëm and the adjacent wood is evident here, as it is in the case of the phloëm-plates of *Bignonia*, with which the islands have already been compared by Hérail¹. Hence we find that the parenchymatous cells lying on the flanks of the island become stretched in the radial direction. The unequal formation of xylem and phloëm further results in the fact that the phloëm-forming portion of the cambium becomes detached from the normal ring, and remains nearer the centre of the stem. Thus the main zone of cambium has now suffered an interruption of its continuity. But this interruption is only temporary. The process just described goes on until the phloëm-island has

¹ For a very full account of the development of the phloëm-plates in *Bignonia*, see Hovelacque, *Recherches sur l'appareil végétatif des Bignoniacées, etc.*, 1888, pp. 60-69.

attained its definitive form. Then the activity of the phloëm-forming cambium slackens, though it does not cease, and so the margin of the wood comes up flush with the outer margin of the phloëm-island. And now those cells of the external bast-parenchyma which have escaped obliteration begin to divide, starting on either side with the cells adjacent to the normal cambial zone. The divisions advance from both sides until the cambium becomes continuous around the outer border of the island, and the normal ring is once more completed (Fig. 9).

The exact position of the cells which divide, in order to complete the cambial zone, varies. They may either lie immediately outside the external sieve-tubes of the island, separated from them only by a layer of obliterated cells; or they may lie further towards the exterior, leaving one or two rows of living parenchyma between the new cambium and the outer border of the actual phloëm. The cambial arc by which the normal ring is completed requires a name. We propose in this, and in all similar cases, to term it *complementary* cambium. A word must be said as to the nature of the cells by the divisions of which it is formed. Hérail speaks of them as belonging to the pericycle. This may be true in some species, in which the pericycle remains largely parenchymatous, but in *S. nux vomica* the inner cells of the pericycle become sclerotic, and the cells which undergo division, as shown by their position and regular radial arrangement, both in transverse and longitudinal sections, are clearly of secondary origin, and come under the head of bast-parenchyma.

The complementary cambium now assumes its normal function as part of the general ring. It begins to form wood, outside the new phloëm, starting on either side (Fig. 10). The wood thus formed becomes continuous, and the phloëm-island is now completely surrounded, and deserves its name.

The cambium on the inner side of the island does not however cease its activity. It goes on for a long time producing new and active phloëm as the old becomes past work, and the

new elements can only find room by the crushing and obliteration of the old. The nearer the island lies to the centre of the stem (i.e. the older it is) the greater of course is the amount of obliteration. In the oldest observed, the mass of crushed elements, which as we have seen always lies on the outer side of the island, may occupy almost half its area (see Fig. 11). Towards the inner side, on the other hand, a distinct cambial layer, with thin tangential cell-walls, is always found. As we have already seen, it is a constant rule that the radial arrangement of the phloëm-elements is most regular in the inner part of the island, and that the radial series can be traced continuously inwards through the cambium into the wood. Towards the outside the radial rows, even when not wholly erased by obliteration, can seldom be traced at all, and never with any regularity. That any signs of radial continuity can ever be seen on the outside is due to the fact that the complementary cambium (in this species at any rate) arises by the division of cells which were themselves of cambial origin.

Some account must be given of the position of the phloëm-islands in the wood; and first, as regards their relation to the medullary rays. A small island often occupies the space between two rays. In other (rarer) cases, a medullary ray can be clearly traced straight through the island. In one case a large ray, three cells thick, was observed to pass through the middle of an island, its cells being thin-walled in this part of its course. At the outer margin of the phloëm the cells of the ray are not obviously distinct from the parenchyma so often found at the outside of an island, but in the external wood the ray goes on again as before. These facts are explained by the development. The complementary cambium has simply formed new ray-cells which approximately fit on to those which the normal cambium had begun to form before its dislocation. Not uncommonly however a broad secondary ray starts from the outer margin of a phloëm-island. In other cases a small ray can be traced to the inner margin of an island and through the cambial layer into its tissue, but it does not reappear on the outside. The explanation of all

these various cases is obvious in the light of the developmental facts.

It is a nearly constant rule that the island is bounded on its outer side by woody parenchyma; its inner boundary is usually, but less constantly, formed by woody fibres. The xylem-elements abutting laterally on the islands may be ray-cells, woody parenchyma, or fibres. We have never found vessels in contact with the islands. On the outer side and on the two flanks the contrast between the thick-walled xylem and the soft phloëm is quite sharp. On the inner side, however, a layer or two of thin-walled cells are generally found between the woody fibres and the actual cambium, and among these cells developing xylem-elements may sometimes be observed. This proves that the phloëm-forming cambium has not wholly lost its capacity for centrifugal formation of wood.

The sectional form of a phloëm-island is circular, or more often somewhat elliptical, with the major axis directed tangentially to the surface of the stem. Its cambial-layer is thus curved, with its convexity towards the centre of the stem. This is due to the fact that during the formation of the island the retardation of the wood-forming activity of its cambium begins at the middle point of the layer.

As regards the minute structure of the phloëm-islands we have nothing to add to de Bary's account, except that the elongated cambial cells on the inner side are very conspicuous in radial section (Fig. 8). The phloëm is made up of parenchyma, sieve-tubes, and companion cells. The first-formed sieve-tubes of the island have approximately transverse sieve-plates (Fig. 8), but those which are developed later on have inclined terminal walls, sometimes bearing three sieve-plates each. The direction of inclination of these walls is variable, as would be expected from the curved course of the cambial layer, and from the great crowding of the cells. Anastomosis of the phloëm-strands in the internodes is certainly rare, if it ever occurs, but they unite with one another at the nodes.

STRUCTURE OF THE ROOT.

We are not acquainted with any previous observations on the *root* of this genus. We were not able to obtain material sufficiently advanced to decide the most interesting question, namely that as to the existence of phloëm-islands in the root. The oldest roots at our disposal had a xylem ring about eighteen cells in radial thickness, whereas in the stem the formation of phloëm-islands does not begin until about double this amount has been formed. Hence no negative conclusion can be drawn. We were able, however, to prove the existence of medullary phloëm in the root of *S. spinosa* (the only species examined), and as this appears to be an uncommon structure among Dicotyledons, it will be desirable to give some account of the anatomy of the roots of this plant.

The roots examined were from two sources, the Royal Gardens at Kew, and the garden of the Society of Apothecaries at Chelsea. The former plant is certainly *S. spinosa*, and the latter in all probability belongs to the same species. The differences in structure between the roots of the two specimens may well be due simply to differences of age. The largest roots examined were about 4 mm. in diameter. They are of polyarch structure, ten being a common number for the xylem or phloëm-groups. The cortex is wide, and persists for a long time. The hypodermal layer is cuticularized, and forms a well-marked exodermis. The subjacent cells often divide to form an external periderm. This is, however, only a temporary structure, for the pericycle ultimately gives rise to an internal periderm of great regularity. In the main roots the pith is relatively very large, the xylem for a long time forming only a relatively narrow ring. The formation of secondary phloëm is most active opposite the primary phloëm-groups, so that the latter become pushed out into the pericycle, causing local compression of tissue. The appearance of these prominent masses of phloëm is quite like that of the phloëm-islands of the stem at an early stage of development, but we have no evidence to show that the phloëm-groups of the root ever become enclosed in the wood.

Small groups of medullary phloëm lie just within some, but not all, of the primary xylem-groups. The cells between the medullary phloëm and the xylem form a distinct cambium (Fig. 12). The development of these phloëm-groups is very unequal. In the same transverse section some are found with fully formed sieve-tubes, while others are only indicated by a few cambial divisions in the outer cells of the pith. It appears then that the medullary phloëm in the root is of relatively late development. Similar structures are found in all the roots which have any pith. In the smallest lateral branches the xylem reaches to the centre, and here, of course, there is no medullary phloëm.

In some roots of the specimen undoubtedly belonging to *S. spinosa* the outer zone of the pith is sclerotic, so that the central parenchymatous portion is of relatively small extent. In such roots there is usually a single excentrically situated medullary phloëm-group. This may be separated by as many as three parenchymatous layers from the nearest sclerotic tissue. Here also a layer of cambium is present on the side towards the xylem. Longitudinal sections show that the medullary phloëm-groups of the root contain typical sieve-tubes and companion cells, the older sieve-tubes having their plates obliterated by callus.

SUMMARY OF RESULTS.

Before going on to compare the phenomena of development in *Strychnos* with those in some other Dicotyledons, we will shortly recapitulate the results of our observations:—

1. The *external phloëm*, though but little developed, contains sieve-tubes and companion cells of normal structure, with the exception that nuclei are found in the mature sieve-tubes. The latter fact is perhaps an indication of their rudimentary character.
2. (a) The *medullary phloëm-groups*, as shown by their development and by their course, form an integral part of

the leaf-trace bundles, which are therefore from the first of bicollateral structure.

(b) These medullary groups grow by means of a special cambium lying on the outer side of each group. The formation of additional elements by the cambium results in the progressive obliteration of the older and effete portions of the phloëm on the side towards the pith.

3. (a) The *phloëm-islands*, or interxylary phloëm-strands, are formed centripetally by certain portions of the normal cambium. They become sunk into the wood owing to the relative retardation of the development of secondary xylem on their inner side. The wood ultimately closes round them in consequence of the formation of a complementary cambium, which arises from the division of cells of the external bast-parenchyma, and thus again completes the cambial ring.

(b) The phloëm-islands continue to grow, after they are enclosed in the wood, by means of the cambial layer on their inner side. This growth is opposite in direction to that of the medullary groups, and results in the obliteration of the older tissues occupying the outer part of the island.

4. The roots, in so far as they have a pith, possess medullary phloëm-groups, similar to, but smaller than, those of the stem, and increased, like the latter, by means of a centrifugally active local cambium.

COMPARATIVE CONSIDERATIONS.

In possessing bicollateral bundles *Strychnos* agrees with a large part of the Loganiaceae¹, and with many other natural orders of the most diverse relationships, among which the Myrtaceae, Onagraceae, Lythraceae, Cucurbitaceae, Melastomaceae, Solanaceae, Asclepiadeae, Apocynae, Cichoriaceae, and Campanulaceae may be mentioned. This is not the place to discuss the systematic importance of this character, a

¹ See Solereder, l. c. pp. 28 and 176.

question which has been sufficiently dealt with by Petersen and Solereder. In several of these cases the normal external phloëm is much reduced, but this peculiarity is more generally characteristic of plants with phloëm-islands in the wood. In *Strychnos*, which is so abundantly provided with both medullary and interxylary phloëm, it can excite no surprise that the external phloëm should remain in a comparatively rudimentary state. The presence of a centrifugal cambium between the xylem and the internal phloëm of bicollateral bundles has already been often recognized. Vesque¹ found it in various Solanaceae, Asclepiadeae, and Apocynae, and Petersen further showed that it occurs among the Myrtaceae, Lythraceae, Cichoriaceae and Campanulaceae². He even states that in *Tragopogon* and *Lactuca* this cambium forms a little centripetal wood. The internal cambium of *Strychnos*, especially of *S. nux vomica*, appears to be exceptionally active in phloëm-formation, so much so that a comparison with *Tecoma* at first suggested itself. There is, however, no centripetal wood in *Strychnos*, and the medullary structures in *Tecoma* must certainly be regarded as constituting a distinct system of bundles, whether cauline as Hérail³ and Hovelacque⁴ believe, or common, as held by Weiss⁵, and not as forming part of the bundles of the normal ring. However, the distinction is not really so sharp as it appears. Transitional cases between internal phloëm and distinct medullary bundles occur in the Melastomaceae, Solanaceae, Cichoriaceae, Campanulaceae⁶, and other families.

As regards the presence of phloëm-islands in the wood, they are now known, chiefly owing to Solereder's work on herbarium material, to occur in no less than twenty-four genera, belonging to ten different natural orders; whereas when de Bary published his 'Vergleichende Anatomie' they were only known in the two genera *Strychnos* and *Dicella*. We will not enumerate all the genera, but will only mention the orders

¹ l. c. p. 146.² l. c. pp. 363 (Pl. IV, Fig 4), 379, 386, and 391.³ l. c. p. 282.⁴ l. c. pp. 12, and 146-179.⁵ l. c. pp. 396, etc.⁶ Cf. Petersen, l. c. pp. 371, 382, 386, 391; also Weiss, l. c. p. 396.

to which they belong. They are : Vochysiaceae, Malpighiaceae, Olacineae, Combretaceae, Melastomaceae, Salvadoraceae, Loganiaceae, Gentianeae, Acanthaceae, and Thymelaeaceae. Thus every sub-class of Dicotyledons is represented. To this list, as we shall presently see, the Onagraceae, Solanaceae, and Goodeniaceae should probably be added, while similar, though not identical structures are also found in the roots of Cruciferae and of Cucurbitaceae. But though the examples are so numerous, only a small minority of the plants in question have been investigated any further than was necessary to establish the bare existence of the anomalous structure. Solereder, who was the first to find interxylary phloëm in sixteen genera, worked entirely on herbarium material,—a fact which he regards as advantageous, on account of the authentic naming of the specimens investigated¹. But accuracy of specific determination, desirable as it is, is no compensation for inexactness in the anatomical results. The examination of histological structure in dry material alone, may afford a useful clue to the empirical identification of species, but is seldom of any use when developmental questions are involved. Solereder's work is of value from the wide field it covers, and is highly suggestive of further research, but his statements as to development rest on no satisfactory basis. He defines interxylary phloëm-groups as 'those islands of soft bast in the wood, which are locally produced on the inner side by a normal cambium belonging to a normal circle of bundles².' This statement contains an unwarranted generalization. In the few cases in which the development has been traced, phloëm-islands are in some formed on the inner side, in others on the outer side of the cambium. We will shortly describe the best investigated instances of each.

Among the Vochysiaceae the phloëm-islands of *Erismia* have been observed and figured by Wille³, who says that they are formed on the inside of the cambium. His figures,

¹ l. c. p. 7.

² l. c. p. 32.

³ Om Stammens og Bladenes Bygning hos Vochysiaceerne, Oversigt K. Dansk. Vidensk. Selskabs Forhandl. 1882-3. French résumé, p. 14.

however, are quite indecisive, and he admits himself that he could not obtain much information from the dry material he examined ¹.

De Bary's investigation of the malpighiaceous *Dicella* ² was also made on dry material. He comes to the same conclusion here as in *Strychnos*, but a re-investigation is obviously required.

Passing over several groups mentioned by Solereder, but of which we have no detailed knowledge as regards the point in question, we come to Salvadoraceae, an order not so very remote from the Loganiaceae. The phloëm-islands of *Salvadora* have been thoroughly worked out by Kolderup-Rosenvinge ³, and we have been able to confirm his statements. In this very interesting plant, which in habit resembles a fruticose *Strychnos*, the phloëm-islands are even more numerous than in that genus, and occur not only in the stem, but in the root and in the petiole of the leaf. The primary bundles, however, are not bicollateral. In the stem the islands resemble those of *Strychnos*, but contain rather more parenchyma. There is no doubt that they are formed centrifugally on the inner side of the normal cambium, and thus form morphologically a part of the wood. After an island is developed the same cambium resumes xylem-formation outside it, and so the phloëm becomes imbedded. In fact, the process which de Bary erroneously supposed to occur in *Strychnos*, actually takes place in *Salvadora*. After the phloëm is imbedded irregular cambial divisions go on, both towards the outer side of the island and elsewhere, and a certain amount of obliteration takes place towards the centre of the group. The external phloëm here is well developed.

In the root the structure is different. Here the islands consist chiefly of parenchyma. They are of large extent, and are often irregularly confluent with one another, as seen in transverse section. It appeared to us that the formation of the

¹ l. c. p. 187.

² l. c. p. 580.

³ Anatomisk Undersøegelse af Vegetationsorganerne hos *Salvadora*, in Oversigt K. Dansk. Selskabs, 1880-81.

small phloëm-groups which are found in the parenchymatous islands is a secondary, or rather a tertiary process, like that of the interxylary bundles in the fleshy roots of Cruciferae, described by Weiss¹. That is to say, certain of the secondary parenchymatous cells divide up to form a group of sieve-tubes and companion cells, which then increase in number by means of a special cambium surrounding the group on all sides. This, however, does not alter the main fact; the interxylary phloëm of the root, as well as of the stem, is developed, whether directly or indirectly, on the inner side of the normal cambium². The accuracy of Kolderup-Rosenvinge's figures renders any illustrations of our own unnecessary.

As regards the Loganiaceae, we need only mention that Solereder found phloëm-islands in two additional genera, *Norrisia* and *Antonia*.

In *Chironia*, one of the Gentianeae, Vesque³ found numerous small interxylary phloëm-islands. From his description and figures it is most probable, though not quite certain, that they are formed on the inner side of the cambium.

In *Thunbergia* and in *Hexacentris* (perhaps a sub-genus of the former) among the Acanthaceae, Vesque⁴ found alternating tangential bands of phloëm and xylem, the origin of which was subsequently more fully investigated by Hérail⁵. He finds that this abnormality depends on the unequal activity of the cambium. Opposite the primary xylem-bundles the cambium forms abundant wood containing vessels, while between them it forms a smaller amount of wood destitute of vessels, but is so much the more active in the centripetal formation of phloëm. Hence the cambium shows a depression in each of these latter

¹ Anat. u. Physiol. fleischig verdickter Wurzeln, in Flora, Bd. lxiii, 1880. Compare especially his figures 1 and 2, of *Cochlearia*.

² Treub describes the formation of secondary vascular bundles from cells of the mature parenchyma in *Myrmecodia*, in which the primary bundle system perishes on the formation of the first internal periderm. From the account he gives it appears that the bundles may be formed from parenchyma, which is itself secondary (phelloderm), as well as from the primary ground-tissue. Treub, Sur le *Myrmecodia echinata*, in Ann. du Jardin bot. de Buitenzorg, T. iii, 1883, p. 139; Pl. xxii, Figs. 3, 4; xxiv, Figs. 8, 9, 10.

³ l. c. p. 147.

⁴ l. c. p. 147.

⁵ l. c. pp. 259-263.

regions. Divisions then take place in the cells of the pericycle outside the phloëm-masses, and thus the normal cambium again forms a regular ring. The process is now repeated. Abundant wood is again formed opposite the primary bundles, while between them a smaller amount of wood and excessive bast is produced, until the cambium closes in a second time. This goes on indefinitely, and so the wood ultimately consists of alternating radial portions quite different in structure. The portions lying opposite the primary xylem-groups consist of normal wood, while the interfascicular regions are made up of successive tangential plates of non-vascular wood and of soft bast. There are four radial masses of each kind in *Thunbergia*. The process only differs from that in *Strychnos* in the facts that in the latter the xylem is of similar structure throughout, and that the phloëm-islands do not all lie in the same radial lines.

In *Goodenia ovata* Vesque¹ found that there is a normal ring of bundles, but as regards five of these the cambium is extrafascicular, the phloëm of these bundles thus becoming buried in the wood. This is a case of what may be termed primary phloëm-islands. It is not mentioned by Solereder under this head, as it obviously does not fall under his definition of interxylary phloëm, but from our point of view this case affords an interesting parallel to the process in *Strychnos* and the Acanthaceae.

Lastly we may mention the phloëm-groups in the xylem of the root of certain Onagraceae, Solanaceae, and Gentianeae described by Weiss². These growths are formed directly from the cambium on its inner side. They never grow subsequently by means of a special cambium of their own, and thus differ from the similar groups in the root of *Salvadora*, and from the interxylary bundles in the roots of Cruciferae and Cucurbitaceae.

These last-mentioned bundles are formed sometimes in the parenchymatous part of the secondary wood at a distance from

¹ l. c. p. 146.

² *Flora*, Bd. lxiii, and *Bot. Centralblatt*, Bd. xv, p. 407.

the cambium, and sometimes in the pith. In the Cruciferae a group of phloëm is first formed, then a ring of cambium surrounding it gives rise to additional phloëm-elements on the inside, and to a little xylem on the outside¹. According to Weiss, these concentric bundles are continuous with leaf-trace bundles of the stem².

In *Bryonia*, on the other hand, where the new formation takes place around a normal group of xylem, the phloëm lies externally, and the xylem internally, with reference to the special cambium³. These interxylary bundles are only indirectly connected with our immediate subject. They bear the same relation to true phloëm-islands as complete medullary bundles bear to the internal phloëm-groups of a normal ring of bicollateral bundles.

Summing up the results of our survey, we see that the few satisfactorily investigated examples of phloëm-islands are about equally divided between the centripetal and centrifugal modes of development. Thus Hérail's 'general law' above cited does not hold good universally, any more than does the opposite generalization of Solereder. Every case must be investigated on its own merits.

It is worth mentioning that interxylary phloëm-islands in the stem generally occur in connection with bicollateral bundles. According to Solereder, the exceptions to this rule are limited to the five genera *Dicella*, *Sarcostigma*, *Salvadora*, *Dobera*, and *Hexacentris*⁴. The same author finds that the occurrence of phloëm-islands is not so constant a character for large groups as is the presence of bicollateral bundles. This is quite what would have been expected *a priori*. Phloëm-islands are a secondary formation arising late in the development, while bicollateral bundles are part of the primary structure formed on the first differentiation of the tissues.

¹ See Figs. 1 and 2 of Weiss's paper in Flora.

² Bot. Centralblatt, xv, p. 407.

³ Flora l. c. Figs. 5 and 6. By an oversight this is wrongly described in the text of the paper, p. 110.

⁴ l. c. p. 33.

It is premature to speculate on the physiological significance of the structure we have been considering. There is certainly a tendency among many Dicotyledons (both climbers and others) to find a more protected position for their conducting tissues than is provided by the typical orientation of wood and bast. To take only two familiar examples: In *Bignonia* all the larger sieve-tubes are contained in the phloëm-plates which are so well shielded by the wood. The sieve-tubes of the external phloëm are comparatively insignificant. Similarly in *Tecoma grandiflora*, and no doubt in some of the other species, the medullary phloëm is better developed than the normal. In this plant the medullary wood is also characterized by its large and numerous conducting elements. Whether the internal position of the conducting, and especially of the proteid-conducting tissues offers any other advantage than that of protection must be left an open question for the present.

Although, as we have seen, Hérail's generalization as to the uniform character of the tissue produced on the same side of the cambium, is not constantly true, yet we now know that in the great majority, even of the anomalous cases, the cambium forms phloëm centripetally and xylem centrifugally. The wood of *Strychnos* was compared by de Bary and van Tieghem¹ with that of the Chenopodiaceae, and the comparison still holds good, though the order of development in both is different from what they supposed. As is well known, the wood of the Chenopodiaceae, Nyctagineae, Phytolaccaceae, and Aizoaceae shows, within the cambium, concentric rings of collateral vascular bundles, imbedded in secondary ground-tissue, which is itself often lignified. In some cases successive cambial rings appear; in others the secondary collateral bundles appear to be all formed by one and the same ring of cambium. According to de Bary's account, the phloëm of these bundles is formed from an initial strand, separated off internally from the cambium², so that in

¹ l. c. p. 797.

² l. c. p. 592.

this numerous class of cases the phloëm-formation appeared to be centrifugal. Morot¹ was the first to show that in various Chenopodiaceae, Nyctagineae, etc., in fact throughout the families in question, the cambium constantly gives rise on its inner side to the wood of the bundles, on its outer side to their bast. The generative zone always passes *between xylem and phloëm*, but only has a temporary activity. In order that other more external bundles may be formed, it is necessary for new generative zones to be produced outside the first one. These new cambial zones may either be entirely distinct from their predecessors, or, as is more frequent, may have more or less numerous points of contact with them. In the latter case the original generative zone may maintain its activity in the intervals between the bundles, but these interfascicular cambial arcs become connected by bridges of meristem passing outside the bast, and destined to replace the generative arcs interposed between phloëm and xylem. As Morot points out, it is the persistence in some cases of the activity of the interfascicular portions of the cambial ring, which led to the belief that the activity of the entire ring is persistent. Thus to Morot belongs the credit of showing that the activity of each cambial ring is perfectly normal throughout the whole of this series.

The conclusions of Morot have been fully confirmed by Hérail², Strasburger³, Petersen⁴, and by the independent observations of one of us on *Mirabilis*, *Bougainvillea*, *Chenopodium*, *Amarantus*, and *Mesembryanthemum*. In all these cases, while the bulk of the secondary tissues is formed centrifugally, the phloëm of each bundle is developed, as in normal cases, centripetally.

It is to be regretted that the recent authors Gheorgieff⁵,

¹ Recherches sur le péricycle, in Ann. des Sci. Nat. Sér. vi, T. xx, 1885, p. 284.

² l. c. p. 247.

³ Das botanische Practicum, 2te Auflage, 1887, p. 170.

⁴ Staengel-bygningen hos *Eggersia buxifolia*, in Botanisk Tidsskrift, Bd. xvi, French résumé, p. 9.

⁵ Beitrag z. vergl. Anat. d. Chenopodiaceen, in Bot. Centralblatt, Bd. xxx and xxxi, 1887.

Heimerl¹, and Pax², who have worked at the anatomy of these families, appear to have paid no special attention to the development. Some of Gheorgieff's figures, however, in Pl. VI and VII of his paper, leave no doubt as to the centripetal development of the phloëm in the plants he examined. He describes and figures obliteration of the phloëm here, similar to that which we have so often mentioned in *Strychnos*.

The phloëm-islands of *Strychnos*, then, in their centripetal development from the cambium, conform to a law of wide though not of universal application.

The occurrence of medullary phloëm in the root affords one more decisive argument that the vascular cylinder of the root should no longer be described as a single vascular bundle, but should be regarded as corresponding to the whole vascular system and pith of the stem.

The material for our investigation was supplied partly from the Royal Gardens at Kew, partly from the Garden of the Society of Apothecaries at Chelsea, and to the heads of both these institutions we tender our thanks. We wish further to thank both the Kew authorities and those of the botanical department of the British Museum, for valuable help in the identification of species.

Some of the preparations, including that from which Fig. 1 is drawn, were made by Miss A. L. Smith, whose help we have pleasure in acknowledging.

¹ On Nyctagineae in Engler u. Prantl's *Die natürlichen Pflanzenfamilien*, Theil III, Abth. 1, 1889.

² On Aizoaceae. *Ibidem*.

EXPLANATION OF FIGURES IN PLATES XVIII AND XIX.

Illustrating Messrs. Scott and Brebner's paper on *Strychnos*.

The following lettering is used throughout:—

- cb^1 = Normal (including complementary) cambium.
- cb^2 = Medullary cambium, adding new elements to the medullary phloëm-groups.
- cb^3 = Cambium from which the phloëm-islands are produced.
- ph^1 = Normal external (rudimentary) phloëm.
- ph^2 = Medullary phloëm.
- ph^3 = Phloëm-islands, ultimately imbedded in the wood.
- x^1 = Primary xylem.
- x^2 = Secondary xylem.
- pc = Pericycle.
- p = Pith.
- lp = Lignified pith.
- r = Medullary ray.
- c = Companion cell.
- s = Sieve-tube.

Fig. 1. *S. spinosa*, Harv. $\times 500$, transverse section. Young vascular bundle, showing external phloëm-groups, and the medullary group in course of formation.

Fig. 2. *S. spinosa*, $\times 920$, transverse section. External phloëm-groups at a slightly older stage. The sieve-tubes (with sieve-plates) and companion cells are shown. Only young unligified xylem is shown.

Fig. 3. *S. spinosa*, $\times 920$, longitudinal section. At the same stage as the last, showing a sieve-tube and companion cell in an external phloëm-group. A nucleus is present in the sieve-tube.

Fig. 4. *S. nux vomica*, L., $\times 333$, transverse section. Shows a medullary phloëm-group. On its outer side is an active cambium, while on the inner side the elements are beginning to become obliterated.

Fig. 5. *S. nux vomica*, $\times 333$, transverse section. More advanced medullary phloëm-group. The cambium is ceasing its activity, and a great mass of obliterated elements is seen on the inner side.

Fig. 6. *S. nux vomica*, $\times 333$, transverse section. First commencement of the formation of a phloëm island. The normal cambium is increasing its activity in this region, and has already produced a few sieve-tubes and companion cells. The compressed elements may be primary phloëm. No retardation of wood-production is as yet to be noticed. This is from an old stem (thickness 5 mm.).

Fig. 7. *S. nux vomica*, $\times 333$, transverse section. More advanced stage. The phloëm-cambium is now quite detached from the normal ring. The obliteration of peripheral elements is making progress. The island is now deeply sunk in the wood.

Fig. 8. *S. nux vomica*, $\times 500$. Longitudinal radial section of a phloëm-island at a similar stage. The cells of the special phloëm-cambium are shown with contents. Sieve-tubes and companion cells are shown.

Fig. 9. *S. nux vomica*, $\times 333$. Transverse section at a later stage. The phloëm-island is now overtopped by xylem on either side, and divisions in the bast-parenchyma have completed the normal cambial ring outside the island. The phloëm-cambium is in full activity, and the continuity of the radial rows of phloëm-cells with those of the internal xylem is especially evident here.

Fig. 10. *S. nux vomica*, $\times 333$. Slightly later stage. The wood is now beginning to close in on the outside of the phloëm-island. The number of obliterated peripheral elements in the latter has increased, but the cambium is still as active as ever.

Fig. 11. *S. nux vomica*, $\times 333$. Very old phloëm-island, completely immersed in wood. An immense mass of obliterated elements is seen on the outside. The cambium shows but little signs of activity. This corresponds to Fig. 5 of the medullary phloëm.

Fig. 12. *S. spinosa*, $\times 333$. Transverse section of root, in which secondary thickening has begun. A medullary phloëm-group is seen in the pith opposite a group of primary xylem. These groups increase slightly by an external cambium as in the stem. Thickness of root about 4 mm.

Note.—Figs. 4, 5, 6, 7, 9, 10, 11, and 12 were drawn under a power of 500 diam. and subsequently reduced to two-thirds.

Fig. 1.

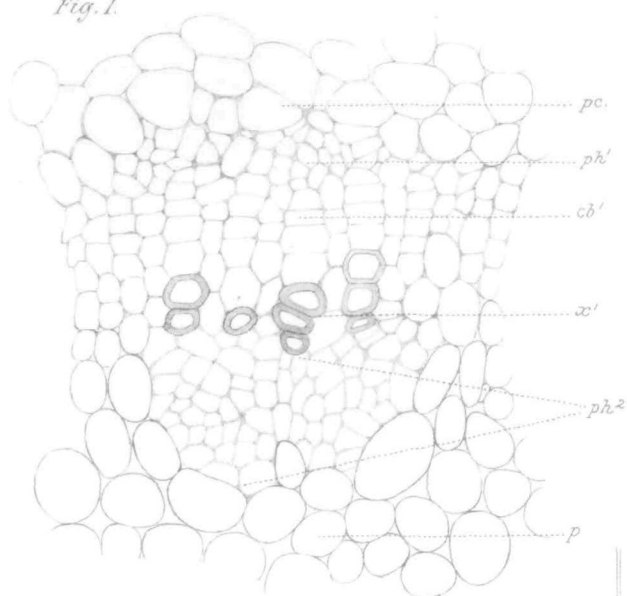


Fig. 2.

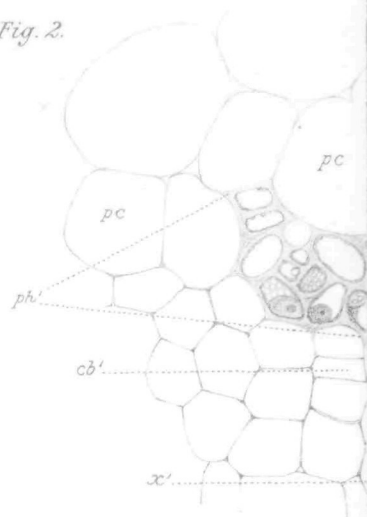


Fig. 5.

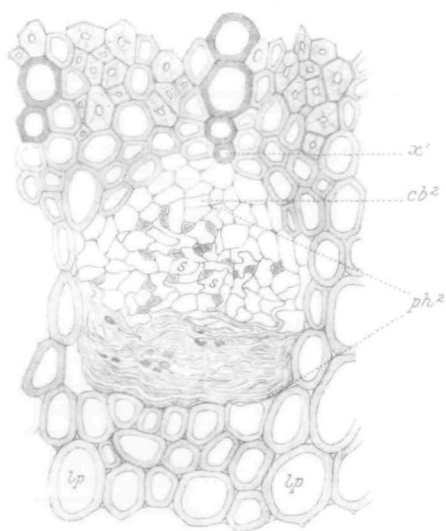
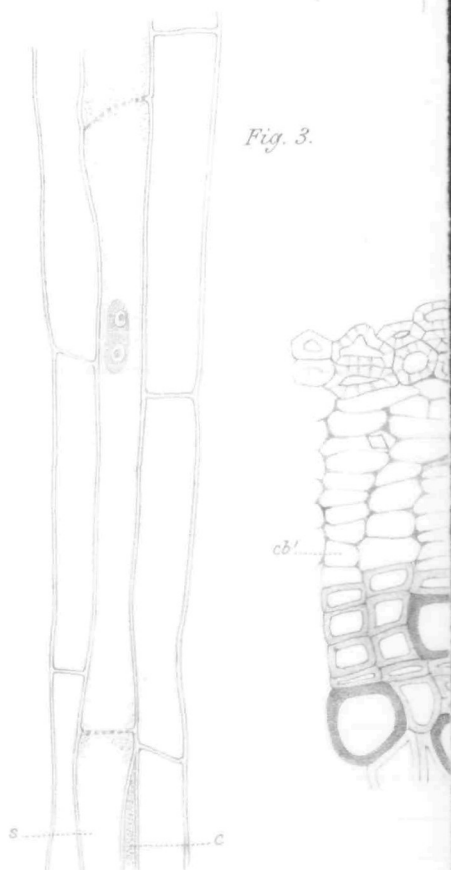


Fig. 3.



G. Brebner del.

Fig. 4.

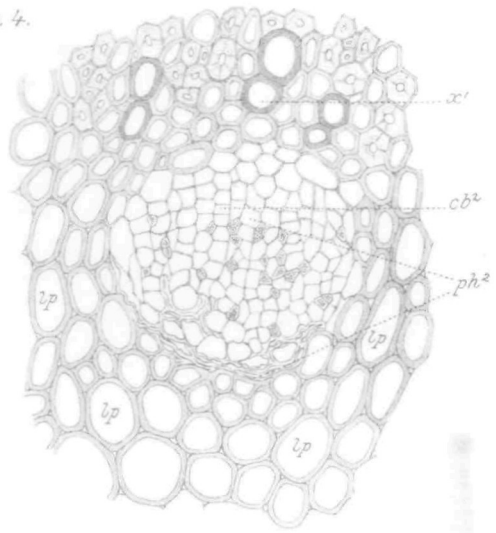


Fig. 7.

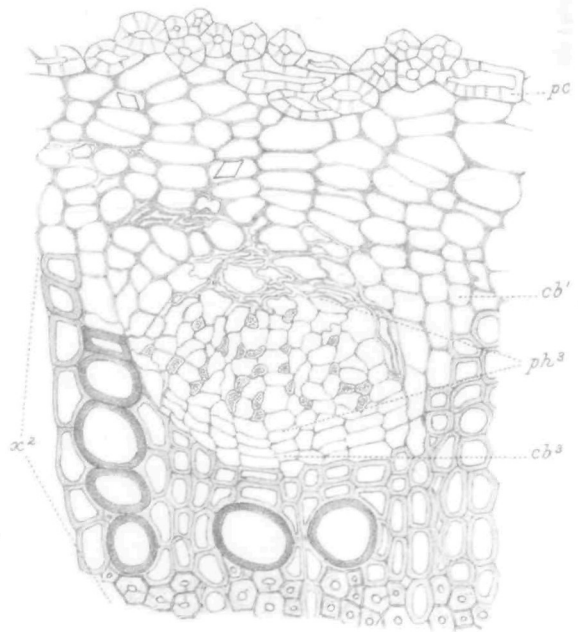
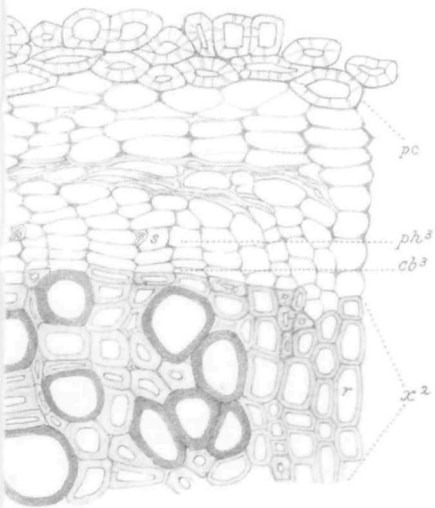


Fig. 6.



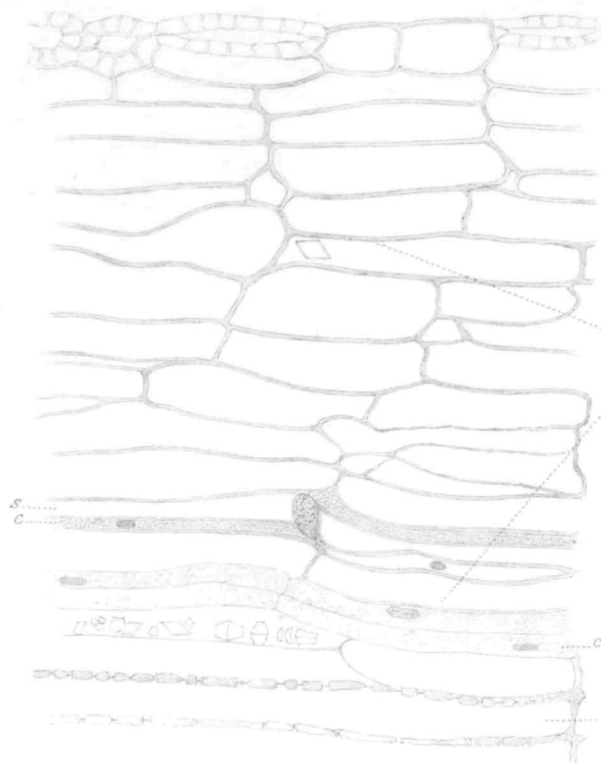


Fig. 8.

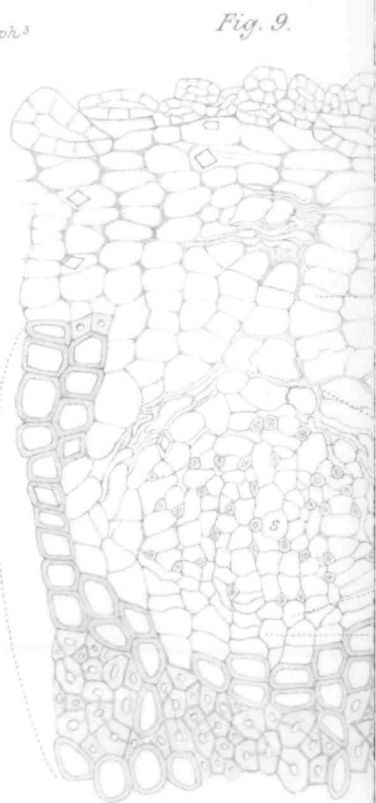


Fig. 9.

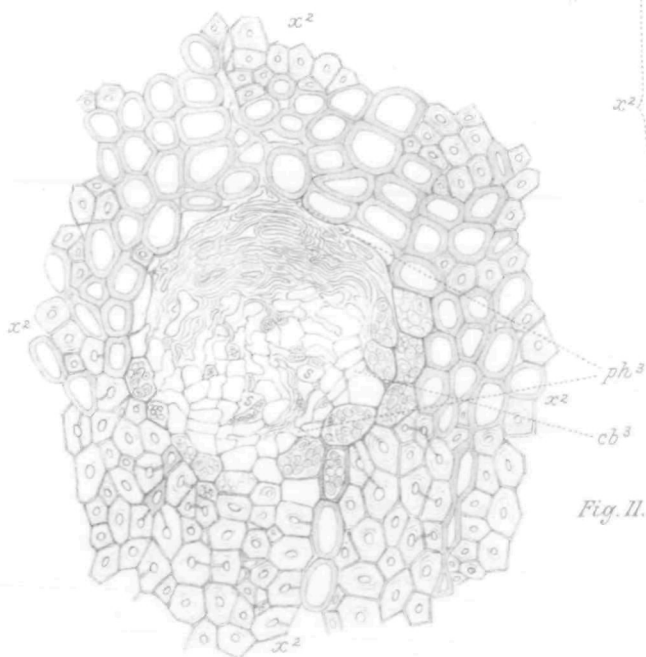


Fig. 11.

G. Brebner del.

Fig. 10.

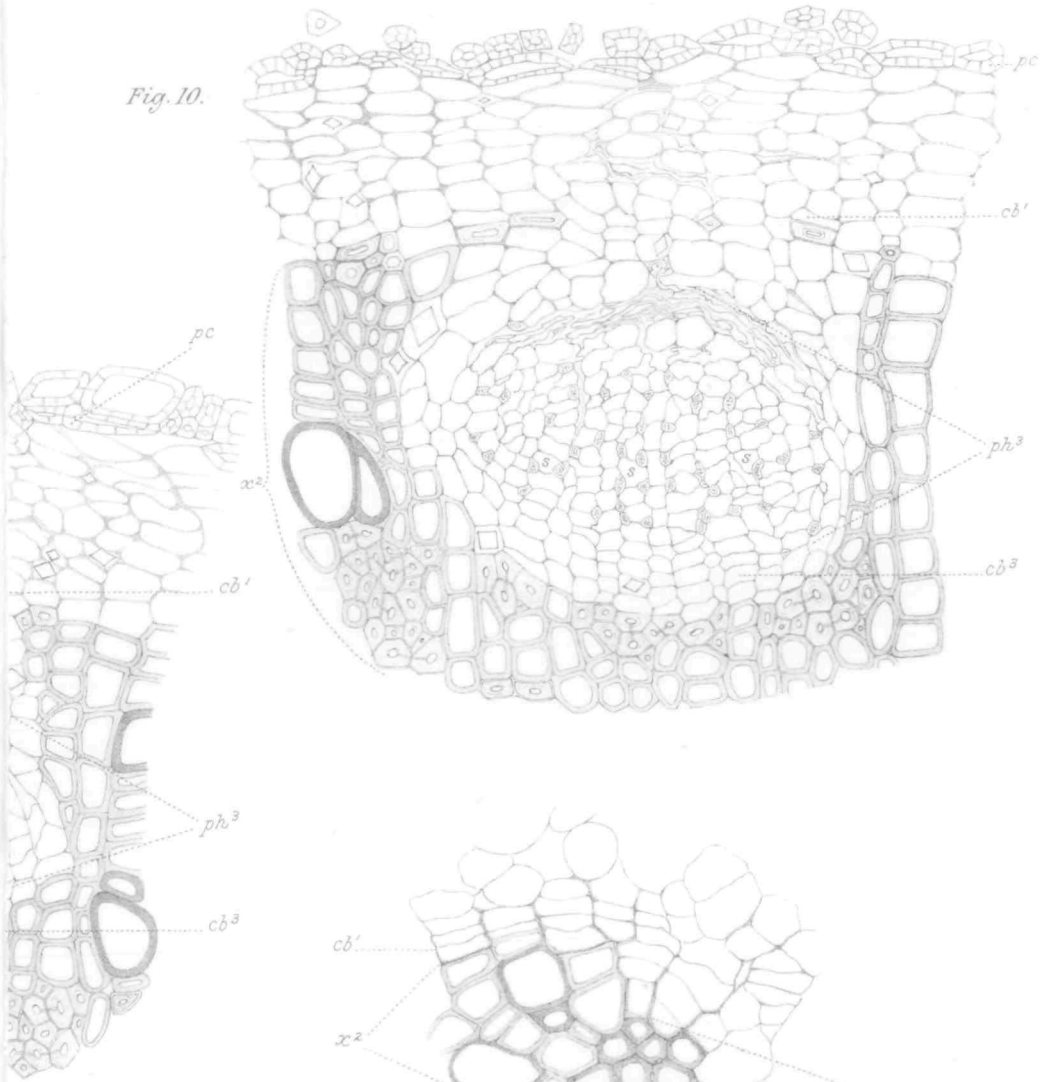


Fig. 12.

