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ON THE

FORMATION OF NODULES IN THE CORTEX OF HEVEA BRASILIENSIS.

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On the Formation of Nodules in the Cortex of Hevea brasiliensis Muell.-Arg.

BY

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WITH the development of the rubber industry and the planting of large areas in the Eastern Tropics under *Hevea brasiliensis*, a striking pathological condition of the cortex was brought to light. In the cortex of certain trees small woody bodies of varying shape and size were found; these bodies were termed "burrs" or "nodules." As the rubber plantations became older and the trees bigger in girth, tapping operations to obtain the latex from the cortex were begun. These burrs or nodules, which were considered to be comparatively rare in untapped trees, now appeared to occur more frequently in trees where tapping had been in progress for some time. However, other circumstances might combine to render their occurrence apparently more frequent; tapping operations would disclose their presence in trees where, perhaps, owing to little outward sign, they had not been suspected before. In parts of the tree not tapped their size, increasing with age, would ultimately result in their discovery.

The presence of nodules of several years' growth is at once detected by the characteristic, gnarled, and knotted appearance of the stem of a tree so affected. Tapping may be seriously interfered with, or even rendered quite impossible in trees badly affected. In a younger stage nodules may cause only a slight swelling externally, and they may then somewhat resemble the callus formed as a result of tapping injuries to the stem wood.

Swellings on the *Hevea* stem were shown by Petch (21) in 1905 to be of two kinds. The first kind is caused by wounding the cambium of the stem, usually by tapping too deeply.

The wound thus produced is closed over in a manner common to trees in general, *i.e.*, the living cambium cells surrounding the wound undergo rapid division and give rise to a callus or cushion of tissue which grows over the wound area and ultimately covers up the wound. A swelling is thus formed over the site of the wound, but this gradually disappears in the subsequent growth in thickness of the stem. Thus, tapping is not interfered with permanently, though care is necessary when again tapping over this point to avoid grazing the woody swelling on the stem wood, if it is not yet merged in the subsequent growth. This healing process is known as "occlusion," and is a method whereby the tree covers up exposed wood areas and re-unites the severed edges of the cambial layer, so that one continuous cambium is again formed, and the stem can continue its normal growth in thickness. The new wood, however, never unites across the wound with the old wood, and in sections across the stem the wound is always visible. The cause of this kind of swelling being known, measures can be adopted to avoid producing it.

The second kind of swelling is due to the production of nodules. About the cause of the production of nodules much difference of opinion prevails; several explanations have been advanced, but none so far has found general acceptance. A nodule at first is a little isolated body of woody tissue lying in the cortex, usually about the size of a "pea" when first observed, and easily "shelled out" with a penknife. There is little to indicate its presence at this stage—occasionally a small protuberance, or a slight cracking of the bark externally. In later stages these "peas" increase to the size of a "hen's egg," or many "peas" fuse together and form an irregular mass; or, again, large sheets of woody tissue are produced. At the same time growing points originate, which grow inwards and unite with the stem wood, and thus ultimately the nodular masses become connected with the stem wood at many points. As the nodules grow larger the stem becomes gnarled; the cortex cracks and latex oozes out; finally, the entire stem to a height of 5 or 6 feet from the ground is affected. In this condition it is impossible to carry on tapping, and the tree is useless.

DISTRIBUTION.

Nodules have been recorded from every country where plantations of *Hevea brasiliensis* have been established; they are found in Ceylon, the Federated Malay States, Singapore, Java, Sumatra, South India. One record (16) comes from Dutch Guiana; this is noteworthy, as Dutch Guiana is on the reverse slope of the Amazon Valley watershed, and probably has *Hevea* indigenous to its flora.

In a report (1) prepared for the Brazilian Government, Akers says of the Malay Peninsula: "The worst pest brought to the notice of the Commissioners was the formation of burrs or nodules in the bark. While these do not materially affect the health of the tree, they are a serious interference to tapping. They occur principally on old trees that have been badly tapped in past years, but they are found also on trees that have never been tapped. Dr. Huber considers that they are the result of suppressed bud expansion combined with bad tapping, and this diagnosis is supported by Mr. Lewton Brain, the Director of Agriculture at Kuala Lumpur. Dr. Huber further thinks that they may be induced by the action of sun on renewed bark causing an irritation ...... It is worthy of note that in the Amazon Valley, where the trees have been hacked about to a merciless extent by the use of the small axe (*machadinho*), these nodules are practically unknown."

It is interesting, in view of the statement contained in the last sentence, to read a report (2) on the Amazon Valley made by Akers for the Brazilian Government: "The older trees are hacked about in disastrous fashion ...... Naturally the trunks have become a mass of wooden warts with only a thin covering of bark." Again, Akers says later: "At every stroke of the axe the cambium is penetrated ...... Moreover, these gashes in a very short time transform the trunk into a mass of knots and warts, half the size of a man's fist, and over these only a thin covering of renewed bark is formed in the course of the next year or two."

As early as 1877 *Hevea* so deformed had been reported from Brazil. Cross in his report (9) to the India Office says: "From the ground up to a height of 10 or 12 feet the trunk was one swollen mass of warty protuberances and knots covered with thick scales and flakes of dry bark." Aker's statement, that nodules are practically unknown in the Amazon Valley, was made before his visit to report on that place, and appears too sweeping. The " warty protuberances and knots " mentioned by Cross, the " mass of knots and warts " mentioned by Akers, and the presence of nodules in Dutch Guiana reported by the Department of Agriculture there are together good evidence that nodules are not " practically unknown in the Amazon Valley." We may conclude that nodules occur in *Hevea* in its native habitat in Brazil.

Previous Records.

Gnarled stems early attracted attention in the East. Ridley in 1904 was the first to describe (25) knots on Para rubber trees : " They are perfectly harmless, and have no connection with any fungus or insect bite, but are due to the irritation caused by suppressed buds in the stem ...... The only objection to them is that they often interfere with the tapping cut, but they are easily knocked out if so, and if left are usually covered up eventually by the later growth of the trunk and so disappear."

Petch in 1905 published a more detailed description (21) : " The structure of these knots is identical with that of the 'maserknollen' (nodules) of beech and other trees. They are formed in the bark by an adventitious cambium, which has no connection with the main cambium of the stem."

In 1907 Ridley discussed (26) burrs more fully, and adduced some detail in support of his hypothesis, that they are derived from the abnormal development of dormant buds. He mentions that on some trees which had been tapped by the Brazilian method burrs had formed on the tapping cuts, and had later sent forth shoots. In the same Bulletin a correspondent describes nodules as occurring on tapped and untapped trees : the nodule begins as a small globule of wood, and has a spur point penetrating the main cambium and joining up with the wood of the tree. The suggestion is made that the pricker chips off and leaves small fragments of wood surrounded by cambium, and thus these unpleasant growths start.

Petch published a Bulletin (22) in 1909 on "Abnormalities in *Hevea brasiliensis*," in which is given the most detailed description of nodules up to that time, and the question of their origin is discussed. He found that nodules arise wholly in the cortex; they increase in size, and may fuse together to form woody plates; as they increase in size a projecting point appears on the inner surface of the nodule, and grows in towards the wood of the stem, with which it ultimately fuses. "The formation of this point appears to be due to the pressure exerted by the developing core, which apparently prevents the formation of normal cortex between it and the wood of the stem at the points of nearest approach." Latex obtained from the cortex over nodules is often of a yellow or chrome colour. Clots of almost dry rubber were obtained from pockets or cavities occurring where the cortex had died and become separated from the wood of the stem. Cross sections of nodules show a central nucleus of dead bark cells or of stone cells; round these a cambium had been developed, and had given rise to a nodule by laying down wood cells and fibres internally and bark cells externally.

Gallagher in 1909 attributed (11) the formation of nodules to early bad tapping, and believed them to be dormant buds. Later (12) he distinguishes three types of burr: his first two types are simply different stages of our nodule, his third type being the swelling due to the formation of wound wood on the main stem following a wound to the stem cambium.

Bancroft in 1911 published a paper (3) on the occurrence of burrs on *Hevea*. He distinguished between nodules proper and swellings due to wounding the stem cambium. The nodules he attributed to the natural habit of the tree to produce dormant buds, which fail to develop into shoots. These are stimulated to activity by tapping, and give rise to nodules. He mentions the production of woody masses in forest trees as a consequence of wounding or of increased illumination after thinning out; these woody masses originate from dormant buds stimulated to growth. "The burrs on *Hevea* are similar in all respects to these above-mentioned structures. They are in their nature and mode of origin buds which have failed to develop into shoots. The most convincing evidence in favour of this is the abnormal occurrence in which shoots can sometimes be produced from such burrs, there being a definite organic connection between the shoot and the core of the burr."

Petch in his book on *Hevea brasiliensis* (23) considers that tapping has some effect in leading to the formation of nodules, and that there is no support for the statement that these burrs "work out" if left alone. "The production of burrs is not a universal habit of *Hevea brasiliensis*; indeed, they are comparatively rare on untapped trees ...... freedom from burrs is a character which should be required in the selection of seed bearers." Petch comes to the conclusion that burrs are not caused by insects or fungi.

Rutgers in Java, in his description of canker in *Hevea* (27) in 1912, says that nodules are an after-result of an attack of canker. From behind the canker areas a brown colouration spreads out in streaks; these streaks reach the inner cortex and then expand and discolour large areas. These brown-coloured streaks and areas are composed of dead cells, and they remain in the bark long after the external cankered area has disappeared. They are apparently not caused by the fungus itself, but rather by poisonous products emanating from the fungus. The living cells round these dead areas begin to divide, and ultimately nodules are formed. Nodules are thus a secondary result of an attack of canker. Rutgers does not explain how the poisonous products, in their passage through the tissue intervening between the cankered area and the inner cortex, leave that intervening tissue unaffected. This appears to be a serious objection to his hypothesis.

Bateson translated (4) and discussed Rutgers' paper in 1913. Later he published a discussion (5) on the formation of nodules, in which he records from his observations that nodules arise on old leaf scars, although some occur between old leaf scars, and many occur at the base of old trees, where the leaf scars are totally obliterated. The vascular strand of the leaf passes through the cortex of the main stem and joins up with the central vascular system. When the leaf falls, the part of the strand in the main cortex remains there more or less isolated, and in the further growth of the main stem it loses its connection with the central vascular system. The cells of the strand are carried sideways in both directions, and become scattered in small fragments along the whole length of the leaf scar. These cells are functionless, and may contain easily decomposable substances; the decomposition products would set up a state of irritation in the surrounding cortical cells. These would begin to divide and a cambium would arise, which would form cells round the point of irritation so as to isolate it from the adjacent healthy cells, and so a nodule would be formed. Bateson points out that this theory accounts only for nodules occurring on leaf scars, and suggests that for the formation of a nodule it is probably necessary to have only a small point of irritation; thus, local death of cortical cells, from various causes, might give rise to nodules in areas outside the leaf scars. He states further that this theory does not account for nodules occurring on tapped surfaces, where the cortex containing remains of leaf bundles is pared away.

A short note by Bateson (6) in a later Bulletin announces his discovery that the irritant present in the cortex is the coagulated latex in old latex vessels. This causes burrs to originate in both untapped and renewing bark.

Kuijper in 1913 gave a detailed account of the structure of nodules (16); he mentions the presence of a brown point or line in the centre of the nodule, consisting of ordinary cortical parenchyma cells, and occasionally a single sclerenchyma cell. These are surrounded by wood elements arranged radially round the brown centre, consisting of wood parenchyma with tracheidal elements and libriform fibres. Towards the periphery of the nodule the wood parenchyma is disposed in groups between other wood elements. Cells resembling wood vessels occur. The whole is enclosed by a cambium. The wood fibres are strongly curved and of irregular outline. In the cortex are found brown points and lines consisting of dead cell groups round which cambial activity sets in; this represents the first stage in the formation of a nodule, but the origin of the dead cell groups is obscure. Kuijper, after close examination, concludes that plant and animal parasites play no part, and that nodule formation is induced by tapping or otherwise wounding the tree.

In two later Bulletins (17 and 18) Kuijper considers that the formation of nodules points to the existence in *Hevea* of a strong tendency to produce abnormal growths, this tendency being accentuated by tapping or otherwise wounding the tree. Normally the cortex is subjected to internal pressure owing to the growth in thickness of the wood of the stem. In nodular cortex there is, in addition, the pressure owing to the growth of the nodules. This must have a disturbing effect on the tender cambium of the main stem, and probably this disturbance is manifested in the uneven, pitted, and ridged surface of the wood of the main stem under areas of nodular cortex. He contends that the pricker has no effect in inducing nodule formation in normal trees.

Rutgers and Arens (28), in a paper printed for the Rubber Exhibition at Batavia (1914), discuss nodules as the result of an attack of canker (*Phytophthora Faberi* Maubl.). The fungus kills small points and lines of cortical tissue, and these areas of dead cells act as an irritant on the surrounding healthy cells, which then divide to form a cambium, and so nodule formation is begun. Rutgers, after a short visit, claimed to have found *Hevea* canker caused by *Phytophthora Faberi* in the Federated Malay States; but this cannot be held to be conclusive, as it is not borne out by the work of Federated Malay States mycologists. *Cf.* Brooks (8). The presence of nodules in the Federated Malay States is well known; thus, under the circumstances, canker cannot be satisfactorily considered as the cause of nodule formation.

Richards and Sutcliffe, in the Straits Settlements, in a pamphlet (24) issued in 1914, consider the question of the formation of nodules. They accept Bateson's theory of the development of nodules on old leaf scars, the stimulus to nodule formation being the irritation set up by the coagulation or decomposition of the latex in the fragments of latex vessels remaining from old leaf traces. They apply the theory to the formation only of pea-like nodules. The plate and sheet nodules are formed round the outer latex vessels, as they are gradually pushed outwards and broken up by the new cortex which is continually being formed by the cambium; the stimulus to nodule formation is again the irritation set up by the decomposition of the contents of these latex vessels. In the course of tapping latex vessels may be severed above and below, and the latex in the remaining portion may coagulate or decompose and so inaugurate nodule formation. The latex does not appear to coagulate in the latex vessels, but rather seems to exude into the surrounding cells. The authors admit the difficulty that only a few leaf traces give rise to nodules, and only a few stems tapped or untapped have nodules present; their theory would require nodule formation to be the rule rather than the exception.

Keuchenius (14) in 1914 discussed the effect of the pricker in inducing the formation of nodules, and came to the conclusion that the pricker was the chief agent, but that nodules might also be formed as the result of injury from fungus or insect attack. The pricker, especially if the teeth are blunt, tears the cortex and pushes cells bodily out of position. The pricker marks are healed up in the usual way; a cambium forms round them, which produces cork cells externally, and so closes the wound in the cortex. The bodily displaced cells, however, become a source of irritation to the surrounding cells, which then begin to divide, and so give rise to a nodule. It can, however, no longer be maintained that the pricker is even the chief cause, as the pricker has fallen into almost complete disuse; yet nodules are found on many trees now in tapping, but to which the pricker has never been applied.

Bateson in 1914, in a later Bulletin (7), expands his theory of the origin of nodules. He states that "Coagulation of latex inside the vessels takes place normally in the outer cortex, and does not apparently give rise to burrs. From this it may be inferred that the cells of the outer cortex have lost their power of responding to this particular stimulus by forming a cambium; the cells of the inner cortex being younger are probably more easily stimulated into a resumption of cambial activity." From the evidence adduced later it will be seen that this statement is open to some doubt, as inception of nodule formation was observed to occur almost invariably in the outer cortex.

Bateson cites three causes which may lead to the isolation of latex vessels, stagnation of movement of the latex in the vessels, and consequent formation of nodules; these are (1) leaf-fall, (2) disease, (3) wounds. In the case of disease, healthy patches of cortex may be isolated by the diseased tissue, and in these patches nodules are found. Exhaustive tapping is considered as a further cause of the development of nodules. His conception of root pressure is faulty, and the assumption of a diurnal vertical movement of the latex in the latex vessel under the influence of this root pressure is unwarranted on the evidence led. The evidence cited applies normally to every *Hevea* tree; we would therefore, on this theory, expect to find nodules occurring as the normal condition; actually they are found only on a very small percentage of trees.

In the present Paper a clear distinction is drawn between "nodules" and "globular shoots." By "nodules" is understood the woody structures formed round altered latex vessels. "Globular shoots" are the spherical woody structures formed as the result of the slow growth of dormant buds, which have lost their vascular connection with the stem. These latter comprise the great majority of the structures found in untapped trees.

Macroscopic Appearance.

Plate 1. * Stems with large nodular growths are externally strongly gnarled and warted. The area of stem affected may range from quite a small patch of a few inches across up to an area comprising the whole circumference of the stem to a height of 5 or 6 feet. The surface of the bark is covered with warts and protuberances; deep cracks and fissures abound, from which latex often of a yellow or chrome colour oozes out and coagulates.

Pl. 2. Fig. 1. * In the early stages the nodules are little spherical or elongated bodies of 1 or 2 millimetres diameter, which can only be detected with difficulty. The first outward indications are a slight raising and cracking of the bark. The
Pl. 2. Fig. 1. Pl. 6 Figs 2, 3. * nodules at this stage are like little "peas" of wood lying in the cortex, from which they can easily be "shelled out" with a penknife. The nodule separates from the cortex along the line of the nodule cambium; between this and the stem cambium there is a layer of normal cortex.

Pl. 2. Fig 1. * Where several small nodules occur close together their cambial layers may meet and unite, thus producing a multiple nodule. Pl. 2 Fig 2. × Often a large nodule in its growth meets and fuses with small nodules, which then appear as excrescences of the large nodule.

The older nodular masses vary considerably in size and shape. Some specimens are much developed in thickness, and project very considerably from the surface of the stem; some of these measure 3 or 4 feet in length, 6 or 7 inches in breadth, and 3 or 4 inches in thickness. At other times a plate or sheet of nodular tissue is formed. One such plate at Peradeniya measures 4 feet 9 inches long, 6 inches broad in the middle, and 1 to 2 inches thick.

Occasionally nodules are obtained which exhibit a network shape strongly resembling the network of a latex vessel cylinder in tangential section. This type of nodule exactly represents what would occur were the latex vessels to be encysted by layers of woody tissue, and as will be seen later this appears actually to be the case.

Pl 6. Fig 1. Pl 7. Fig 2. Pl 10. Figs 1, 2. × At a very young stage nodules of only a few millimetres diameter may develop a vascular connection toward the wood of the stem; some nodules apparently never develop any vascular connection. This vascular connection ultimately reaches the wood of the main stem, the cambial layers unite, and the wood of the nodule thus becomes united with the stem wood. As the nodule grows more vascular connections are formed, and thus large nodules become united with the stem wood at many points. In the case of thick, massive nodules large areas of the nodule may become united with the stem wood, but no cases have been observed of complete fusion between nodule and stem. In the case of plate and sheet nodules fusion occurs to a lesser extent, the vascular connections remaining more or less isolated. Hence between such large nodules and the stem wood there are considerable areas of the original cortex.

Similar vascular connections are sometimes developed from the stem cambium and proceed in an outward direction toward the nodule. In addition, the surface of the stem wood is pitted, these pits corresponding in position with the vascular connections from the nodule. The surface of the stem wood

and of the nodule is irregular, corresponding with irregularities on the adjacent cortical surface, the condition being due to unequal cambial activity under the abnormal state of the tissues. The surfaces of nodules are marked with raised
Pl. 2. Figs 1, 2. × ridges running in parallel undulating lines and in places describing whorls. Similar raised undulating lines can be traced on the stem wood in many instances.

Pl. 11. Figs 1, 2. × On cutting into nodular cortex, pockets or cavities of several inches diameter containing rubber are frequently encountered; occasionally these are lenticular in form. Petch (23) states as follows: "I have taken three ounces of almost dry rubber from such a situation." These cavities may have been formed by the rupture of the cortex under the internal strains set up by the developing nodule. Latex would then flow from the ruptured latex vessels into the cavity and would coagulate there. Such pockets of rubber are likewise found in trees subsequent to attack by parasitic fungi, more particularly after attacks of canker (*Phytophthora Faberi*).

Nodules do not extend to the parts of the plant below ground; they are not found on the roots even when these are exposed to the air, though the stem may be badly affected down to the ground level.

Nodule formation appears to spread out in all directions over the stem from the point of origin.

Untapped trees up to eleven years old have been examined in large numbers, but not one case of large, massive nodular growths has been found by the writer on such trees.

STRUCTURE.

Transverse sections of nodules show three zones of tissue :—

(*a*) A central core, dark brown in colour, appearing as a
Pl. 6. Fig 1. Pl. 9. Fig 1. × point or line. It consists of cortical elements, and represents that portion of the original cortical tissue round which cambial activity started in the formation of the nodule.

Pl. 6. Fig 1. Pl. 7. Fig 1 × (*b*) Surrounding the core is a zone of wood elements derived from the nodule cambium. These form the bulk of the substance of the nodule.

Pl. 7 Fig 1. Pl. 21 Fig 1. × (*c*) On the outside is the nodule cambium with the few cortical cells which it cuts off externally.

(a) Central Core.

The central core, in transverse sections, appears to the naked eye as a dark brown point or line, and in longitudinal sections as a brown line or plate respectively. It consists of one or Pl 8. Figs 1.2.3. × several latex vessels surrounded by cortical cells containing a dark brown tannin, and outside these a few cortical cells without tannin.

In normal cortex transverse sections show the latex vessels Pl 3. Fig 1. × disposed in ~~concentric rings~~ parallel rows; thus, in a length of stem they could be represented diagrammatically by a series of cylinders fitting one inside another, but separated from one another by approximately equal spaces. While the latex vessels of any one cylinder branch and anastomose abundantly within that Plate 4. × cylinder, they do not form any connections with latex vessels of neighbouring cylinders. Each cylinder is thus completely isolated from adjacent cylinders. The latex vessels are accompanied by prosenchymatous cells, some of which have a tannin content; such tannin cells are isolated or occur in little rows. The latex vessels with their prosenchymatous cells and the sieve tubes and companion cells pursue a parallel course; when they encounter a medullary ray in their vertical Pl 3. Figs 2.3. × course in the cortex, they diverge and pass round it. In tangential sections, therefore, the medullary rays appear to lie in pockets or enclosed areas formed by the latex vessels, Pl. 3. Fig 4. × prosenchymatous cells, sieve tubes, and companion cells.

In a nodule the central core shows all these points of structure. The latex vessels in the core are derived from Pl. 8. Figs 1.2. × only one latex cylinder, as there is only a single row of them. They are accompanied by prosenchymatous cells, and in longitudinal sections the medullary rays are observed to Pl. 14. Figs 1.2. × lie in pockets formed by the latex vessels, prosenchymatous cells, sieve tubes, and companion cells. The tannin cells here Pl. 8. Fig 1 Pl. 15. Fig. 2. × completely surround the latex vessels in varying numbers, but much more abundantly than in normal cortex. The Pl. 14. Figs 1.2.3. × central core thus consists of a patch of cortical tissue, which has been encysted by the formation round it of a cambium which produces wood cells.

Pl. 12. Figs 1.2.3. Pl. 13. Figs 1.2. Pl. 15. Fig 3. × The presence of latex vessels can be demonstrated by staining and maceration. The rubber content stains pink with tincture of alcannin, and reddish orange with Sudan glycerine, and the characteristic, contorted appearance of a strand of rubber is plainly evident. Digestion of sections in Schulze's maceration mixture for 30 minutes in the cold leaves the rubber content intact, while other cell contents are dissolved. Sections of nodules freshly taken from a tree show that the latex vessel content is already coagulated; no latex oozes out from the cut surface of the central core.

Pl. 8. Figs 1.2. Pl. 9. Figs 1.2.3. * Tannin cells surround the latex vessels of the core in a layer of varying depth. Some cells contain a yellowish tannin, which readily turns blue with ferrous sulphate solution, and appears not to differ from tannin in normal cortex. Similarly, just as in normal cortex, cells with a dark brown tannin content are present. A few of these readily turn blue with ferrous sulphate, but the majority are acted on only very slowly, and apparently contain an insoluble tannin or tannin compound, which is highly resistant even to Schulze's maceration mixture.

In the core the cell walls of the latex vessels, the latex vessel content, and the cell walls of the tannin cells and of the Pl. 9. Fig 2. x neighbouring cortical cells are all of a yellow colour. This colouration appears to be due to the infiltration of some coloured substance. In some places only the middle lamella is coloured, and occasionally the colouring matter is found occupying neighbouring intercellular spaces. Again, only the secondary thickening layers of a cell wall may be coloured. Generally, however, the whole wall is coloured. The colouring matter permeates the tissue in such a way as to suggest diffusion from the latex vessels of the core. The colouring matter is not acted on by iron salts; in a tannin cell the content turns blue, but the wall remains yellow. It is insoluble in alcohol. With 1 per cent. osmic acid the tannin content rapidly turns blue or black, but the walls darken only very slightly and slowly. The yellow colouration is probably due to the production of some decomposition product in the latex vessels; its subsequent diffusion into the surrounding cells results in the staining of the cell walls. This is the first symptom of the change in the latex vessel content. Sections Pl. 17. Fig 1. Pl. 19. Figs 1.2. x of nodular cortex showing very early stages have been obtained; and these show the inception of nodule formation round latex vessels belonging to the same latex vessel cylinder. Some latex vessels are surrounded by cortical cells, whose walls show the yellow colouration only. Round adjacent latex vessels the cortical cells have yellow coloured walls and, in addition, an abundant tannin content. Further, some of these last show cell division beginning in the neighbouring cortical cells. The diffusion of this yellow colouring matter appears to stimulate the cells to the production of tannin; possibly the tannin is secreted as a means of protection against the poisonous effects of the yellow colouring matter.

Pl. 12 Fig 1. Pl. 21. Fig 3. * The cell walls of the latex vessels and other elements in the central core are thickened, often strongly thickened. The cell walls are lignified and take on all the lignin stains. The fact that the latex vessel walls are lignified indicates that the lignification occurs subsequently to the inception of the nodule. The other lignified cells are ordinary cortical cells, and have no resemblance to the stone cells of the cortex; their thickened walls are not striated and pitted as are the walls of stone cells. Stone-cell groups occasionally occur in the core as accidental inclusions.

Pl. 13. Fig 1. * Starch is found in the core in varying quantity, and crystals of calcium oxalate may also be seen.

(*b*) *Wood Elements.*

Pl. 16. Figs 1.2. * These consist of cubical wood parenchyma cells, medullary rays, tracheides, short tortuous vessels, and fibres.

Pl. 13. Fig 1. * The cubical wood parenchyma cells are the first productions of the nodule cambium, and immediately surround the central core. They are disposed in a regular manner radiating out Pl. 14. Fig 2. * from the centre.

The medullary rays are similar to normal medullary rays, * Pl 5. Figs 1.2.3. and also radiate out from the centre. They can often be Pl. 21. Fig 1 } Pl. 7. Fig 2 } * traced continuously from the cortex into the nodule, right Pl. 7. Figs 1.4. * across the nodule, and into the cortex beyond again. The nodule cambium thus lays down medullary ray cells continuous with those in the cortex. This facilitates the transport of food material into the nodule and its storage as starch, which is sometimes very abundant. A little tannin may Pl. 7 Fig 1. * occur in the medullary rays.

Pl. 6 Fig 1. * Near the centre wood vessels are absent, but they are produced in increasing number toward the outside. They are a little narrower in lumen than normal vessels, and are Pl. 16. Fig 2. * extremely tortuous. They have a longitudinal course in the nodule, and terminate abruptly at each end. They have large bordered pits as in normal wood.

Pl. 16. Fig 1. * The libriform fibres are found at the ends of the nodule mainly, where the surface is very sharply curved. At these points wood parenchyma cells are at first produced, but the growth of the nodule entails a very rapid increase in surface. Pl. 9. Fig 3. * To meet this the cambium cells elongate, and cut off correspondingly elongated wood parenchyma cells. The elongation continues, and long prosenchymatous cells are produced. Pl. 9. Fig 1. * These cells are interwoven with one another, due perhaps to irregular elongation or curving of the cambium cells under the internal strains set up in the tissue by the growing nodule. Isolated cells can be obtained by maceration; they exhibit Pl. 16. Fig 1. * many fantastic and bizarre shapes. These are the libriform fibres, but it is possible that in elongating some of the prosenchymatous cells develop abnormal shapes, or that tracheides may also be thus changed.

Over the rest of the surface of the nodule, with increasing girth, the wood parenchyma cells undergo a similar elongation, but to a lesser extent. A cambium cell undergoes for a time ordinary tangential division and consequent elongation; it then divides radially, so that two daughter cambium cells are formed in its place. These undergo the same cycle in the further growth of the nodule.

In large nodules the outer layers are nearly normal. Twisted and curved elements disappear, the vessels pursue a straighter course, and there is little to distinguish the sections Pl. 5. Figs 1, 2, 3. * from normal wood.

The central core is sometimes excentric, owing to more rapid growth on one side of the nodule than on the other.

The starch content of the wood parenchyma and medullary rays is often abundant.

Pl. 6. Fig 1. Pl. 7. Fig 3. Pl. 10. Figs 1, 2. * The vascular connections of nodules, which ultimately join up with the stem wood, are exactly similar to the vascular connections on globular shoots. The vestiges of such vascular connections are frequently found completely overlaid by layers of wood tissue produced in the subsequent growth of the globular shoot. Exactly the same feature is found in some typical nodules, where aborted vascular connections occur completely sunk in the tissue of the nodule. In globular shoots, under suitable change of conditions, growth may be resumed, and disconnected vascular connections again become connected with the stem wood. The vascular connections of nodules arise under conditions of activity in the cortex, and their whole appearance and occurrence suggest a close analogy with those of globular shoots.

(c) *Nodule Cambium.*

The nodule cambium arises from cortical cells, which become active and begin to divide. It cuts off wood cells internally and cortical cells externally, the latter only to a small extent. Latex vessels are produced externally by the nodule cambium only after a long period of division, and then only sparingly. In the cortex overlying old nodules the latex vessels are scanty ; this is very noticeable in sections ; and in the field, in tapping such cortex, a poor yield of latex is obtained. It will be seen from the following that such cortex may with good reason be considered as entirely the product of the nodule cambium.

In normal cortex two zones can be quite clearly distinguished, *i.e.*, the inner cortex and the outer cortex. The inner cortex in longitudinal section exhibits well-developed latex vessels, sieve tubes, cortical cells mostly prosenchymatous, comparatively few cells with tannin content, no stone cells ; and the medullary rays are quite distinct. The outer cortex is marked by the presence of abundant stone cells, fragmentary remains of latex vessels, and abundant tannin cells ; the medullary rays are indistinct, and the cortical cells are hexagonal or isodiametric.

In the cortex overlying old nodules the inner cortex is normal. The outer cortex differs strongly from the normal in the almost entire absence of stone cells and the much greater abundance of tannin cells. The absence of stone cells is very noticeable in cutting sections ; it is extremely difficult to obtain sections of normal cortex, whereas nodular cortex cuts easily. Correlated with the absence of stone cells in the outer cortex are the following:—The medullary rays are distinct, the latex vessels are continuous, and the difference between inner and outer cortex disappears to some extent. There is, however, a slight difference, in that the outer cortex has a greater abundance of tannin cells, and the cortical cells are isodiametric. Such differences in the structure of the cortex, more particularly the absence of stone cells in the outer cortex, could not be brought about by changes in the original cortex. Further, old nodules of large size effectively exclude the stem cambium for contributing cells towards the renewal of the cortex; hence, in the course of time nodules would be exposed by the gradual shedding of the cortex as bark. Tissue thus shed as bark cannot be made good, unless the nodule cambium cuts off cortical cells. The fact that old nodules are not exposed, and the abnormal structure of the cortex covering them, indicate that the nodule cambium produces cortical tissue. This cortex produced by the nodule cambium may become very thick; some specimens are almost twice the thickness of normal cortex.

Pl. 6. Fig. 1. Pl. 7. Fig. 2.

After a longer or shorter period of growth the nodule cambium develops a projection directed towards the stem cambium. The two cambia finally meet, merge into one another, and continue to produce wood cells internally. Thus, a bridge of wood cells is formed joining up the wood of the nodule with the wood of the stem. This may proceed simultaneously at several points on the same nodule and several connections be formed, but these remain isolated, hence the inner surface of the nodule never becomes wholly fused to the wood of the stem. In old nodules there are many connections, but there still remain areas of cortical tissue between the nodule and the stem wood.

The writer has obtained radial sections of cortex in which the inward-growing projection of a nodule had a corresponding projection proceeding outward from the stem cambium to meet it.

Sections show that the inward-growing projection of a nodule may cause the stem cambium to lag behind in activity of division in its vicinity, so that a depression or pit is gradually formed in the stem wood. Generally the abnormal strains set up in the cortex by the growth of the nodule would result in irregular cambial activity, and thus ultimately in a pitted and warty surface. This is probably the mode of origin of the majority of the pittings on the stem wood and on the nodule.

NODULAR CORTEX.

Under this heading will be considered cortex in which
nodules are developing. Sections of nodular cortex showing
Pl. 17. Figs 1,2,3. *early stages of nodule formation can be readily obtained.
Pl. 18. Figs 1,2,3. Round a developing nodule the cortical tissue is much com-
pressed and distorted. Cells are pushed outwards from the
Pl. 19. Fig 1. *centre of formation and come to lie concentrically round the
nodule. Sometimes stone-cell groups are thus displaced and
Pl. 19. Fig 1. *form an almost complete ring, or an entirely complete ring,
round the young developing nodule. It is obvious that the
formation of a nodule sets up in the surrounding cortical
Pl. 20. Figs 1,2,3. *tissue unusual internal strains, which would have an imme-
diate effect on dividing cells and even on mature cells. This
probably accounts for the abnormal shape of cells and the
abnormal curvature of cell walls often seen. The inner
Pl. 21. Fig 2. *cortex is in nearly every case quite normal; nodules originate
in the outer cortex at varying distances from the inner cortex,
Pl. 18. Fig 1. *or very rarely in the inner cortex.

Old nodules are often of considerable size and of various
forms; roughly, they form either plates or rounded masses of
nodule tissue. Sections through the central core show that
Pl. 8. Fig 1. *cell division begins simultaneously round several adjacent
latex vessels in the same cylinder, and that the several cambia
Compare Pl. 37. Figs 2,3. *on coming into contact merge into one another and form one
continuous cambium round the whole. A large nodule in its
development may come in contact with small nodules near it
and fuse with them. This is plainly seen in the external
appearance of some nodules which seem to have small nodules
adhering to them; sections show that the central core of the
small nodule is not connected with that of the large nodule.
Pl. 2. Fig 2. *By such continued fusion, plate or sheet nodules may arise;
but more often these appear to arise by the growth of a nodule
from its point of origin along the ramifications of a latex
vessel cylinder or by simultaneous encrusting of the latex

vessels over a large area. Nodules occur, which branch and have a distinct net structure; there are open meshes where growth has proceeded along the latex vessels only, and left the intervening cortical tissue unchanged. This intervening cortical tissue consists of medullary rays, as the meshes formed by the ramifications of the latex vessels in normal cortex are occupied by the medullary rays.

Pl. 15. Fig 1. x In gouging a nodule out of the cortex a brown point is frequently observed at each end of the nodule, and this is seen to coincide with a similar brown point in the cortex. These brown points are the altered latex vessels and their neighbouring cells. The central core of the nodule is here continuous with the cortical tissue; the nodule would probably continue its growth along the latex vessels thus altered.

In nodular cortex, which is still more or less normal, longi- Pl. 6. Figs 2, 3. Pl. 19. Fig 3. x tudinal sections show the presence of vertical areas of abnormal tissue consisting entirely of parenchymatous cells. These areas differ from the surrounding tissue in being free from tannin and stone cells, and in having abnormally curved cell walls. They appear to arise as the result of indefinite cell division over a small area, and occur generally between the inner and outer cortex. The medullary rays are quite distinct in the cortical tissue on either side of the abnormal area, and can sometimes be traced through it. This indicates that these areas arise subsequently in the cortex. They stand out prominently in sections as white areas amid the surrounding tannin-stained tissue. It might be suggested that the cortex is stimulated to this indefinite cell division by the presence of irritant substances diffused from the altered latex Pl. 18. Fig 1. x vessels, or that bud primordia are stimulated to growth and Pl. 14. Fig 1. develop abnormally. x Such abnormal areas have no definite cambium, and twisted cells with curved cell walls occur, which resemble the twisted tracheides of nodules, but are not lignified. Occasionally these areas are produced in the inner cortex near the stem cambium, when the cells of the inner cortex may be displaced and disposed in undulating lines, giving a tissue which strongly resembles that in the vicinity of developing vascular connections. In one case sections showed a developing bud structure with a definite cambium

Pl. 18. Fig 3. ×situated inside an area of abnormal cortex. In other cases the abnormal areas consist of twisted and curved cells with abundant tannin content; often these cells are disposed in the form of a whorl, and have been derived from cortical cells by indefinite division, the tannin content apparently not having any inhibitory action on cell division. The cortical cells surrounding abnormal areas always have an abundant tannin content.

Pl. 17. Fig 3 Pl. 18. Figs 1, 2. × A case was observed where altered latex vessels occurred in the inner cortex near the stem cambium; they were surrounded by a layer of tannin cells, and cell division had just set in. The same section showed a developing globular shoot with its vascular connection almost joined to the stem wood, the whole being in contact with some altered latex vessels in the inner cortex. This appears to be a satisfactory case of the production of a globular shoot from an adventitious bud in tissue stimulated to activity by the presence of altered latex vessels.

Sections of both nodular cortex and normal cortex frequently exhibit brownish-coloured streaks. These coloured streaks are most abundant in nodular cortex, and occasionally are seen in the above-mentioned areas of abnormal tissue and near developing nodules. This brown colouration appears to be confined to the walls of the latex vessels; it gives no reaction with iron salts.

Pl. 9. Fig 2. × The bright yellow colouration and highly refractive walls of altered latex vessels in nodular cortex are quite distinct from the brownish-coloured cell walls above described. The yellow walls of latex vessels in nodular cortex have no doubt some connection with the chrome-yellow latex sometimes obtained from nodular trees; normal latex is white. It would appear probable that some substance in the altered latex vessels of nodular cortex is of a yellow colour, and imparts this colour to the walls. In some cases nodular cortex yields a normal white latex; here probably the alteration of the latex vessel content has ceased.

Nodules to a small extent are shed with the bark scales. On old *Hevea* trees in the Royal Botanic Gardens, Peradeniya, the writer has found dead nodules of fair size in dead bark scales which were on the point of dropping to the ground. One such nodule was 2 inches long. Other large nodules were

Compare Pl. 39. figs 2, 3. Pl. 40. figs 1, 2, 3.

partially protruding from the bark, and were exposed on their outer surface. The exposed side was dead and dried up; the inner side was still in living connection with the cortical tissue. It would be merely a matter of time till these nodules dried up completely and fell away with the bark scales. The writer has observed a similar condition on trees on estates, where the trees were much younger. In both cases other nodules were present which had joined up with the stem wood.

In cutting sections of nodular cortex one may find, in the outer cortex, small reddish-black points, which are extremely brittle, and crumble away before the razor. They appear almost as foreign bodies lying in the cortex, and easily separate from the surrounding tissue. They consist of portions of the cortex, including abundant stone cells and some cortical cells and latex vessels, all saturated with tannin. Sections can with difficulty be obtained, and require treatment with concentrated nitric acid to render them transparent, the tannin being then dissolved. Stone cells are by far the most abundant; the remaining tissue is normal. The tannin here is probably secreted as a means of protection against some injurious effect emanating from these points. The nature of these reddish-black points has not been determined.

Nodules in Untapped Trees.

The first material collected from an untapped tree consisted of two specimens obtained from near the base of a five-year old *Hevea* on the Government Experiment Station at Peradeniya. Sections of these showed no latex vessels in the core, and the tannin cells so characteristic of nodules were entirely absent. These specimens were undoubtedly globular shoots derived from latent buds.

It became evident that the statement that nodules occur on untapped trees required some definite proof of its accuracy. Accordingly, 2,000 trees seven years old and untapped were examined. These trees formed part of a field on an estate. The result was as follows :—

121 trees had globular shoots, *i.e.*, 6·05 per cent.

6 trees had nodular structures of various types, *i.e.*, ·30 per cent.

No trees had true nodules.

In the 2,000 trees not one case of large nodular masses was observed, nor have such cases ever been noticed in untapped trees examined on many estates in various parts of Ceylon. It may be objected that untapped trees are too young to show nodule formation on a large scale. On one estate eleven-year old trees which had been in tapping only two weeks were examined; no trees showed large nodular masses. On the Experiment Station, Peradeniya, six-year old trees were brought into tapping in 1910, and in 1912, when eight years old, had developed large nodular masses in many cases. Tapping thus apparently supplies conditions favouring the rapid growth of nodules, though it is not necessarily an essential factor in their inception, and age is a negligible factor.

Nodules can be distinguished from globular shoots with certainty only under the microscope. A nodule when cut Pl. 6. fig 1. × through the centre exhibits a dark brown point or line at the centre of the cut surface, and this can be used as a rough means Pl. 28. fig 2. × of distinguishing it from a globular shoot, which has no such colouring. In the nodule the dark brown colour is due to the presence of the tannin cells surrounding the altered latex vessels. Globular shoots in untapped trees have evidently been frequently mistaken for nodules, and probably are usually the bodies in question when nodules are stated to occur in untapped trees.

Of the six cases of nodular structures obtained in the 2,000 untapped trees, three were found in the callus at the edge of Pl. 23. figs 1.2.3. × Pl. 24. figs 1.2. long vertical wounds. In these the structure was not typically nodular; the rubber strands in the core occupied a cavity into which the latex had evidently oozed and coagulated. The cavity may have originated through internal lesions in the cortex, or through slight wounding by some external agency.

Pl. 22. figs 1.2.3. × In the fourth case there was a large cavity filled with rubber at the base of a globular shoot; the cavity was closed over by subsequent layers of wood elements. The wood tissue of the structure at this point showed signs of a former callus nature, and without doubt this was a case of a globular shoot which had become exposed, possibly through the natural shedding of the bark, or through some injury, as this case was obtained from the callus of a vertical wound. This exposure was accompanied by outpouring of latex, and the callus formed at the exposed area of the globular shoot included the coagulated latex in the process of occlusion.

Pl. 27. Fig 1,2. * The fifth case showed no central cavity. In its place there was a core resembling somewhat a leaf-trace and coloured greenish-yellow like the colour of latex vessels in the core of true nodules. Surrounding this core was a shallow layer of tannin cells. Maceration failed to disclose the presence of rubber in the core.

Pl. 26. Fig 1,2. * The last case had a core composed of a fairly large portion of cortical tissue with several stone cells present. Maceration showed up two small particles of rubber indicating the presence of latex vessels, but these were in nowise altered, and cannot be taken as being the cause of the formation of the woody sphere. Surrounding the core, again, was a shallow layer of tannin cells, and the neighbouring wood tissue also had a considerable number of cells with tannin contents.

These last two cases are of considerable interest, as here we have instances of the encysting of cortical tissue under conditions other than the alteration of latex vessel content. This condition approaches very closely the condition in beech nodules described by Krick (15).

Here may be mentioned another type of nodule found in nodular trees generally and of not uncommon occurrence. In this type maceration of transverse sections shows the cells Pl. 25. Figs 1.2.3. * of the core embedded, so to speak, in rubber. There is no lesion of tissue. The latex has apparently oozed out of the latex vessels and coagulated in the neighbouring intercellular spaces. Richards and Sutcliffe (24), amongst an excellent series of microphotographs, show a good example of this type of nodule.

Globular Shoots.

Pl. 28. Figs 1,2,3. * Under globular shoots are considered those spherical woody bodies which are found isolated in the cortex, and do not possess a core as in nodules.

Where *Hevea* has been pollarded, strongly growing adventitious shoots develop just below the cut surface. They appear at first as spherical woody protuberances, which attain some size, and then send out a shoot. The protuberances in early stages have no connection with the stem wood, and therefore are derived from dormant or latent buds, and not from adventitious buds, which arise endogenously, and would thus have their vascular strand in connection with the vascular system of the stem. Very often the spherical woody body produced by the continued growth of such dormant buds, after they have lost their connection with the wood of the stem, can be detected at the base of shoots developing near the cut surface of pollarded trees. Sections through such developing shoots show that they consist of wood parenchyma, wood fibres, tracheides, and vessels. The tracheides are curved and the vessels somewhat tortuous, but they are continuous. Later a vascular strand, consisting mostly of tracheides and wood parenchyma, connects the developing shoot with the stem wood. In the centre of the base of the shoot the fibres are much curved and irregular, but become normal in the outer layers, the irregular structure indicating the position of the spherical woody body from which the shoot developed. The vascular connection with the stem wood is formed by a growing point directed inwards from the developing shoot tissue towards the stem wood.

Sections show that the spherical bodies are composed of twisted tracheides and wood fibres, with here and there a tortuous vessel, the several elements being interwoven in a highly irregular manner at the centre and becoming normal towards the outside. A cambium is present which produces a small amount of cortical tissue and latex vessels, the latter being determined as the product of the nodule cambium by their concentric disposition round the spherical body. On the inner side and directed towards the stem there is frequently a tapering point consisting of wood elements and resembling closely the vascular strand of a shoot. This undoubtedly represents the former connection with the wood, but in many cases it is entirely wanting. In some of these cases sections disclose the former connection completely sunk in the tissue of the spherical body; the tapering point has ceased growth, and has been covered over by the subsequent layers of tissue laid down by the cambium of the spherical body. In other cases no trace of a former connection can be found, and here no doubt the bud primordium has lost connection with the stem at a very early stage before the appearance of vascular elements in the connection. Occasionally, amongst the last-named cases, a small protuberance may be found on the surface of the spherical body, apparently an attempt by the spherical body to develop a vascular connection with the stem. Under favourable conditions, as, for example, if the tree were pollarded, this protuberance would join up with the stem and the spherical body would grow forth as a shoot. Some specimens of these spherical bodies have vestiges of a shoot directed outwards, and sections have been procured which show a typical vegetative cone with leaf rudiments and rudimentary axillary buds.

The spherical bodies are thus shoots, and might be called globular shoots, as described by Strasburger (29). The sprouting of nodules mentioned by Ridley (26) and Bancroft (3) were probably cases of globular shoots stimulated to further growth by changed conditions. A specimen at Peradeniya shows a globular shoot of spherical outline without any external vestige of a connection with the stem, which has developed a shoot 4 inches long bearing a small leaf at its apex.

The material collected from the 2,000 untapped trees already referred to was classified as follows :—

(1) Material collected from old leaf-scars.
(2) Material collected from areas where the bark exhibited no marking.
(3) Material collected from wound callus.
(4) Material collected from the fork of trees with forked stems.

(1) *Material from Leaf-scars.*

The leaf-scars remain distinct on old stems up to six or seven years of age; they appear as a horizontal line of depression 4 or 5 inches long, with a shallow pit in the middle. Generally, buds if present are dormant, and give no external evidence of their presence. In some cases, however, these dormant or latent buds of the old leaf axils lose their connection with the stem wood, but continue a process of growth, (Pl. 28. Fig 3.) × which results in the production of globular shoots lying isolated in the cortex. These bodies vary from the smallest (Pl. 29. Fig 1. Pl. 33. Fig 3. Pl. 40. Fig 1.) × size up to 3 or 4 centimetres diameter, and may be single, or several may be fused together in a horizontal row along the leaf-scar. Globular shoots have been obtained from the cortex of seven-year old trees; hence the rate of development appears to be much more rapid in *Hevea* than in the beech, where similar bodies are found.

(2) *Material collected from Areas where the Bark exhibited no External Marks.*

This material agreed with the leaf-scar material; in fact, it is highly probable that it should be considered as leaf-scar material, the leaf-scars having disappeared in the older bark from which this was obtained. Cases occurred where the globular shoots had fused together in a horizontal row, exactly as in the case of leaf-scars.

(Pl. 39. Fig 1.) × Two specimens were obtained which showed a deposit of tannin in scattered cells in the centre. This unusual secretion of tannin may have been due to conditions present before the latent bud had resumed activity resulting in the formation of a globular shoot. The tannin content was light coloured and readily turned blue with ferrous sulphate solution.

These first two classes of material comprised nearly the whole of the collection from the 2,000 trees.

(3) *Material collected from Wound Callus.*

Only seven specimens were obtained, and these were typical globular shoots save one, which was considerably elongated.

(4) *Material collected from the Fork of Trees with forked Stems.*

A few globular shoots were obtained which resembled in all respects leaf-scar and wound-callus material.

Trees are frequently seen which have been blown over by the wind or have otherwise been caused to fall; they may have only a few lateral roots still in the ground, yet along the whole upper surface of the stem a copious production of new shoots occurs. These are derived from the latent buds which are stimulated to growth by the altered conditions. This indicates the readiness with which *Hevea brasiliensis* responds to changed conditions, the latent buds and globular shoots if present growing out into normal shoots. Similarly, standing trees if scorched by fire throw out large numbers of shoots from the adjacent unharmed cortex.

On leaf-scars a row of globular shoots may be found fused together to the number of five or six individual shoots; this demonstrates that several buds are laid down in each leaf axil and remain latent, unless conditions change and become suitable for a resumption of activity.

In both tapped and untapped trees globular shoots are occasionally obtained which have a central core of very small Pl. 31. figs 1,2,3. Pl. 32. figs 1,2. Pl. 33. figs 1,2,3. × cells with strongly thickened walls. In these the vascular connections are completely wanting, nor do any cases occur where the vascular connection has been covered over in the subsequent growth of the shoot. Here undoubtedly the bud has lain dormant for some time and has slowly developed thickened walls, while at the same time the pressure of the surrounding tissue has prevented the cells from increasing in size. The absence of any point which might represent a vestigial vascular connection with the stem shows that the bud early lost connection with the stem and remained in a completely dormant state. Later, under some change of conditions, cell activity set in in the cells adjacent to the mass of small thickened cells of the bud, and resulted in the production of a globular shoot.

Pl. 30. figs 1,2,3. × Many globular shoots consist entirely of wood elements, more or less tortuous, and show no traces of a former connection with the stem wood. In these the bud primordium may have become separated from the stem wood at a very early stage before the vascular connection had become differentiated into wood elements.

In the course of growth globular shoots are pushed outwards, Pl. 40. figs 1,2,3. × and may come to have their outer surface exposed. In many Pl. 33. fig 1. Pl. 39. figs 2,3. × cases the exposed surfaces are again covered over with tissue, but they are readily distinguished in sections owing to the abundant deposit of tannin in the adjacent cells, and the arrangement of the cells in the covering layers as in the callus in wounds. Latex may ooze out and coagulate on the exposed surface and later be included within the covering layers, and thus give the structure a fictitious resemblance to a nodule.

Large nodules in their development may meet with globular shoots, or may stimulate dormant buds to activity. These fuse with the tissue of the nodule on coming into contact with it, and later throw out vascular projections towards the stem wood. In some cases vascular projections might already be present when fusion occurred with the nodule. This does not account for all vascular connections of nodules, as in some nodules the vascular connection can be traced right into the (Pl. 10. Figs 1, 2. ×) altered latex vessel region of the core. It is possible, however, that even in these cases, at the inception of cell division near (Pl. 18. Figs 1, 2. ×) the altered latex vessels, a bud primordium was present, or that the cortical cells on being stimulated to activity developed bud or shoot characters.

Globular shoots never develop into large masses of woody tissue. The largest specimens obtained measured approximately 1 inch in diameter.

General.

Isolated wood bodies occur in the cortex of other trees. Sorauer's investigations (19, p. 183) on nodules in apple trees showed that the central core consisted either of hard bast elements or of cortical parenchyma cells ; the outer layers of wood elements were similar in structure to the wood elements of *Hevea* nodules. Sorauer was of opinion that apple nodules arise as a consequence of wounding, as they are readily formed in the vicinity of wounds. He describes short woody strands which he found in the cortex of pear trees ; these had a central core as in apple nodules, but the wood elements were arranged parallel to those in the adjacent wood. Sorauer considered these strands to be new formations.

Krick (15) minutely described the woody nodules found in the cortex of the beech, and distinguishes two types : (1) nodules bearing buds or shoots ; the wood of the bud or shoot can be traced continuously right through into the nodule ;

and (2) nodules independent of buds, which are again divided according as the central core consists of wood elements, of bast elements, and of cork tissue. Wood elements form the core in the majority of nodules, cork tissue is found in some, and bast elements were observed in only a single case. The nodules which occur in connection with dormant buds or abortive shoots, which have subsequently become separated from the stem wood, must be clearly distinguished from those nodules which originate as isolated bodies in the cortex. Krick thus considers beech nodules to arise from dormant buds and abortive shoots, or to be new formations.

Frank (10) comes to a similar conclusion from his own observations, and from a discussion of the papers of Krick, Sorauer, and earlier authors.

Under Kuster's (19) arrangement of plant pathology *Hevea* nodules would come under Hyperplasie, sub-section Heteroplastic Tissue, and would be classed near wound wood as "tissue resembling wound wood," included in which section are nodules of beech, pear, and apple. This classification is not quite satisfactory, as the structures described as "tissue resembling wound wood" appear sufficiently distinct to merit a more detailed definition.

The presence of globular shoots in *Hevea brasiliensis* can be fully accounted for within the normal life of the plant. "Every plant-body forms more primordia of organs than it is able to bring to maturity. Just as by far the greater number of seeds which are annually formed are destroyed, sometimes because they do not find favourable environment for their development, sometimes because they are overcome by other organisms in their 'struggle for existence,' so also some of the primordia of organs remain undeveloped because the plastic material which they require for their unfolding is taken by others which exercise a stronger attraction upon it" (Goebel, p. 207). Thus, of the buds laid down in a leaf axil one develops into a shoot, while its correlation with the other buds in the leaf axil results in their suffering arrest in development. That these arrested buds remain capable of development is seen in the abundant production of new shoots from old stems under suitable change of conditions; consequently these buds experience only temporary retardation. At a later date they may begin a slow process of growth, but having lost their connection with the stem and receiving an inadequate supply of food material, they are unable to develop normally, and thus globular shoots are produced.

The case of nodules is somewhat different, and here we undoubtedly have a new formation. The production of these nodular bodies is induced by a definite determining cause, namely, the alteration in the latex vessel content, where under normal conditions they would not be produced. As this alteration in the latex vessel content advances along the latex vessels, it is accompanied by the laying down of nodular wood round the latex vessels; this is illustrated in the flat plate-like nodules of net structure with projecting points at the top and bottom ends.

In tapping operations on estates numerous opportunities occur for the transference of this abnormal nodular condition, if it is transferable, from affected trees to non-affected trees. From the small number of trees affected it must be concluded that it is not transferable, but rather that affected trees have a predisposition to alteration in the latex vessel content. This would affect estate practice, in that great care should be taken to select seed for planting from trees free from nodules, as recommended by Petch in 1906.

The question arises as to whether the alteration in the latex vessel content is brought about by external causes or by unknown internal influences; it must be admitted that this point is still obscure. The evidence, however, lends support to the view that wounding (*e.g.*, tapping) has some effect in inducing the alteration in the latex vessel content in trees which are predisposed to this condition. In support of this view we have the fact that out of a large number of untapped trees systematically examined not one showed development of nodules, though this number includes trees up to eleven years of age. Out of 2,000 untapped trees eleven years old, six yielded nodular structures of about the size of a pea. Microscopic examination showed in four trees, where the structures were obtained from wound callus, that the structures were built up round cavities filled with coagulated latex.

Thus, in the absence of altered latex vessels in the core, these are not typical nodules, nor are they to be classed with nodules. In two trees structures were obtained which showed the central core to be composed of portions of cortical tissue without latex vessels, and thus these differ still more widely from typical nodules. These latter were obtained from the cortex where the bark had no special markings externally.

It would appear therefore that *Hevea* cortex is capable of developing woody bodies as the result of various disturbances in the cortex.

In the production of vascular connections with the stem nodules may exhibit a sort of polarity, as in the production of vascular connections by globular shoots on their inner surface. Some of the vascular connections of nodules may be derived from latent buds or globular shoots which have been caught up and absorbed by the nodule in its development.

There still remains to be determined the nature and cause of the alteration in the latex vessel content, and any advance in this direction will depend on advance in our knowledge of the constitution of latex and its function in the internal economy of *Hevea brasiliensis*.

Summary.

1. Nodules are produced in the cortex of *Hevea brasiliensis* as the result of an alteration in the latex vessel content.

2. This alteration has not been connected with the attack of any parasitic organism, but appears rather to be due to physiological changes in the latex.

3. The tendency to suffer alteration in the latex vessel content appears to be confined to certain individual trees which have a predisposition to develop this condition.

4. Four types of nodule have been distinguished :—

- (*a*) Nodules formed round altered latex vessels.
- (*b*) Nodules formed round lesions in the cortex into which latex has oozed and coagulated. May occur in any *Hevea* tree.

(c) Nodules formed round areas into which latex has oozed and coagulated ; the coagulated latex occupies the intercellular spaces without lesion of tissue. May occur in any *Hevea* tree.

(d) Nodules formed under unknown conditions round areas of cortex from which latex may be entirely absent. Rare.

5. Globular shoots formed by the subsequent growth of latent buds after these have lost their connection with the stem occur in both tapped and untapped trees. They are distinguished from nodules by the absence of a core, and never form large masses of woody tissue as nodules do.

6. Nodules do not occur on untapped trees.

7. Nodules occur on *Hevea* in its native habitat in Brazil, and in Tropical America and the Eastern Tropics where it has been grown in plantations.

8. The percentage of trees which develop nodules is very small.

9. Tapping appears to induce nodule formation in predisposed trees.

10. This abnormal condition is apparently not infectious.

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On the Formation of Nodules in the Cortex of Hevea brasiliensis.

Appendix. (Unpublished).

Globular Shoots.

It has already been indicated that globular shoots are found in the cortex generally, and also in special positions as in leaf scars, in wound callus and in the fork of branches. In the case of material found in leaf scars it may be concluded that it is derived from latent buds, which have been laid down in the axil of a leaf primordium but failed to develop into shoots, and, having in due course lost their vascular connection with the stem wood, by a slow process of growth have developed into roughly spherical bodies of wood tissue.

Examples of leaf scar material are to be seen in Plate 29, Fig. 1, and in Plate 33, Fig. 3. In the former a globular shoot is seen in section, the apex being directed toward the stem wood and the base toward the exterior, while the whole is surrounded by the cortex. The apex is the vestige of the lost connection with the stem, and from it, traversing the globular shoot, runs what may be termed the bud trace or vascular strand, now completely enclosed by layers of wood tissue. On reaching the cortex the bud trace expands into a more or less spherical or conical mass of small-celled cortical tissue, which may be considered as the vegetative point of the globular shoot (Plate 41, Fig. 1. b). In Plate 41, Fig. 2. b and Fig. 3. b, this vegetative point has maintained an activity of cell division and growth sufficient to form a vascular strand of some length, travers[redacted] the stem cortex and directed toward the outside, and to well in advance of the main mass of woody tissue of the globular shoot. which

This may be taken as a simple case of the effect of correlation in growth between buds. The leaf scars on the bark of old trees must have originated when the main stem was of a corresponding height and was clothed with leaves. In other words the leaf scars originated when the tree was one or two years old. They persist and can be found in many trees up to about 10 years of age. The primordia from which the globular shoots are derived were accordingly laid down at the vegetative point of the leading shoot of the main stem, when the tree was one or two years old and was growing vigorously. Of the 4 or 5 primordia laid down in a leaf axil, that one which first started growth and thus got ahead of the other [redacted] primordia of the same leaf axil, would attract more and more of the plastic material supplied to the growing point, and would ultimately become a vigorously growing shoot. The unsuccessful [redacted] primordia deprived more and more of the plastic materials supplied to the growing point suffer an arrest in development and pass into a latent condition; being, however, still capable of growth, and as small quantities of plastic material reach them, they commence a limited process of slow growth, which amounts only to the slow accretion of layers of wood tissue round the primordium. Thus in the present instance the primordium was laid down about 6 years before, and the globular shoot when collected measured only about 3 mm. diameter. It is evident that slight variations as to the length of time the primordia in the axil of any leaf primordium are fully supplied with plastic material will result in their reaching different stages of development. Goebel states (Organography of Plants Pt. 1. p. 57) that "arrest may take place earlier or later in one and the same organ, and consequently the construction of arrested organs varies in an extraordinary degree". The point of time therefore, at which one primordium gets ahead of the others and causes arrest in their development, determines the degree of development of the other primordia at which they enter on the globular shoot stage. In the latter of two cases referred to above namely Plate 33, Fig. 3, the primordium has not reached as advanced a degree of development as in the case of Plate 29, Fig. 1. Indeed the primordium has remained an undifferentiated meristem, until in the course of time, slow growth has transformed it into a globular shoot, consisting merely of a spherical mass of undifferentiated wood tissue enclosing a core of compressed and lignified cells, which represent the original primordium.

In the two cases discussed above, both collected from old leaf scars, we have two types of globular shoot derived from latent buds. In the case of globular shoots collected from the general cortex, these may partly be derived from cortex which has lost the external marks of its leaf scars, and they would then owe their origin as in the previous cases to latent buds. The origin of other globular shoots may reasonably be attributed to the formation of adventitious buds in the cortex, under conditions which do not permit of their development into normal shoots. Globular shoots are therefore to be considered as having arisen from primordia laid down either originally at the vegetative point or later on adventitiously in the cortex.

Globular shoots, which have reached a more advanced stage of development than that illustrated in Plate 29, Fig. 1, are to be seen on Plate 34, Fig. 1, 2, 3, and Plate 35. The vegetative point is clearly present, and the primordia of organs are distinct. It is to be expected that such globular shoots, given conditions favourable to sprouting, would send out a shoot as in the globular shoot on Plate 42. This last example in section exhibited a mass of wood tissue similar to that in the globular shoots on Plate 28, Fig. 3, the leafy shoot arising exogenously from the globular woody tissue.

Primordia may be laid down in close proximity to one another in the cortex, as will be seen from the proximity of the globular shoots in Plate 28, Fig. 3. Fusion frequently occurs when two such globular shoots grow into contact with one another. Fusion may occur at a much earlier date, and a globular shoot with an apparently double core be thus produced as seen in Plate 37, Fig. 2, and Fig. 3. In some cases the original primordium has not been completely converted into wood tissue as in Plate 31, Figs. 1 and 2, Plate 32, Figs. 1 and 2, Plate 33, Fig. 3. The cells of the meristem have probably lain dormant for a considerable period during which time the pressure of neighbouring tissue has compressed the cells, which have in addition become lignified, till some change to more favourable conditions has occurred and growth has been resumed with the formation of a globular shoot. Other globular shoots exhibit a core of considerable size of apparently unchanged meristem (Plate 38, Figs. 2 and 3, Plate 39, Fig. 1), in which cases it may be assumed that growth was very slow, but that it commenced at an early date after separation from the parent vegetative point. The supply of plastic material must have been considerably reduced, as with even a moderate supply it is to be expected that some growth in length would be possible and consequently that a vascular strand would be produced. The absence of any compression of the core cells or of lignification of the walls in Plate 38, Fig. 2 would indicate that the meristematic mass did not lie dormant for any considerable period. In Plate 38, Fig. 3, the cell walls of the core are somewhat lignified, indicating subsequent lignification or some delay in the resumption of cell division after separation from the vegetative point.

The globular shoots in Plate 33, Figs. 1 and 2 have developed wood tissue from almost the whole of the original primordium. Again in Plate 30, Figs. 1, 2, and 3 practically no trace of the [redacted] primordium remains.

Globular shoots are thus derived from [redacted] primordia which, when first formed, suffered an arrest in development due to correlation in growth with adjacent and more vigorously growing organs or primordia of organs, and later having lost their vascular connection with the stem and being furnished with meagre and uncertain food supplies are capable only of limited growth.

PLATE 1.

Plate 1.

Nodules on Hevea stem 2 years after
inception.
From a negative in the possession of
Mr. T. Petch.

PLATE 1.

Plate 2.

Fig. 1. Nodules extracted from Hevea cortex. x 1.
Fig. 2. Nodules extracted from Hevea cortex. x ½.

From negatives in the possession of Mr. T. Petch.

(a) Surface markings.
(b) Multiple nodules.
(c) Nodules lying in cortex.
(d) Interior surface.
(e) Exterior surface.

PLATE 2.

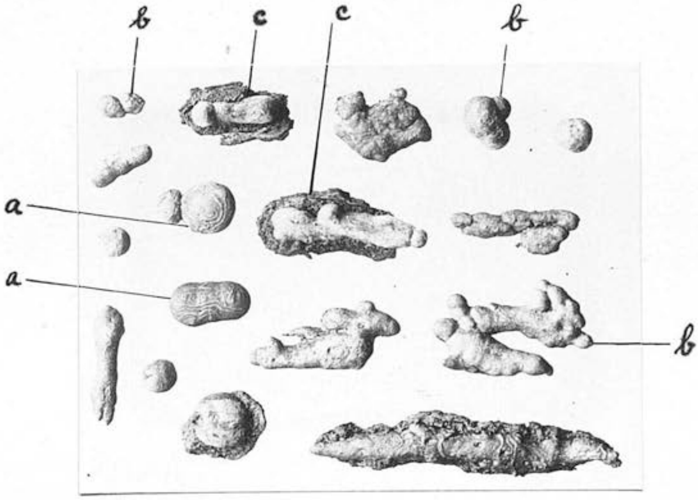


Fig. 1.

Fig. 2.

Plate 3.

Fig. 1. Normal cortex. Trans. Sect.x 10.
Fig. 2. Normal cortex. Tang. Sect. x 35.
Fig. 3. The same x 200.
Fig. 4. Normal cortex. Note tannin cells. Tang. Sect. between latex vessel rows. x 35.

(a) Inner cortex.
(b) Outer cortex.
(c) Stem cambium.
(d) Latex vessel rows.
(e) Stone cell groups.
(f) Latex vessels.
(g) Medullary rays.
(h) Vestiges of separating wall between adjacent latex vessels.
(i) Coagulated latex.
(k) Tannin cells.

PLATE 3.

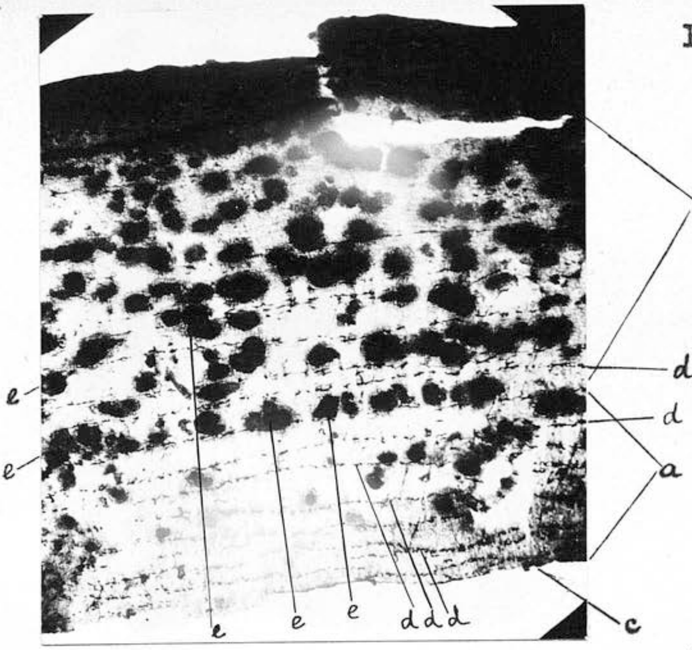
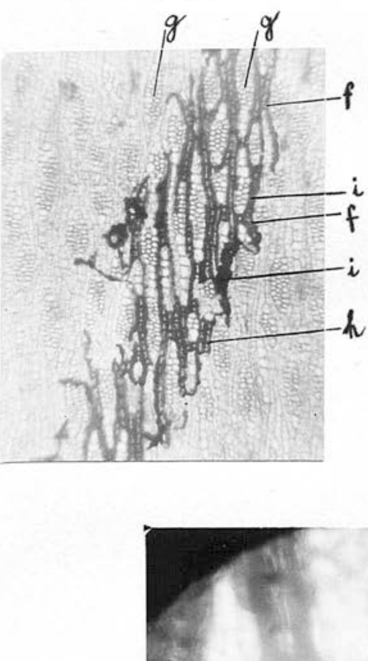


Fig. 1.

2.



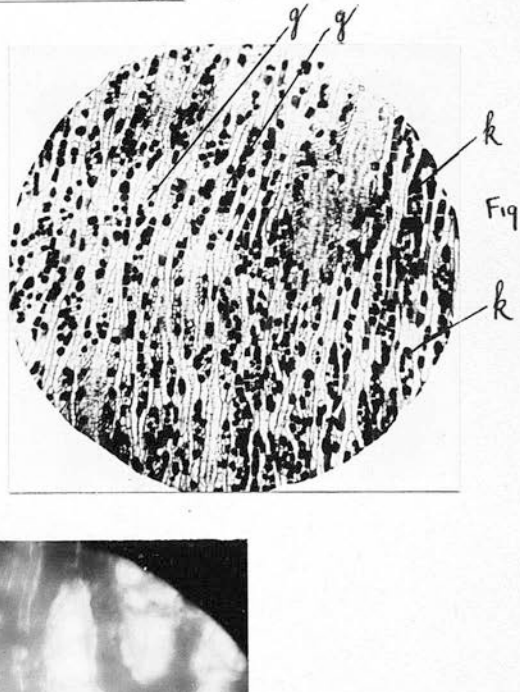


Fig. 4

Fig. 3.

Plate 4.

Normal cortex. Radial Sect. x 35.

(a) Inner cortex.
(b) Outer cortex.
(c) Stem cambium.
(d) Latex vessels containing coagulated latex.
(e) Stone cell groups.
(f) Medullary rays.

PLATE 4.

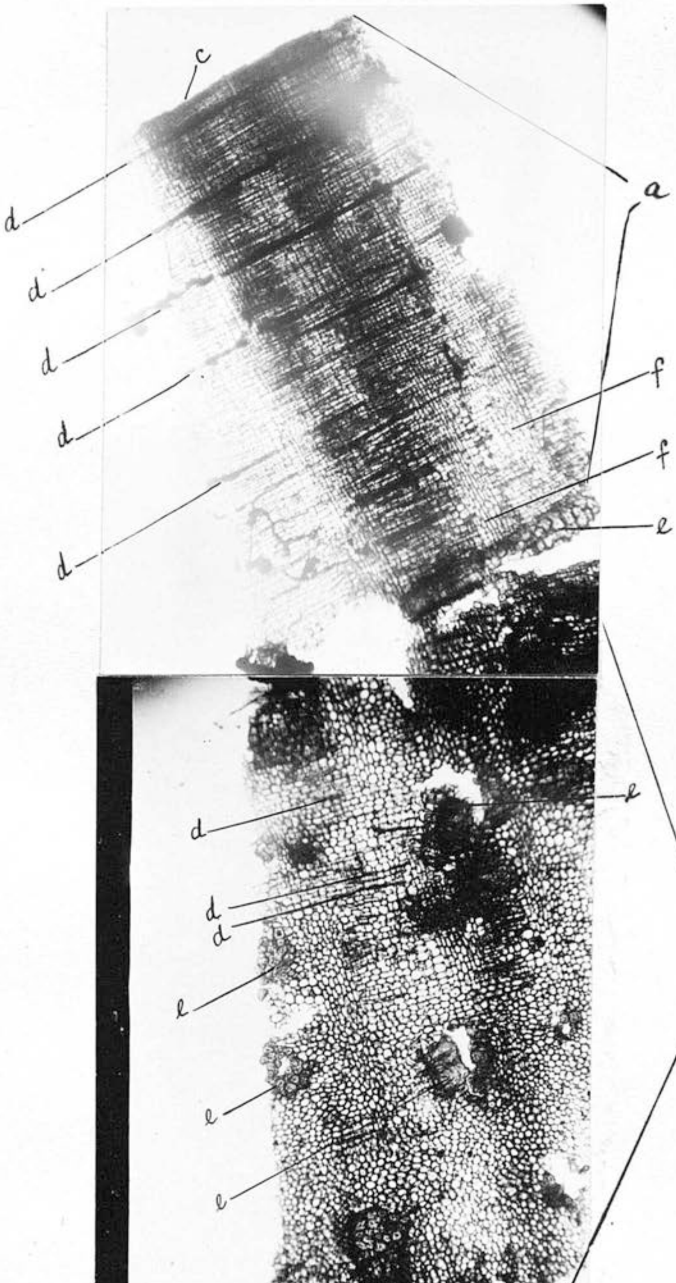


Plate 5.

Fig. 1. Normal wood. Trans. Sect. x 120.
Fig. 2. -do- Radial Sect. x 30.
Fig. 3. -do- Tan. Sect. x 30.

(a) Vessels.
(b) Wood fibres.
(c) Medullary rays.
(d) Wood parenchyma.

PLATE 5.

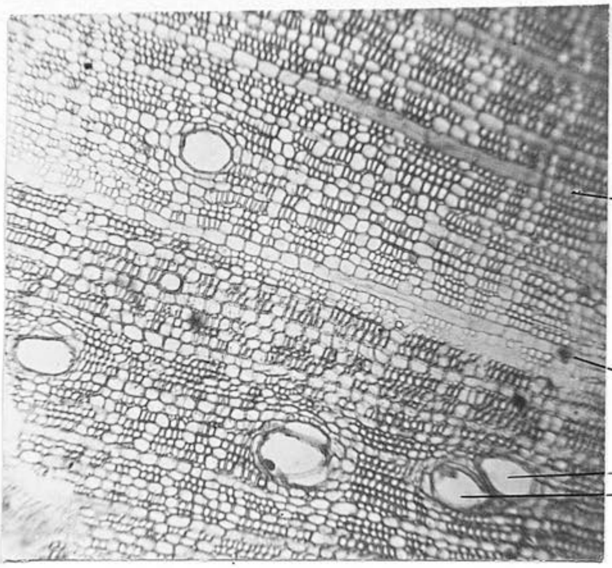


Fig. 1.

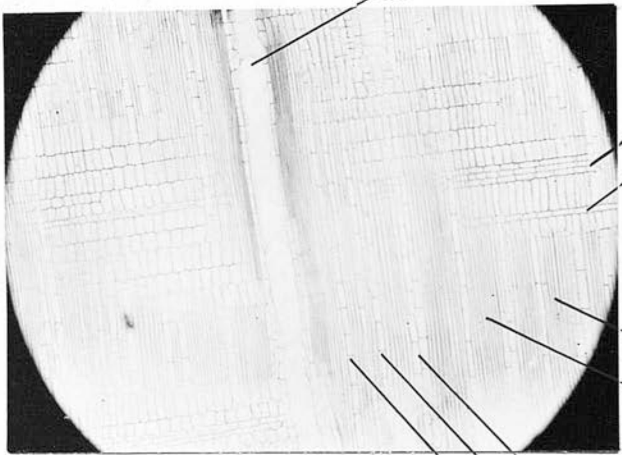


Fig. 2.

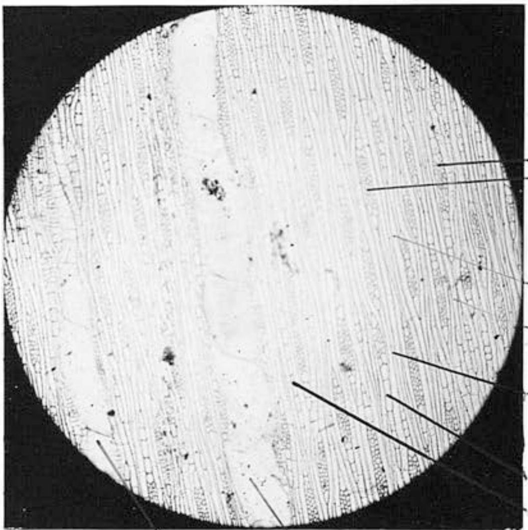


Fig. 3.

Plate 6.

Fig. 1. Nodule in cortex. Projection of vascular tissue toward stem wood Trans. Sect. x 10.

Fig. 2. Nodule in cortex. Radial Sect. x 10.

Fig. 3. The same x 20.

(a) Core of nodule.
(b) Wood tissue.
(c) Abnormal cortex.
(d) Inner cortex.
(e) Vascular projections.
(f) Wood vessels.
(g) nodule cambium
(h) Outer cortex

PLATE 6.

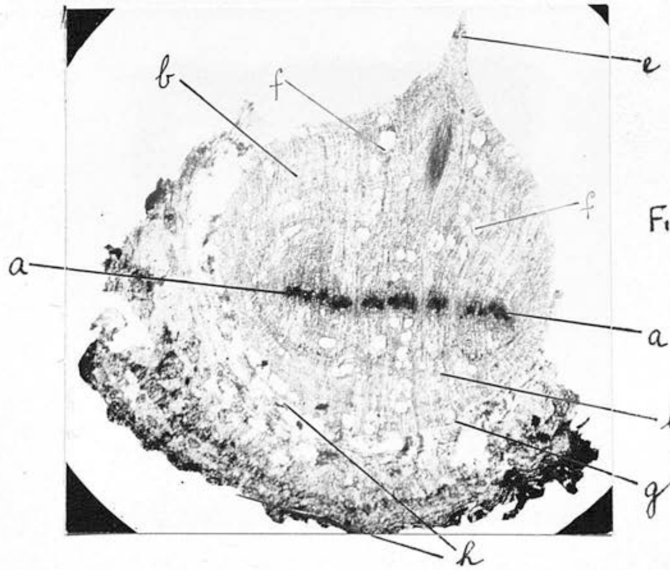


Fig. 1.

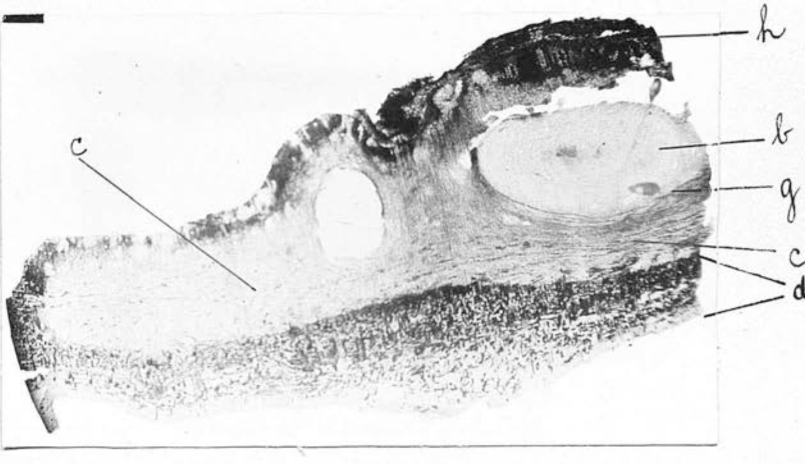


Fig. 2

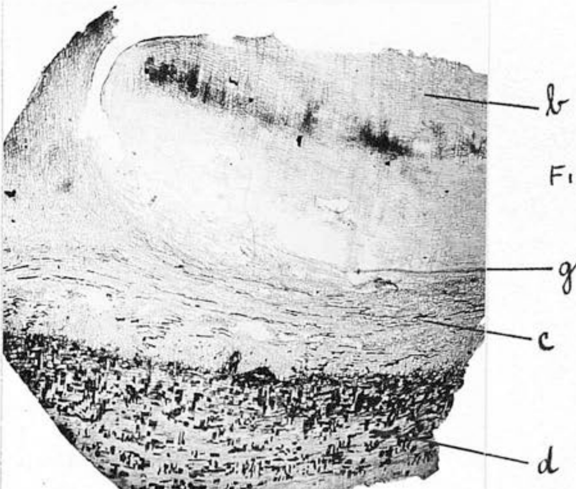


Fig. 3.

Plate 8.

Fig. 1. Nodule. Trans. Sect. x 50.
Fig. 2. Nodule. Trans. Sect. x 35.
Fig. 3. Nodule. Note latex vessels of core displaced by cell division at inception of nodule. Trans. Sect. x 35.

(a) Latex vessels of core.
(b) Tannin cells of core.
(c) Wood tissue.

PLATE 8.

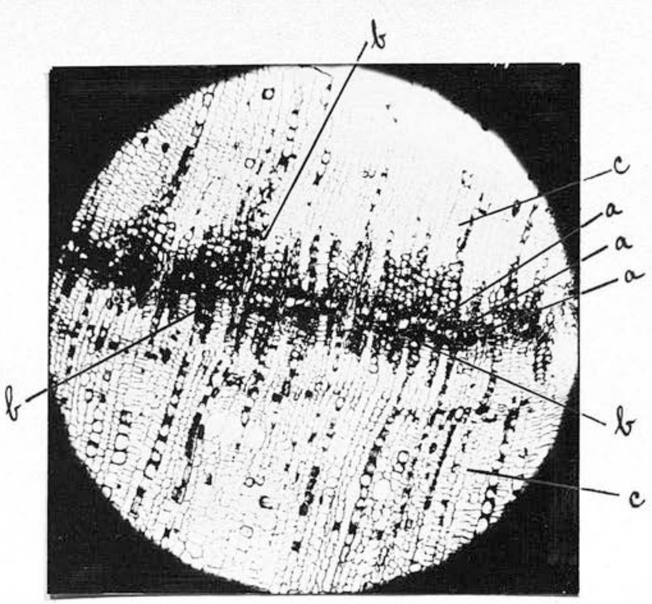


Fig. 1.

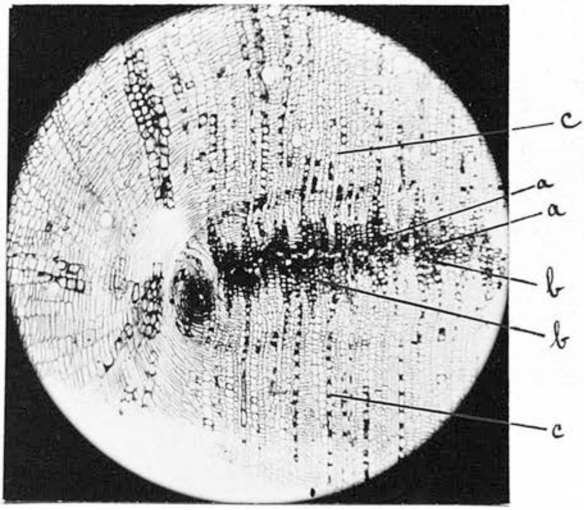


Fig. 2.

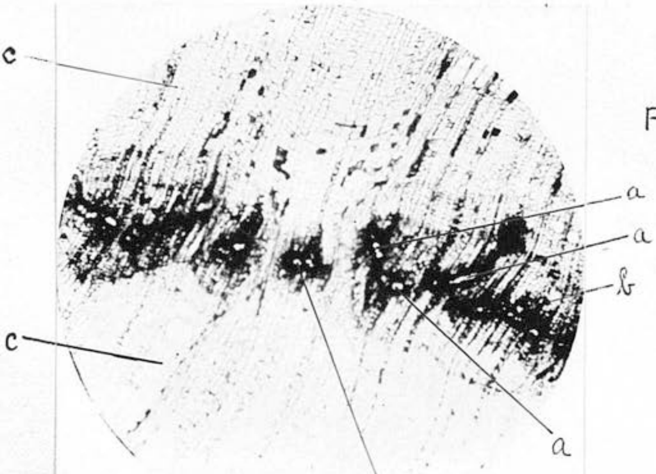


Fig. 3.

Plate 7.

Fig. 1. Nodule and cortex. Medullary rays continuous across nodule core. Trans. Sect. x 15.
Fig. 2. The same x 25. Medullary rays of nodule continued into cortex.
Fig. 3. Nodule with vascular projection. Radial Sect. x 12.
Fig. 4. Nodule. Medullary rays continuous across core. Trans. Sect. x 50.

(a) Nodule core.
(b) Wood tissue of nodule.
(c) Medullary rays.
(d) Vessels of wood.
(e) Tannin cells of core.
(f) Latex vessels of core.
(g) Cortex.
(h) Nodule cambium.

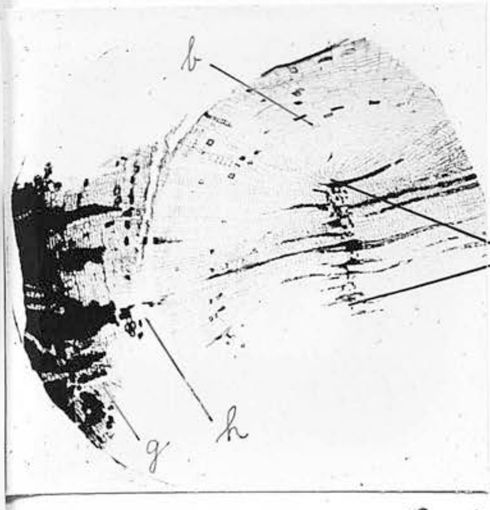


Fig. 1.

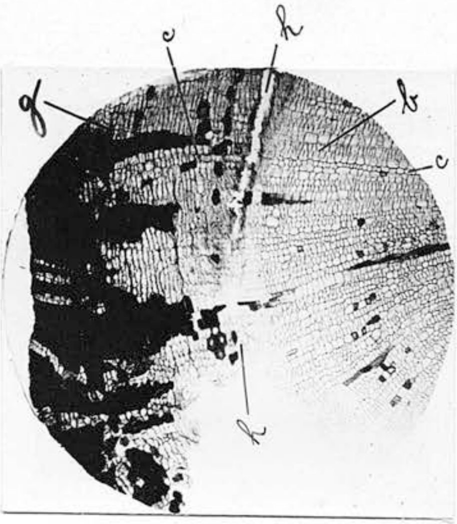


Fig. 2.

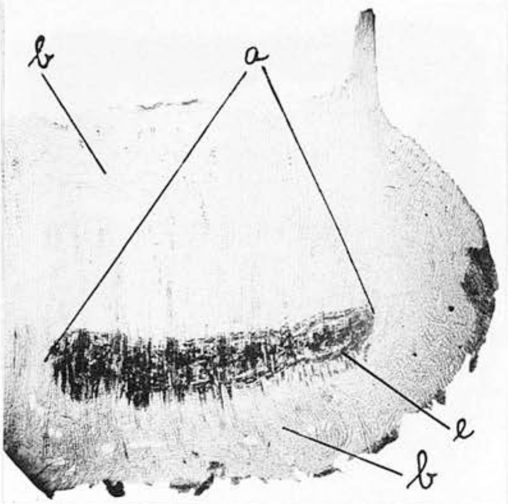


Fig. 3

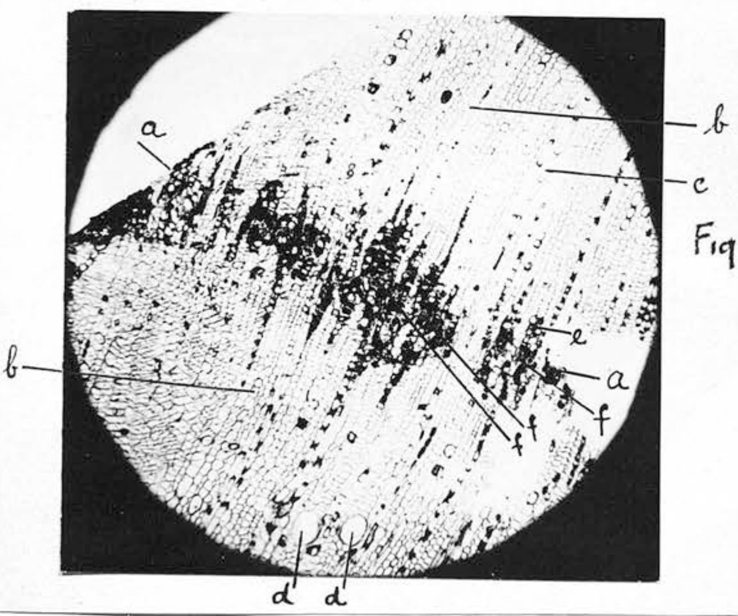


Fig. 4

Plate 9.

Fig. 1. Nodule. Core circular. Note lengthening of wood cells at the sharply curved end of the nodule. Trans. Sect. x 50.

Fig. 2. Nodule. Note highly refractive, translucent walls of core cells. Trans. Sect. x 30.

Fig. 3. Nodule. Trans. Sect. x 35.

Curving cells at end of nodule.

(a) Curved wood elements.

(b) Nodule core.

(c) Translucent walls of core cells.

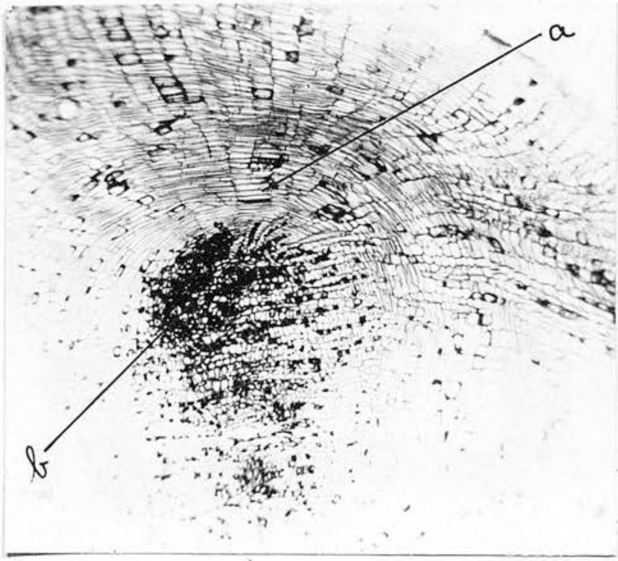


Fig. 1.

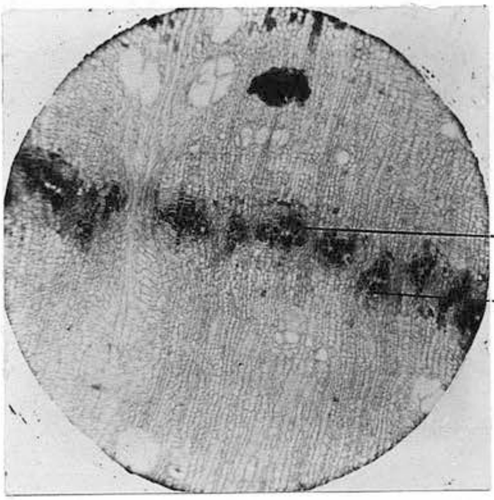


Fig. 2

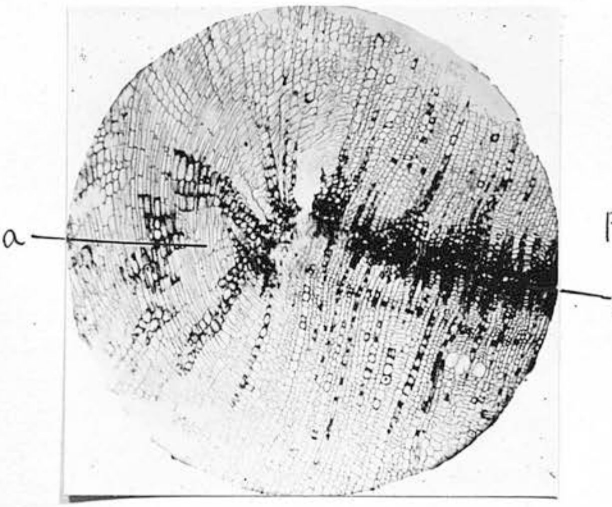


Fig. 3.

Plate 10.

Fig. 1. Nodule with vascular strand directed toward stem occluded by growth of nodule. Long. Sec. x 35.

Fig. 2. Nodule with two vascular strands similarly occluded. Long. Sect. x 35.

(a) Wood tissue of nodule.
(b) Nodule core.
(c) Vascular strands.

PLATE 10.

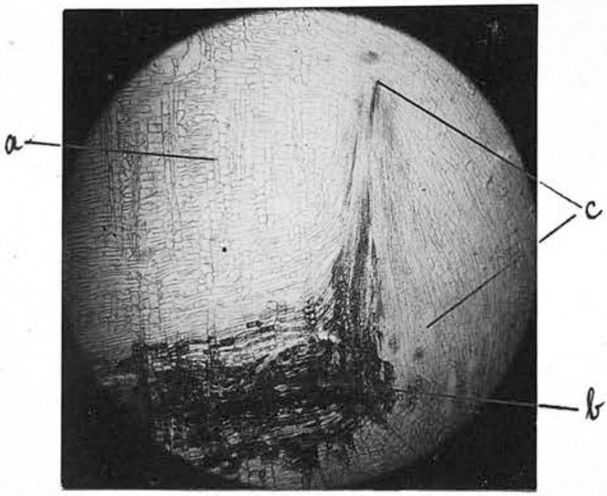


Fig 1.

Fig 2.

Plate 11.

Fig. 1. Nodule with latex vessels in core and in addition cortical lesion containing coagulated latex. Trans. Sect. x 20.

Fig. 2. The same x 50.

(a) Latex vessel of core.
(b) Cortex.
(c) Lesion in cortex.
(d) Coagulated latex in lesion.

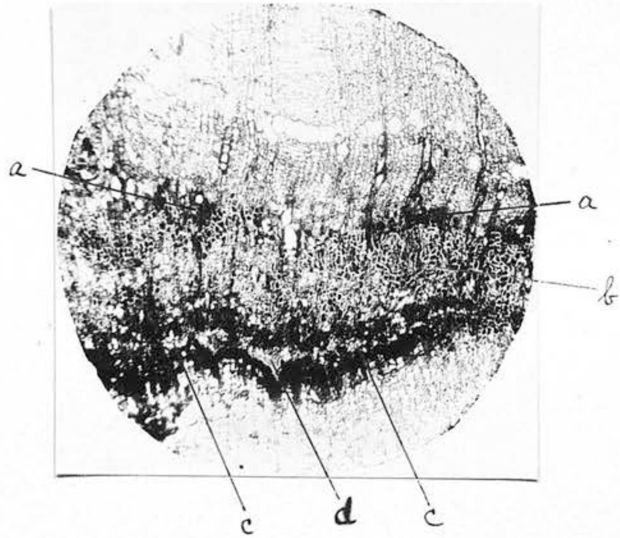


Fig. 1.

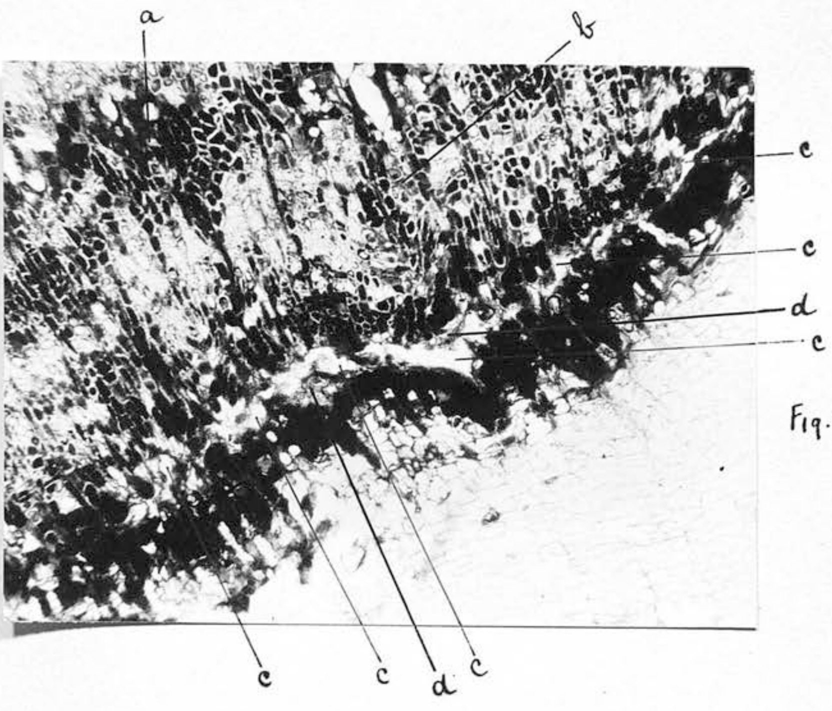


Fig. 2.

Plate 12.

Fig. 1. Core of nodule. Trans. Sect.
x 250.
Fig. 2. Core of nodule. Trans. Sect.
x 250.
Fig. 3. Core of nodule. Trans. Sect.
x 250.

(a) Latex vessels of core.
(b) Coagulated latex.
(c) Tannin cells.
(d) Wood cells of nodule.
(e) Thickened walls of latex vessel.

PLATE 12.

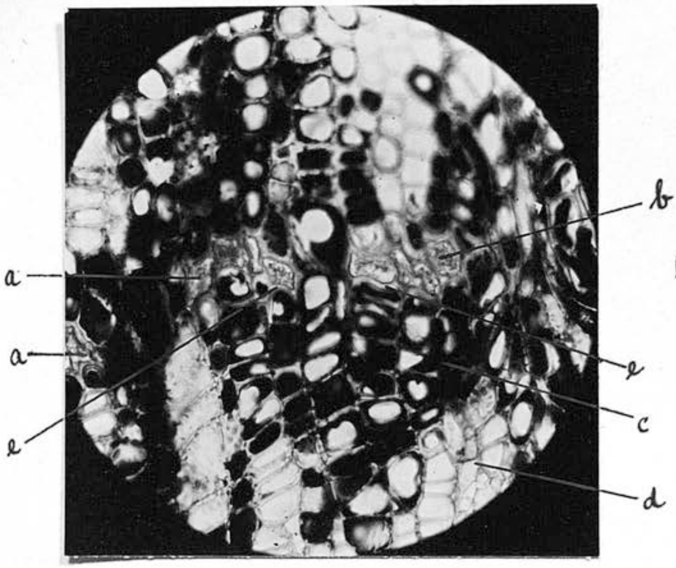


Fig. 1.

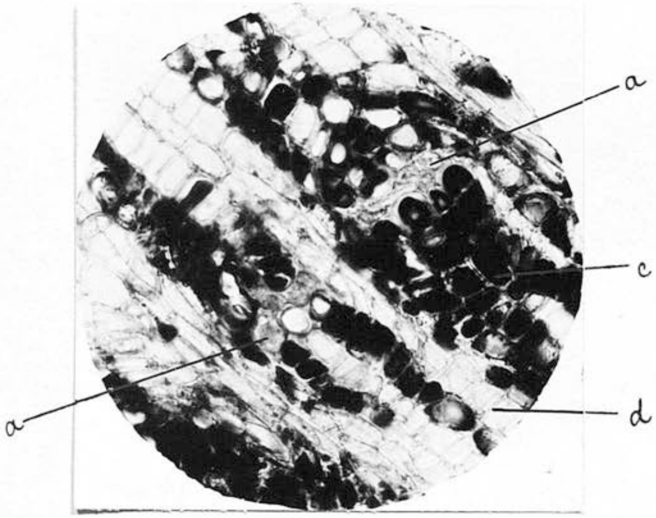


Fig. 2

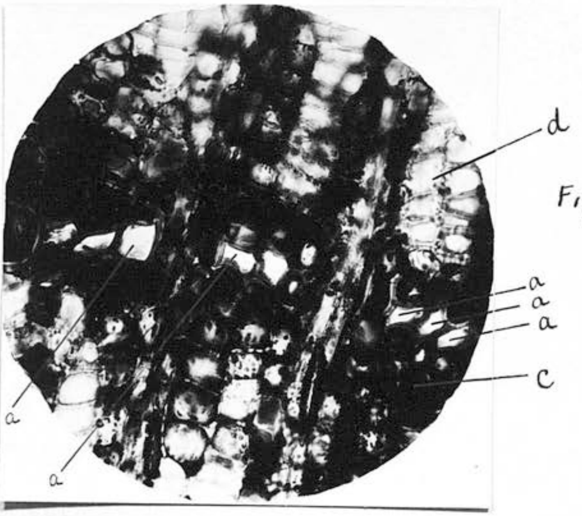


Fig. 3.

Plate 13.

Fig. 1. Core of nodule. Trans. Sect. x 250.
Fig. 2. Core of nodule. Tan. Sect. x 250.

(a) Latex vessels of core.
(b) Tannin cells.
(c) Wood cells of nodule.
(d) ~~(e)~~ Starch grains.
(e) ~~(f)~~ Vestiges of dividing wall between adjacent latex vessels.

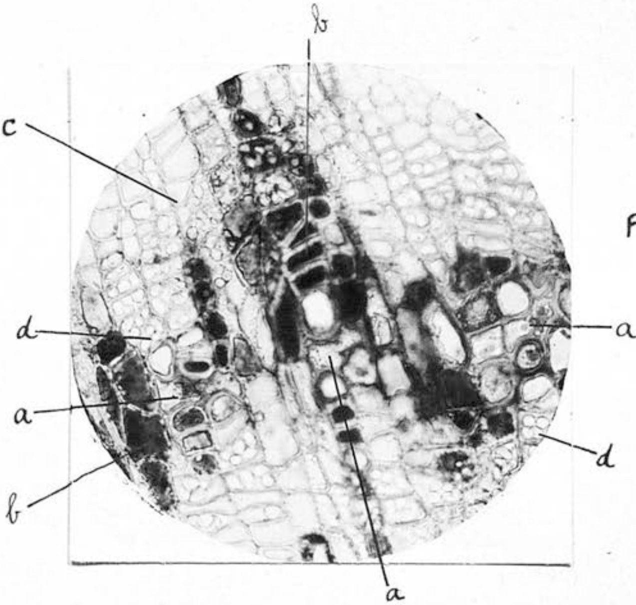


Fig. 1.

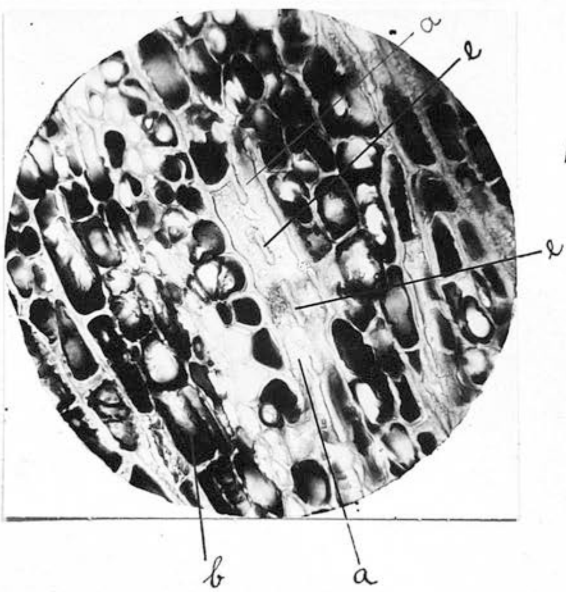


Fig. 2.

Plate 14.

Fig. 1. Nodule. Tan. Sect. x 40.
Fig. 2. Nodule. Tan. Sect. x 35.
Fig. 3. Nodule. Digested with Schulze's maceration mixture. Tan. Sect. x 30.

(a) Tissue of core.
(b) Latex vessels.
(c) Zone of confused cell division.
(d) Wood tissue of nodule.

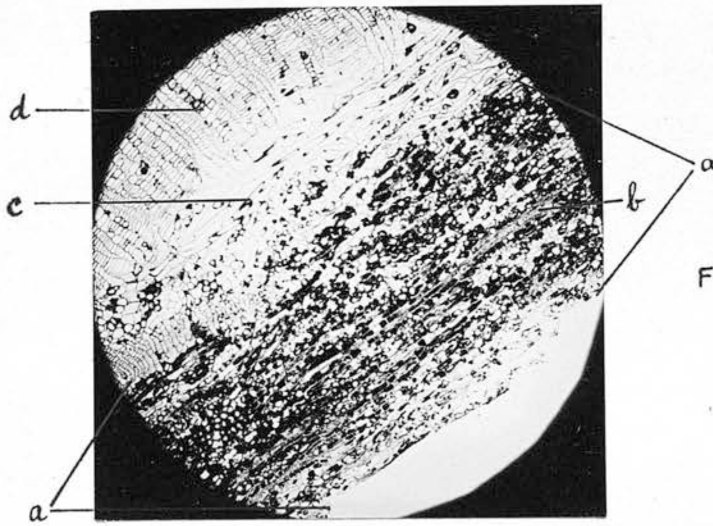


Fig. 1.

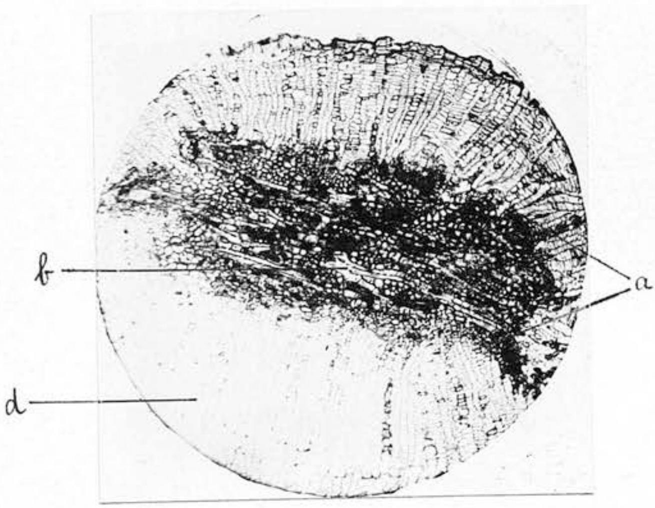


Fig. 2.

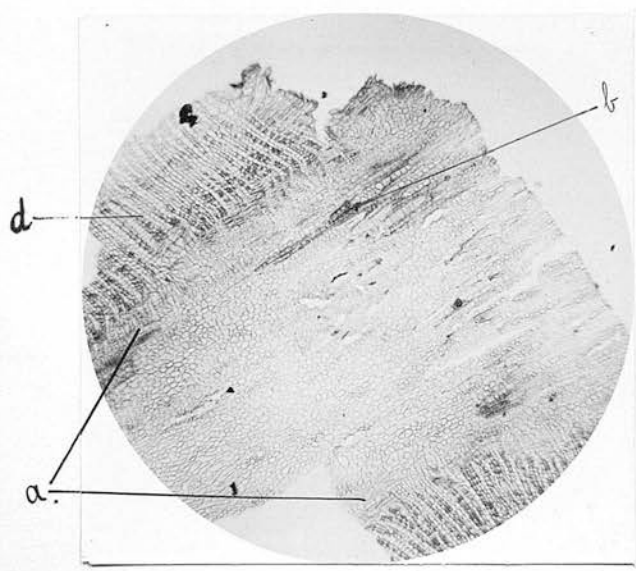


Fig. 3.

Plate 15.

Fig. 1. Nodule apex with nodular cortex
not yet occluded by wood tissue.
Trans. Sect. x 50.

Fig. 2. Nodule. Long. Sect. x 35.

Fig. 3. Nodule. Tan. Sect. x 40.

(a) Latex vessel.
(b) Wood cells of nodule.

PLATE 15.

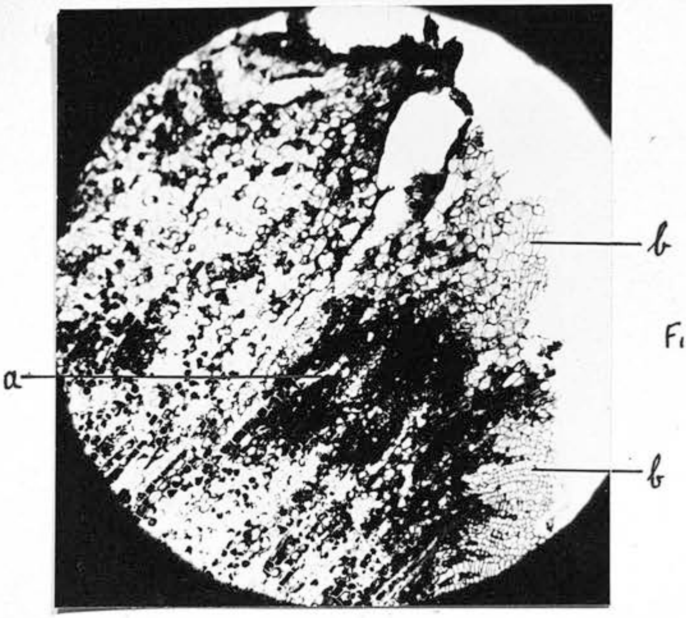


Fig. 1.

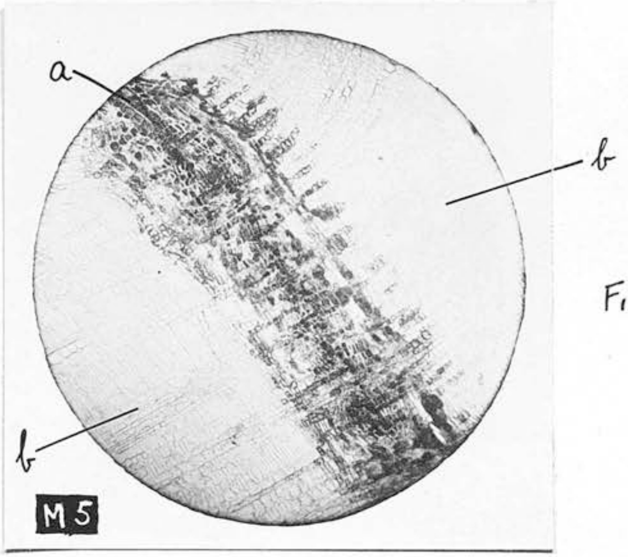


Fig. 2.

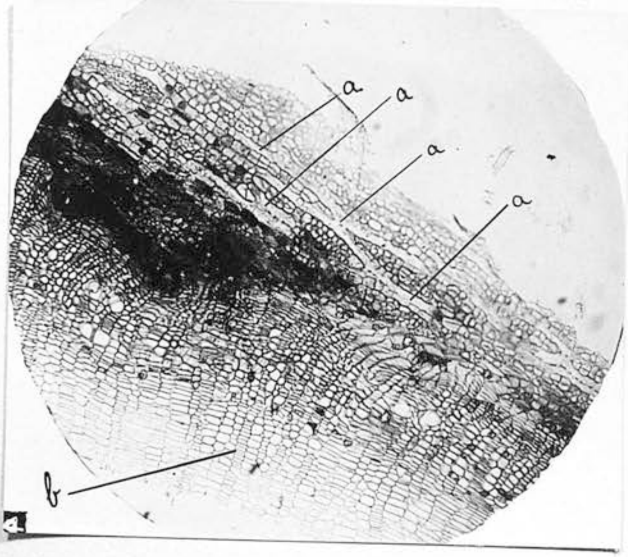


Fig. 3.

Plate 16.

Fig. 1. Wood tissue of nodule showing tortuous fibres and vessel. Tan. Sect. x 35.

~~Fig. 2. Normal cortex Tan. Sect. x 30.~~

Fig. 2. Wood tissue of nodule showing tortuous fibres and vessels.

(a) Fibres.
(b) Vessels.
(c) Medullary Rays

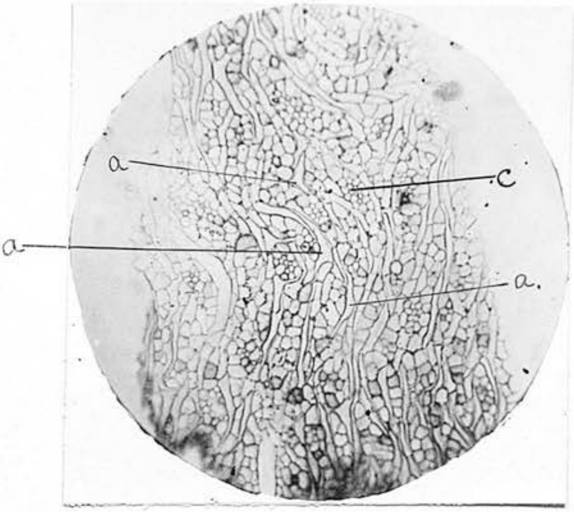


Fig. 1.

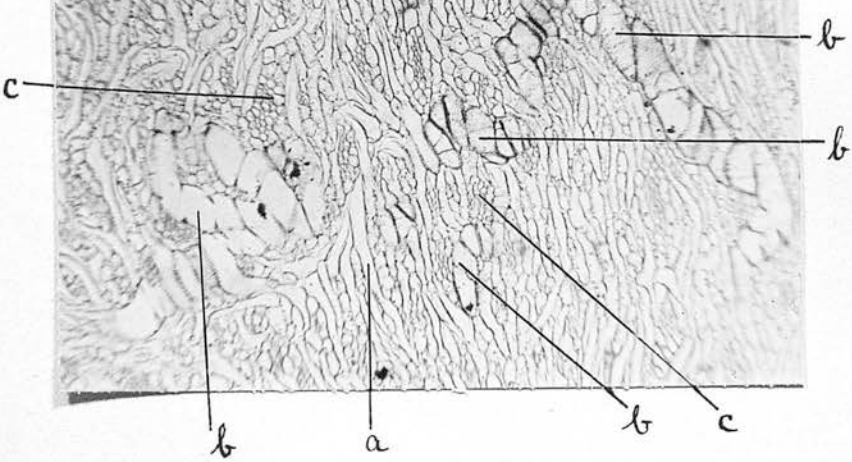


Fig. 2.

Plate 17.

Fig. 1. Nodular cortex showing inception of two nodules. Note absence of stone cell groups. Tans. Sect. x 30.

Fig. 2. The same x 60.

Fig. 3. Nodular cortex with altered latex vessel, and early cell division of nodule. Radial Sect. x 35.

(a) Stem cambium.
(b) Latex vessel.
(c) Cell division.

PLATE 17.

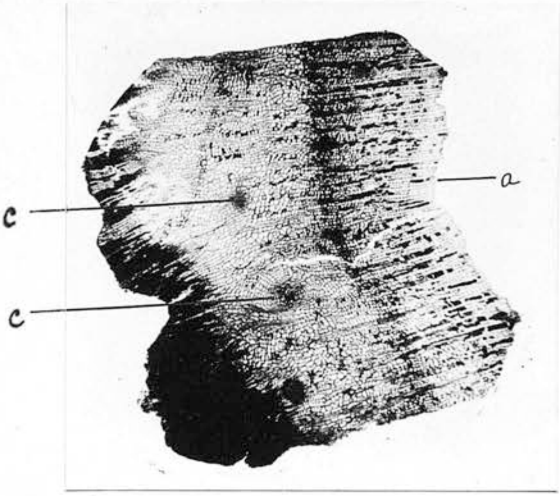


Fig. 1.

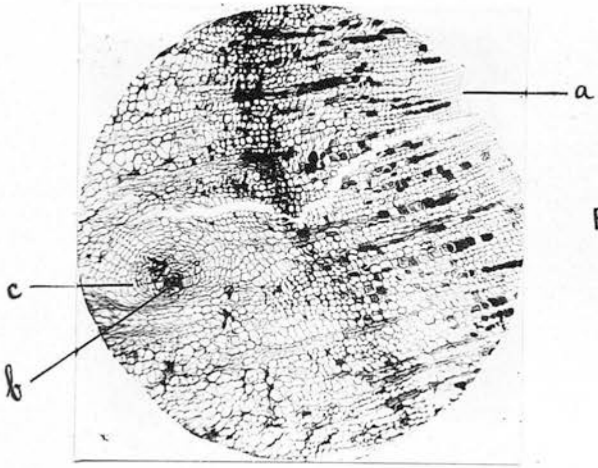


Fig. 2.

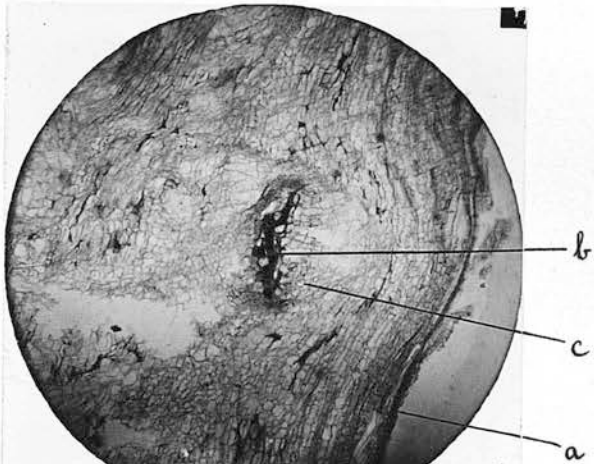


Fig. 3.

Plate 18.

Fig. 1. Nodular cortex. Radial Sect. x 15.
Fig. 2. The same x 35.
Fig. 3. Nodular cortex. Radial Sect. x 40.

(a) Altered latex vessels.
(b) Stem cambium.
(c) Globular shoot stimulated to growth.
(f) Early division in cortical cells tangential to young nodule.
(d) Globular shoot vestiges of vascular connection with stem.
(e) Meristematic cells developing into wood tissue of nodule.

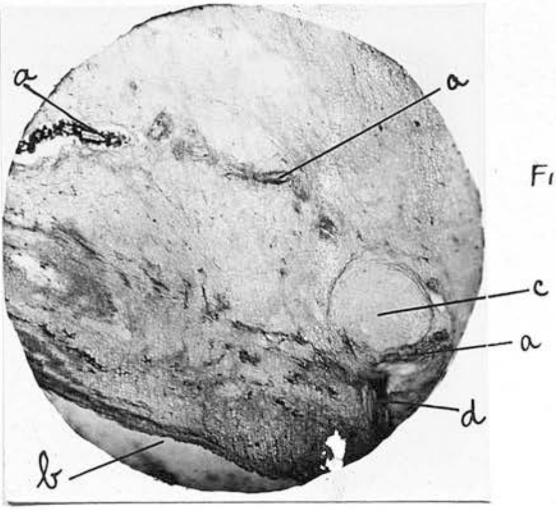


Fig. 1.

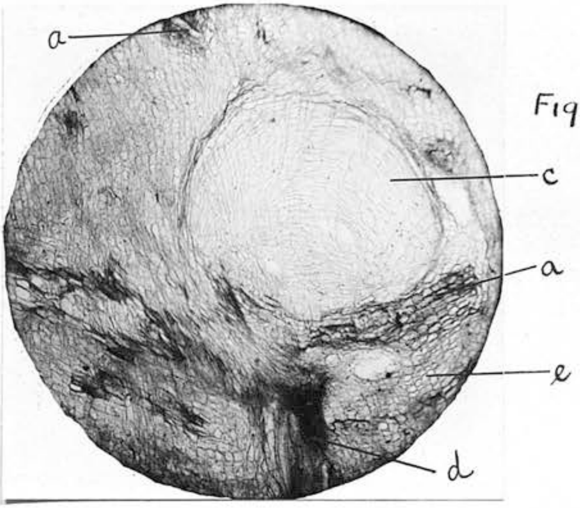


Fig. 2.

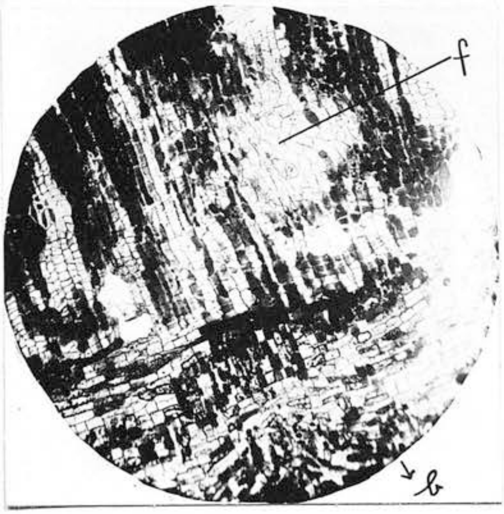


Fig. 3

Plate 19.

Fig. 1. Nodular cortex showing altered latex vessel and early cell division. Radial sect. x 70.

Fig. 2. Nodular cortex showing altered latex vessel and tannin cells. Radial sect. x 35.

Fig. 3. Nodular cortex showing normal inner cortex and abnormal outer cortex. Radial sect. x 50.

(a) Latex vessels.
(b) Tannin cells.
(c) Stone cells.
(d) Dividing cells i.e. inception of nodule cambium.
(e) Normal region of cortex.
(f) Abnormal region of cortex; note absence of stone cells.

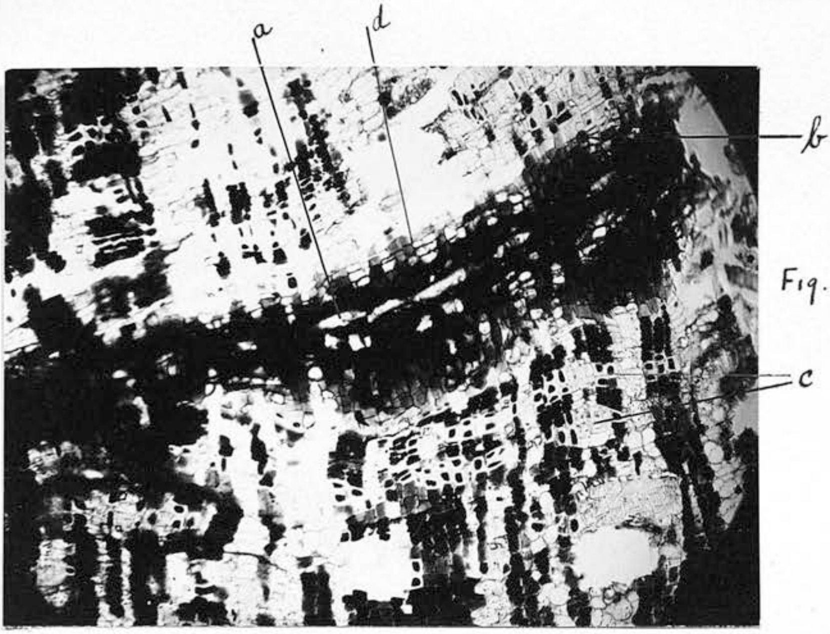


Fig. 1.

Fig. 2.

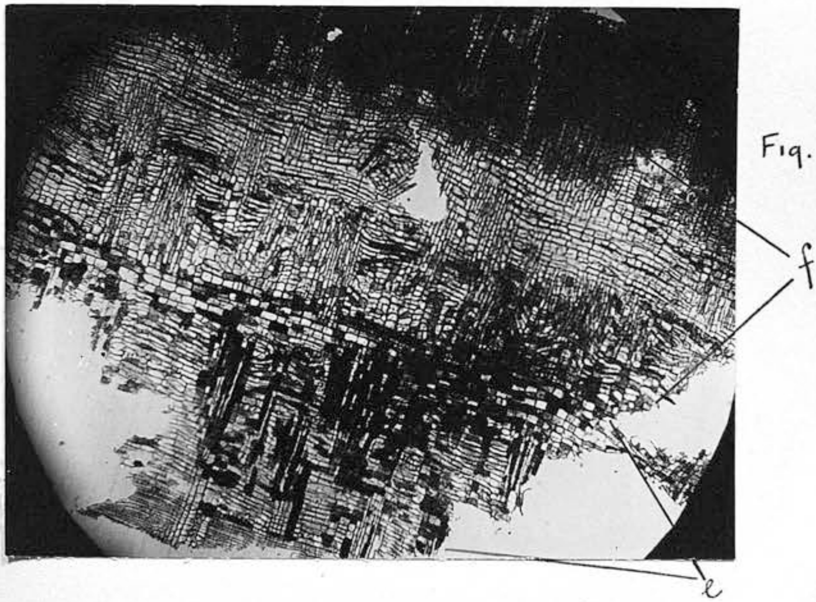


Fig. 3.

Plate 20.

Fig. 1. Nodular cortex with abundant tannin cells and rudiment of vascular strand. Radial sect. x 35.

Fig. 2. Nodular cortex. Note absence of stone cell groups. Radial sect. x 20.

Fig. 3. Nodular cortex. Stone cell groups present, but less numerous than in normal cortex. Trans. Sect. x 20.

(a) Stem cambium.
(b) Inner cortex.
(c) Outer cortex.
(d) Stone cell groups.
(e) Vascular strand. Vestiges of.

Fig. 1.

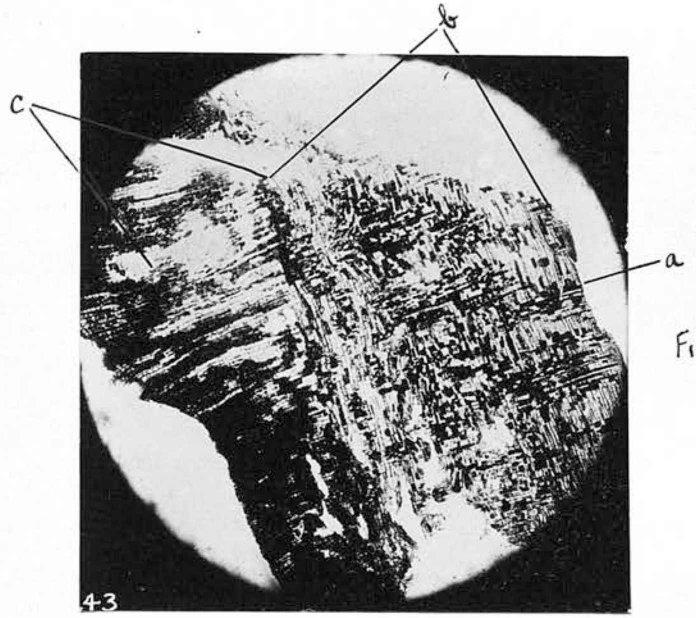


Fig. 2.

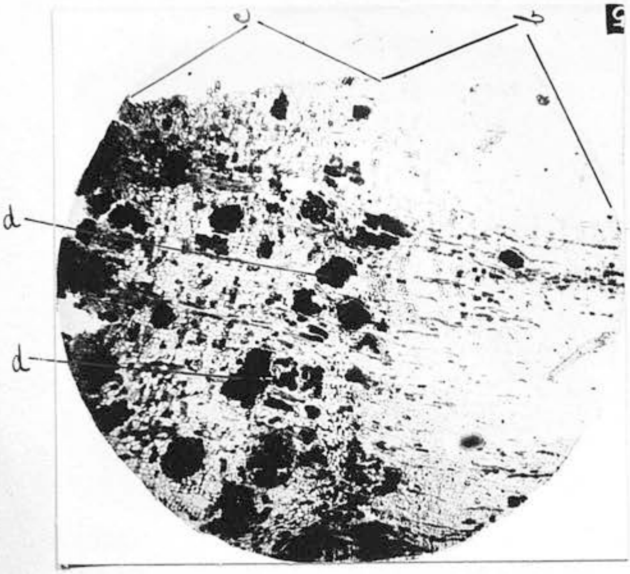


Fig. 3

Plate 21.

Fig. 1. Nodule and nodule cortex. Trans. sect. x 60.

Fig. 2. Nodular cortex; inner cortex normal. Radial sect. x 35.

Fig. 3. Nodular cortex; inner cortex with latex vessel walls somewhat thickened. Trans. sect x 50.

(a) Nodule wood tissue.
(b) Nodule cambium.
(c) Nodule cortex.
(d) Isolated stone cells.
(e) Stem cambium.
(f) Latex vessels.

PLATE 21.

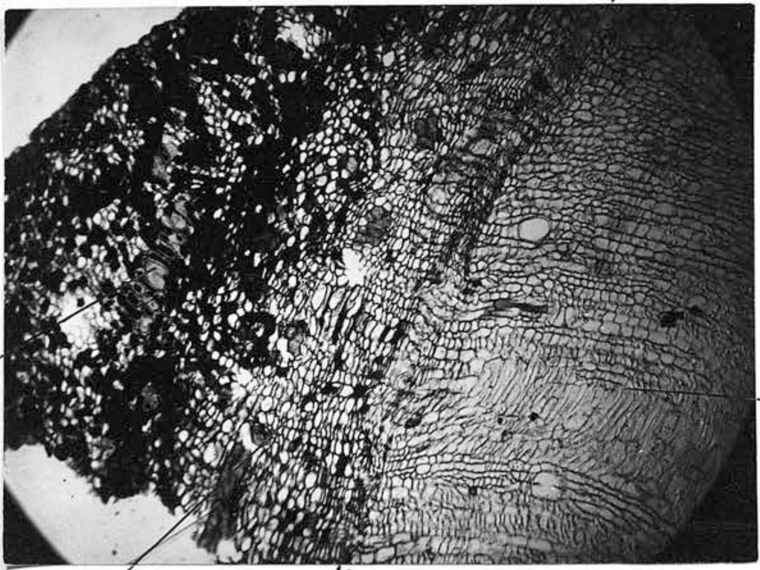


Fig. 1.

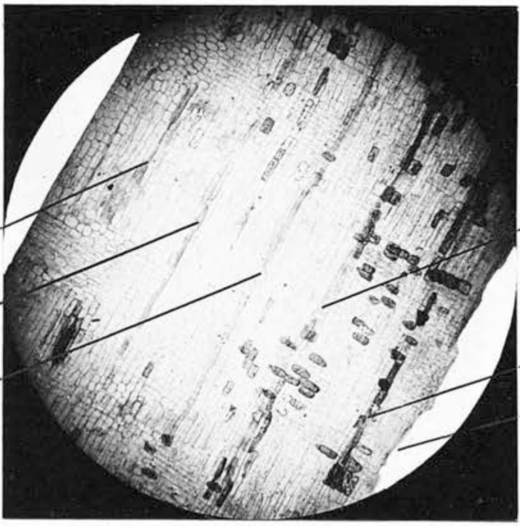


Fig. 2.

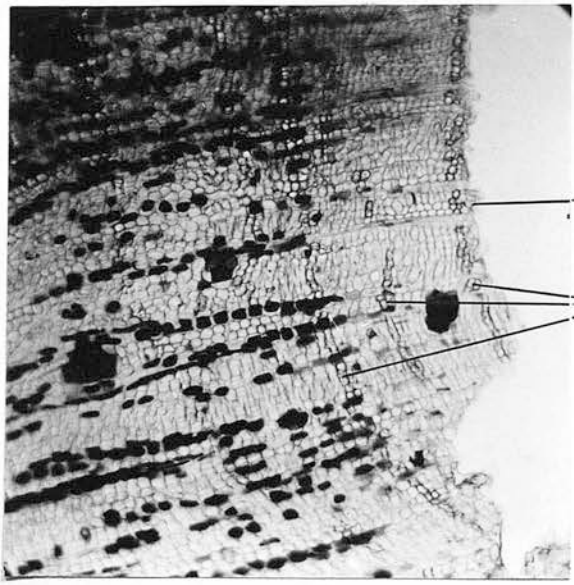


Fig. 3.

Plate 22.

Fig. 1. Nodule derived from cortical lesion containing coagulated latex. Taken from wound callus on main stem. Trans. sect. x 20.

Fig. 2. The same x 50.

Fig. 3. The same x 150.

(a) Cortical lesion.
(b) Coagulated latex.
(c) Tannin cells.
(d) Wood fibres.
(e) Wood tissue of nodule.
(f) Lacerated edge of lesion with torn ends of fibrous cells projecting into coagulated latex.

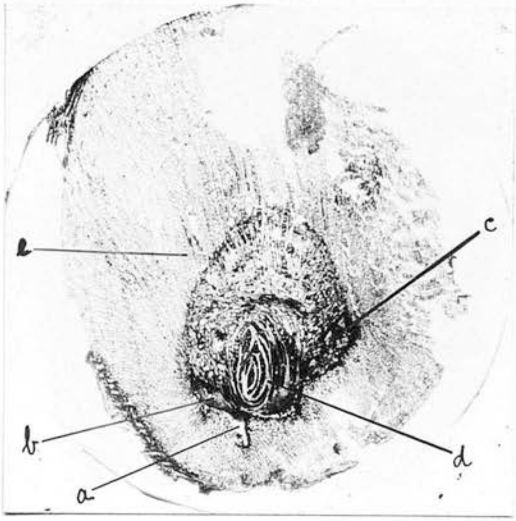


Fig. 1.

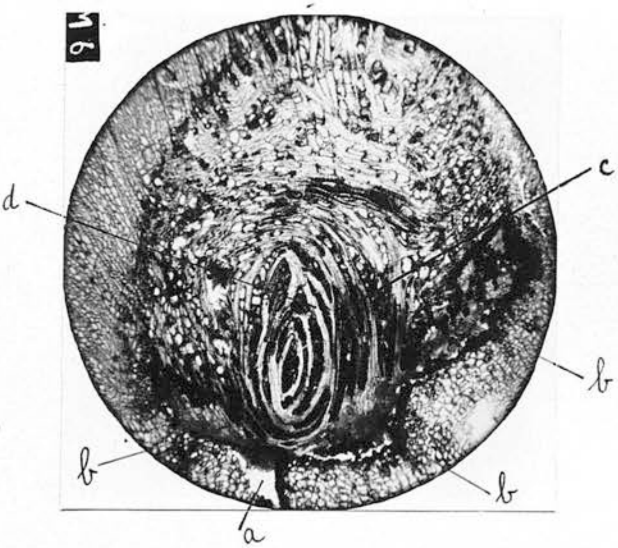


Fig. 2.

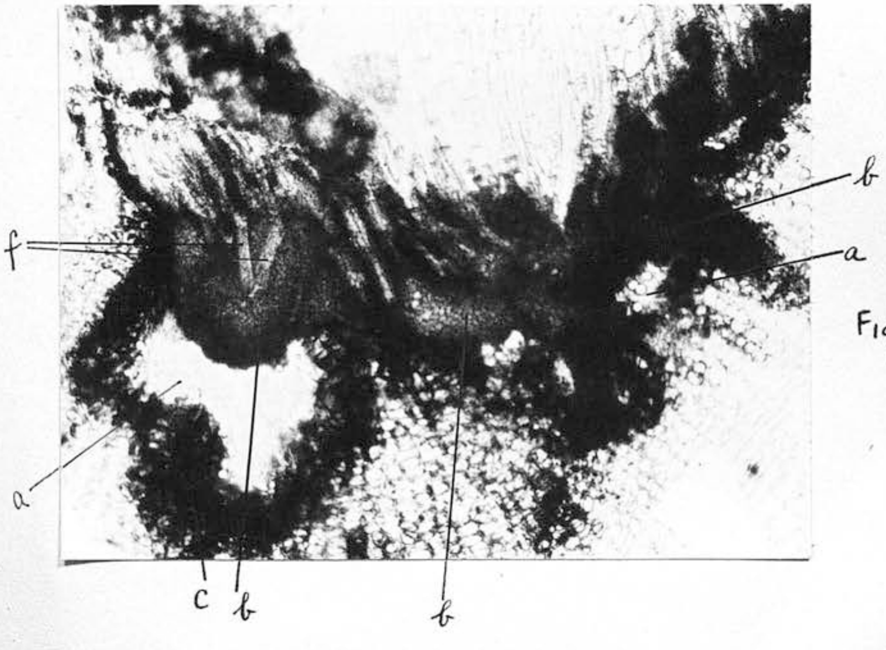


Fig. 3.

Plate 23.

Fig. 1. Nodule derived from cortical lesion containing coagulated latex. Taken from wound callus on main stem. Trans. sect. x 35.

Fig. 2. The same x 35.

Fig. 3. The same x 40.

Fig. 4. The same treated with Schulze's maceration mixture x 70.

(a) Cortical lesion.
(b) Coagulated latex.
(c) Tannin cells.
(d) Wood tissue of nodule.

PLATE 23.

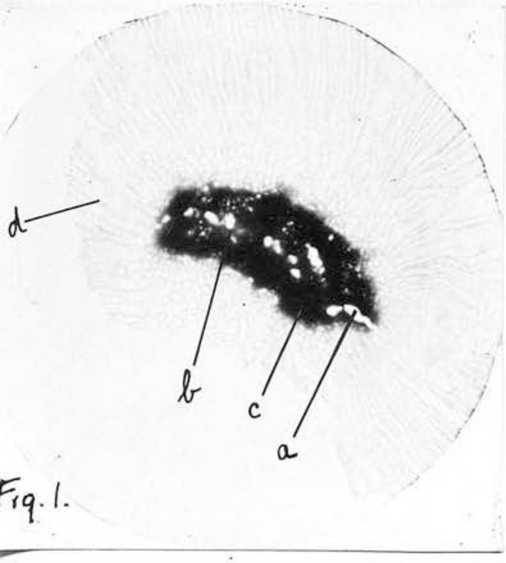


Fig. 1.

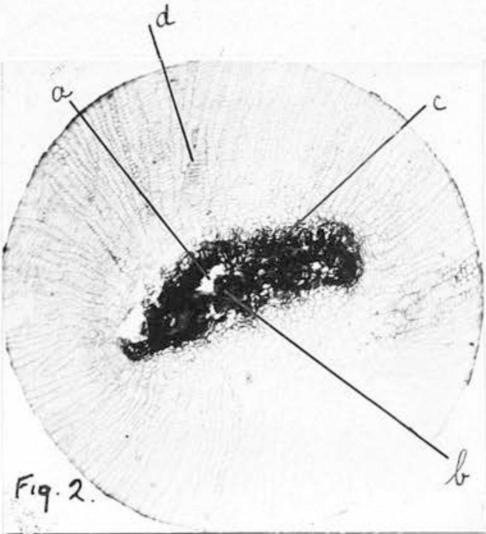


Fig. 2.

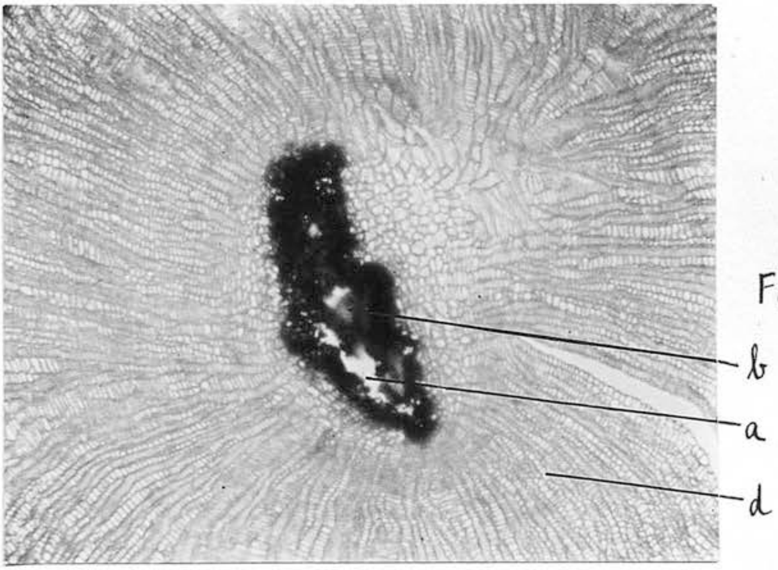


Fig. 3.

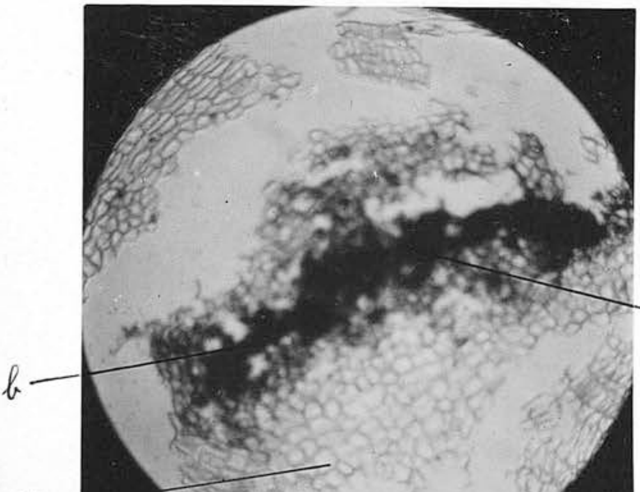


Fig. 4.

Plate 24.

Fig. 1. Nodule derived from cortical lesion containing coagulated latex. Taken from wound callus on main stem. Trans. sect. x 30.

Fig. 2. The same x 40.

Fig. 3. The same x 75.

(a) Cortical lesion.
(b) Coagulated latex.
(c) Tannin cells.
(d) Wood tissue of nodule.

PLATE 24.

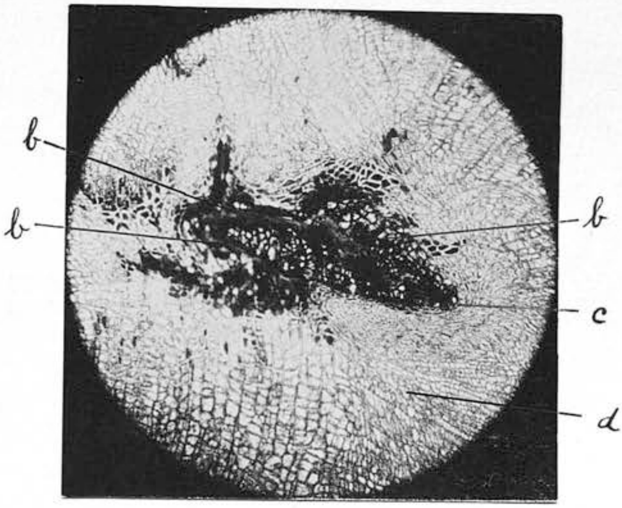


Fig. 1.

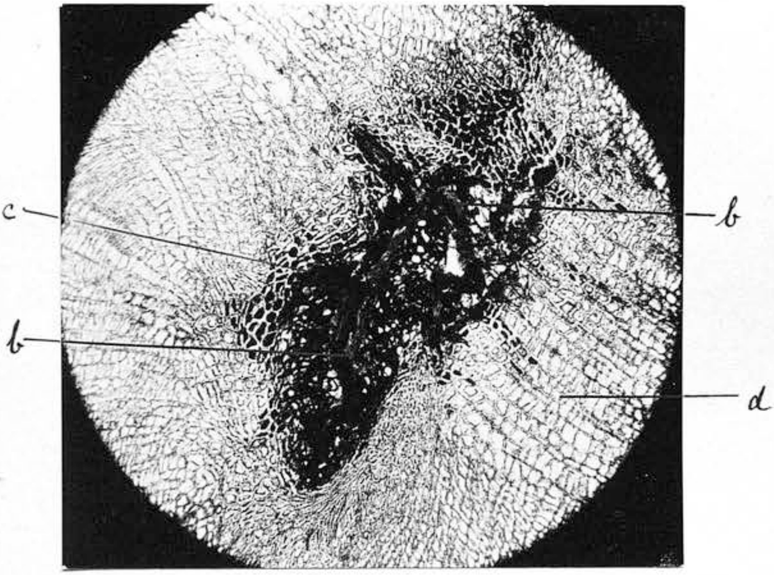


Fig. 2.

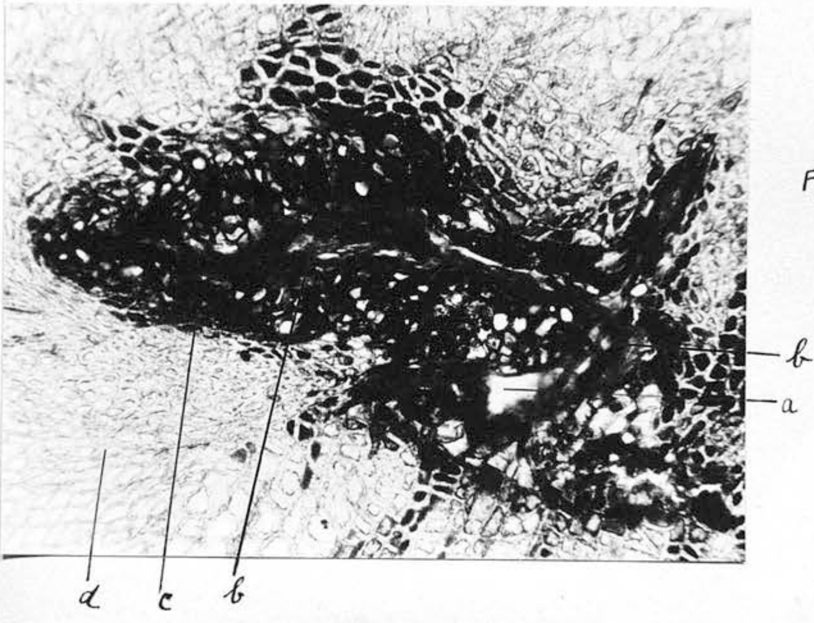


Fig. 3.

Plate 25.

Fig. 1. Nodule derived from cortical tissue with intercellular infiltration of latex without lesion. Trans. sect. x 35.

Fig. 2. The same treated with Schulze's maceration mixture x 70.

Fig. 3. The same after maceration x 300.

(a) Coagulated latex.
(b) Cortical cells.
(c) Wood tissue of nodule.
(d) Early cambial divisions.

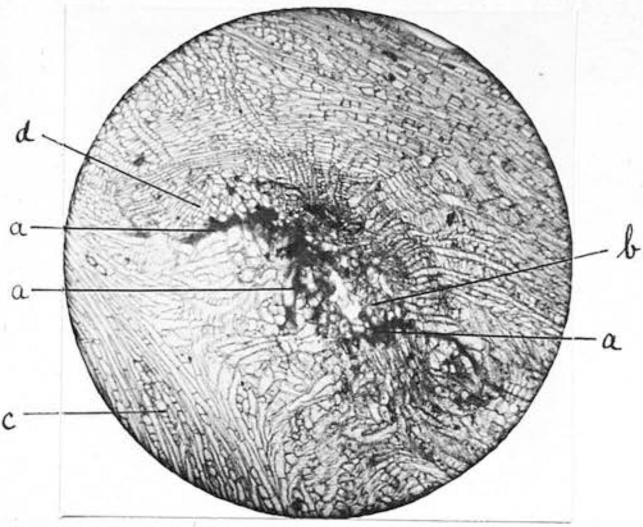


Fig. 1.

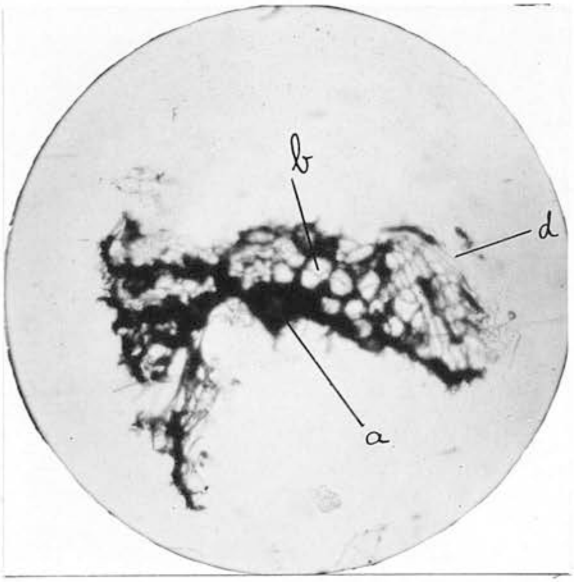


Fig. 2.

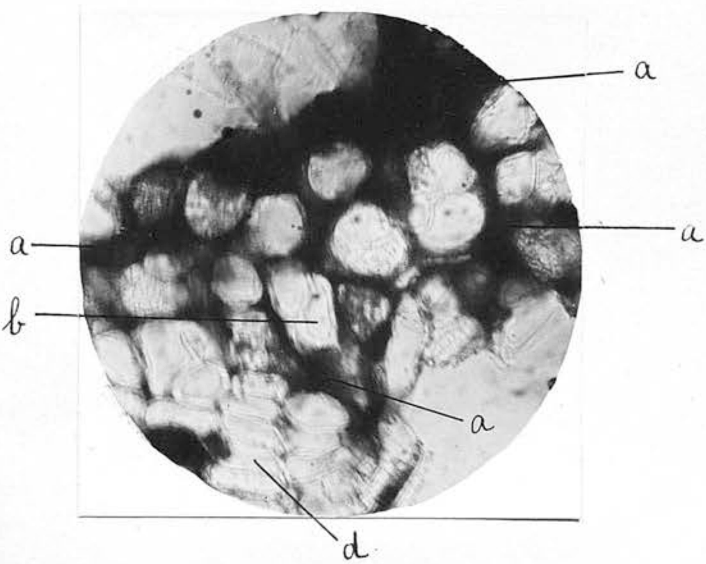


Fig. 3

Plate 26.

Fig. 1. Nodule formed round necrotic cortical tissue. From general cortex. Trans. sect. x 30.

Fig. 2. The same x 120.

(a) Limits of necrotic cortical tissue.

(b) Wood tissue of nodule.

(c) Stone cells.

(d) Earliest cell divisions.

(e) Tannin cells

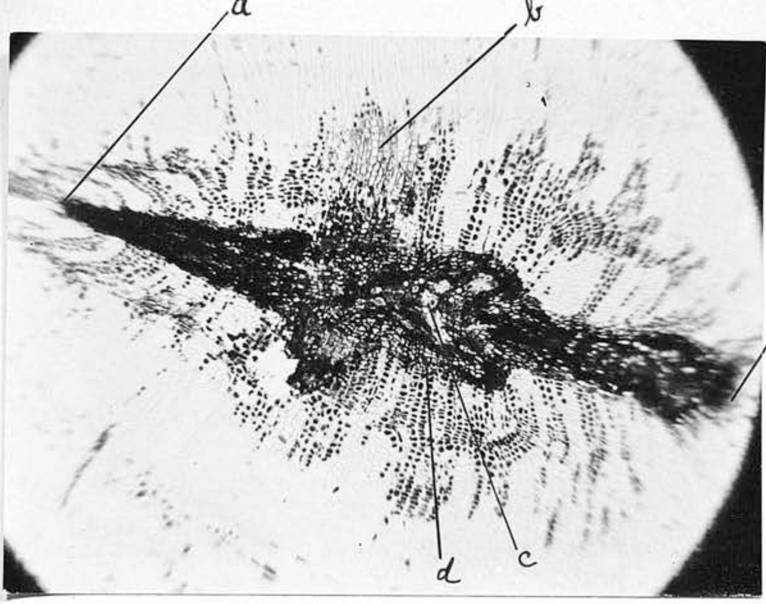


Fig. 1.

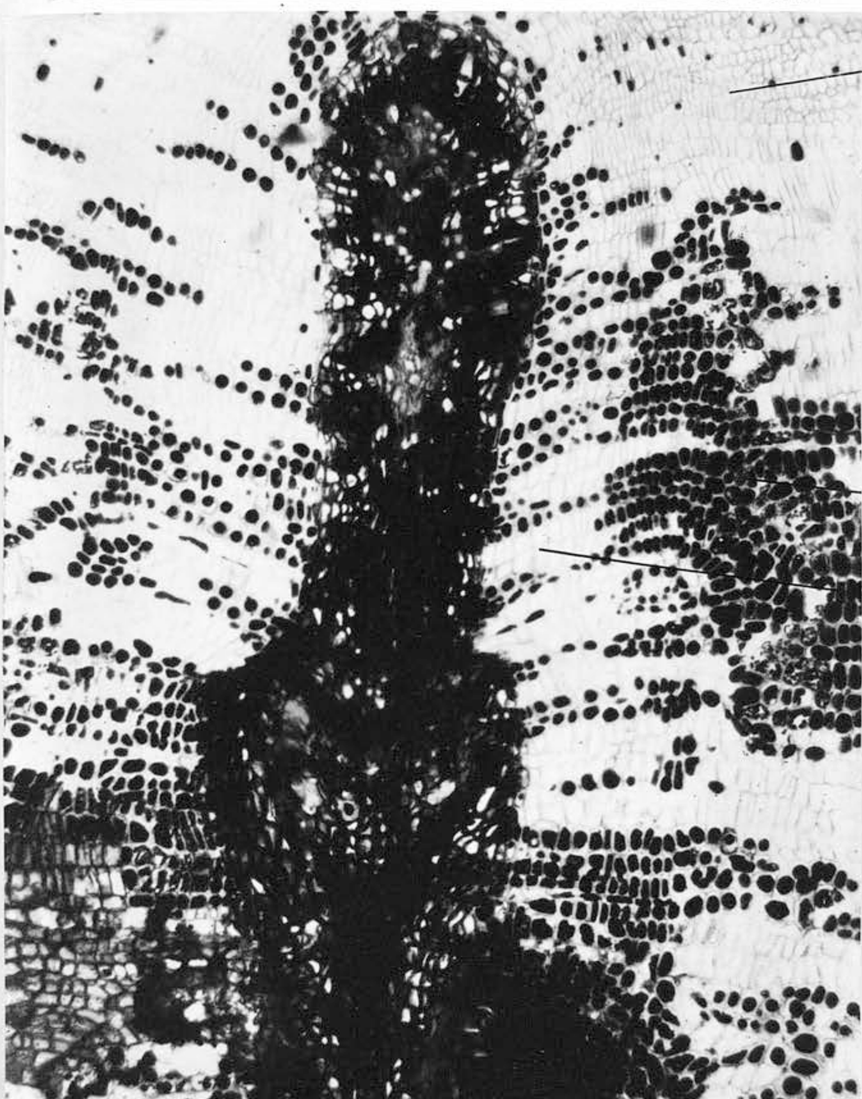


Fig. 2.

Plate 27.

Fig. 1. Nodule formed round necrotic cortical tissue. From general cortex. Trans. sect. x 30.

Fig. 2. The same. Trated with Schulze's maceration mixture. Trans. sect. x 30.

(a) necrotic cortical tissue.

(b) wood tissue of nodule.

(c) Tannin cells.

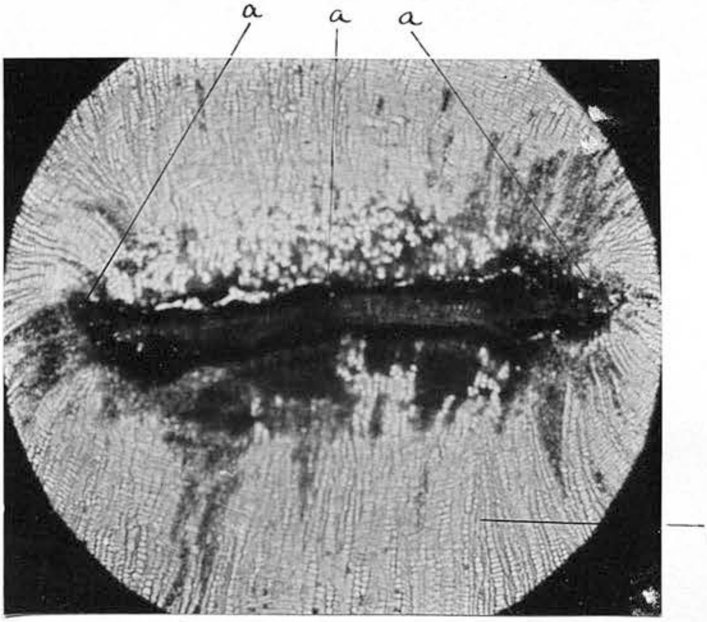


Fig. 1.

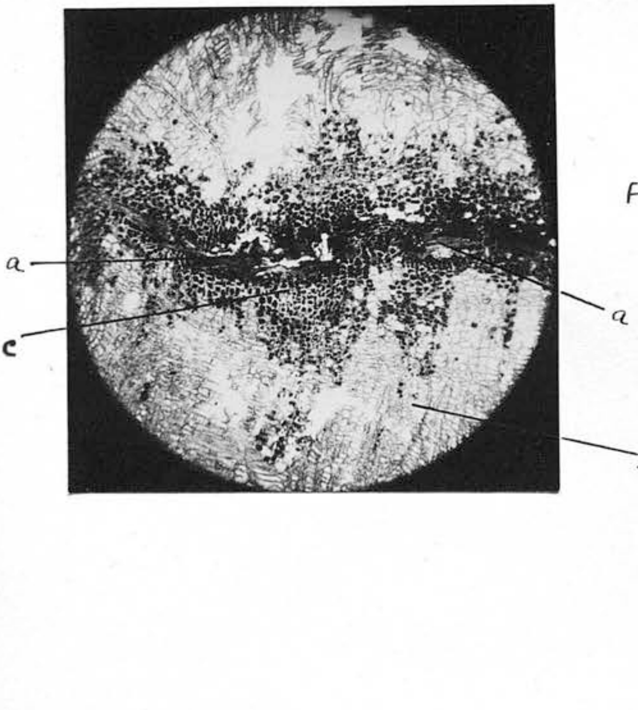


Fig. 2.

Plate 28.

Fig. 1. Globular shoot. x 10.
Fig. 2. Globular shoot with adjacent cortex and vascular projection toward stem. Trans. sect. x 6.
Fig. 3. Globular shoots in cortex. Trans. Sect. x 12.

(a) Vascular projection.
(b) Bud Trace.

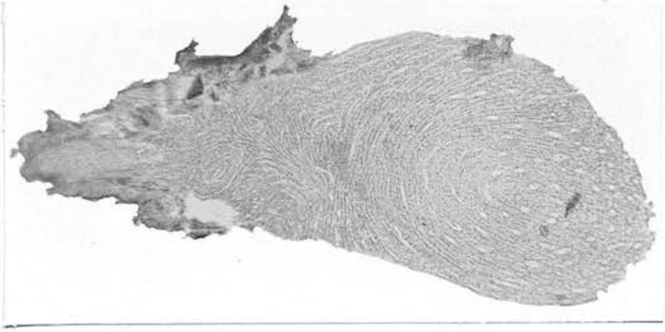


Fig. 1.

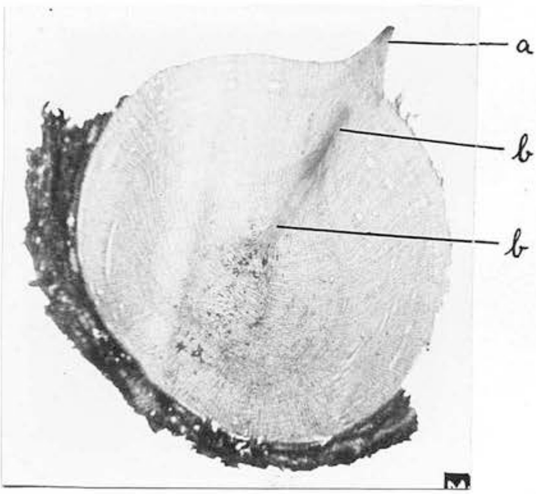


Fig. 2.

Fig. 3.

Plate 29.

Fig. 1. Globular shoot. The apex is directed inwards toward the stem. Taken from an old leaf scar. Trans. sect. x 20.

Fig. 2. Globular shoot with bud trace traversing the wood tissue. Trans. sect. x 8.

Fig. 3. Globular shoot containing bud trace. Trans. sect. x 10.

(a) Bud trace.
(b) Apex.
(c) Bud trace expanding on reaching the cortex.
(d) Wood tissue.
(e) Vessels.

PLATE 29.

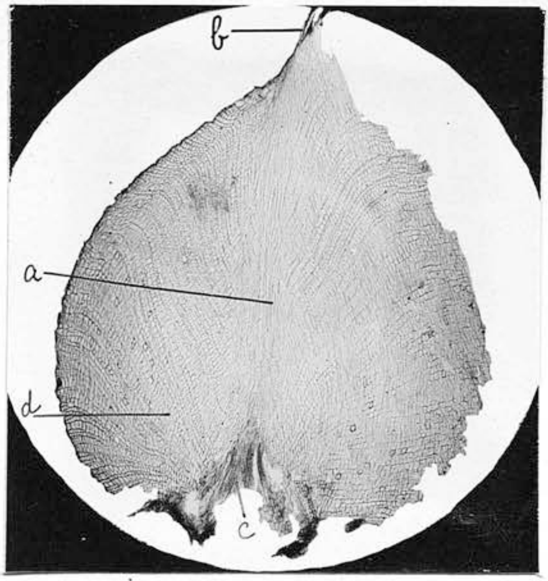


Fig. 1.

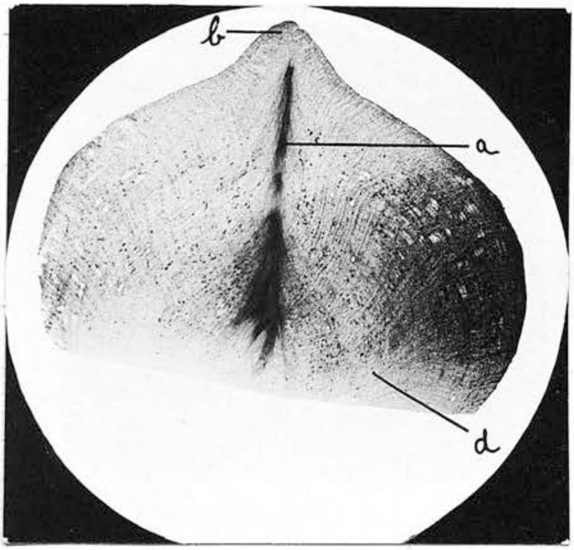


Fig. 2.

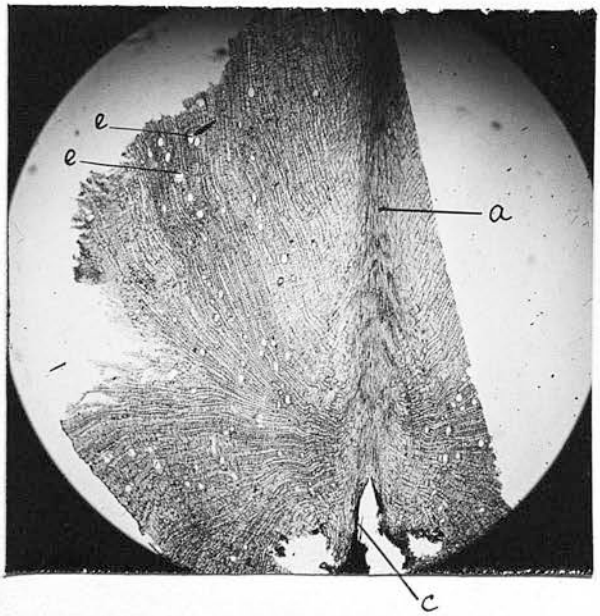


Fig. 3.

Plate 30.

Fig. 1. Globular shoot with core of wood tissue. Trans. sect. x 20.
Fig. 2. Globular shoot with core of wood tissue. Trans. sect. x 20.
Fig. 3. Globular shoot with eccentric core of lignified cells.[redacted]. Trans. sect. x 25.

(a) Core.
(b) Vestiges of vascular connection, i.e. Bud Trace.
(c) Wood tissue.

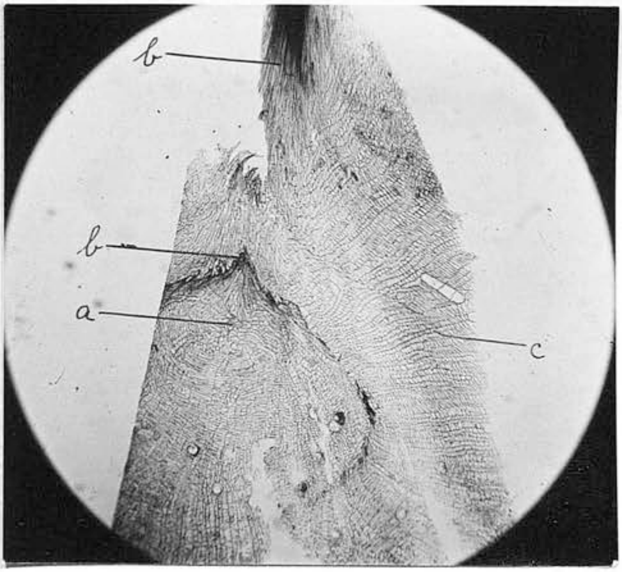


Fig. 1.

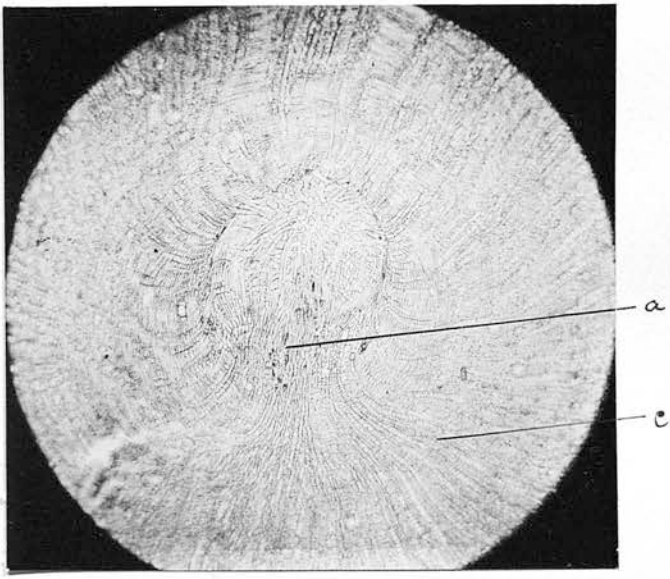


Fig. 2.

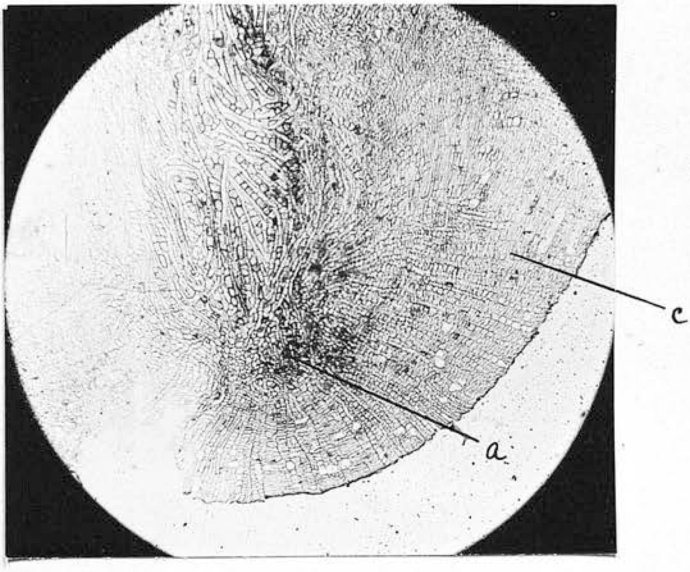


Fig. 3.

Plate 31.

Fig. 1. Globular shoot with core of compressed and lignified cells of latent bud. [redacted]. Trans. sect. x 30.

Fig. 2. The same x 60.

Fig. 3. Globular shoot with core of compressed and lignified cells of latent bud. [redacted]. Trans. sect. x 45.

(a) Core.
(b) Wood tissue of globular shoot.

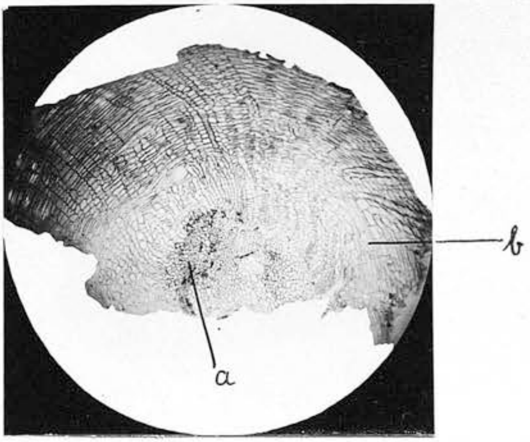


Fig. 1.

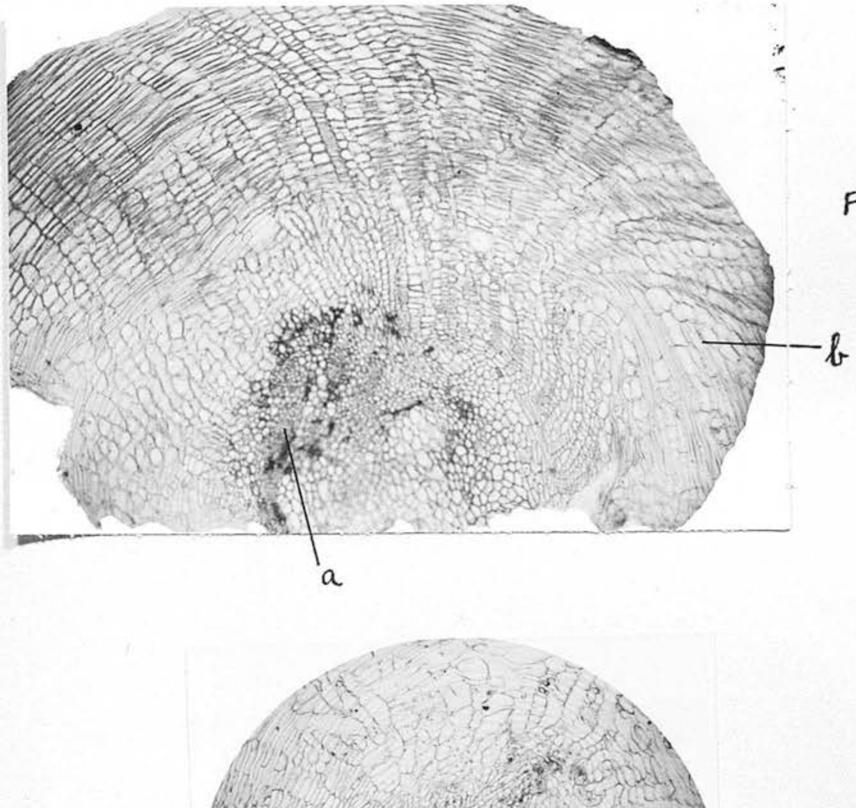


Fig. 2.

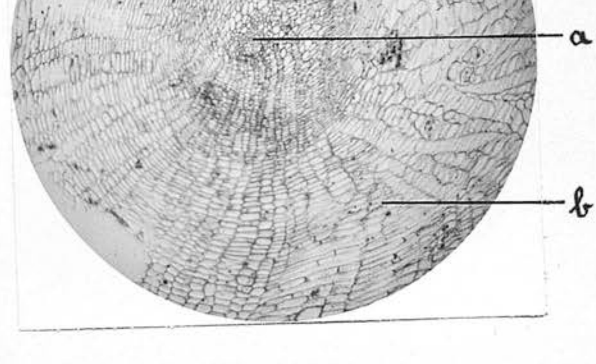


Fig. 3

Plate 32.

Fig. 1. Globular shoot with core of compressed and lignified cells of latent bud, [redacted]. Trans. sect. x 50.

Fig. 2. Globular shoot with core of compressed and lignified cells of latent bud. [redacted]. Trans. sect. x 35.

~~Fig. 3. The same~~

(a) Core.
(b) Cells with tannin content.
(c) Wood tissue of globular shoot.

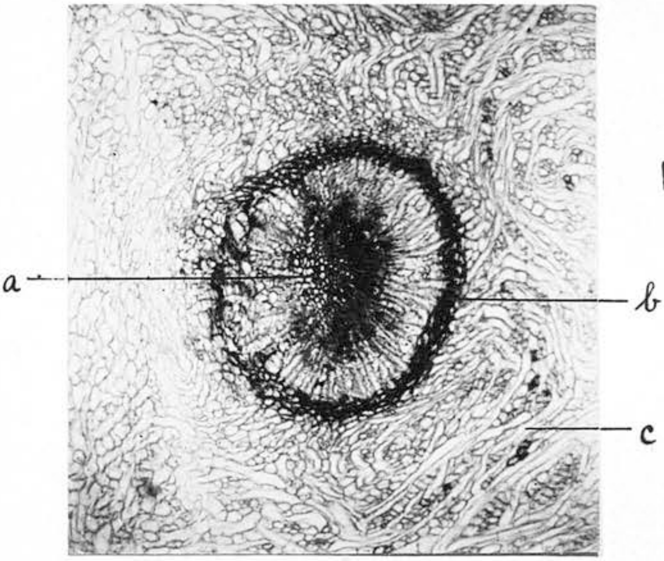


Fig. 1.

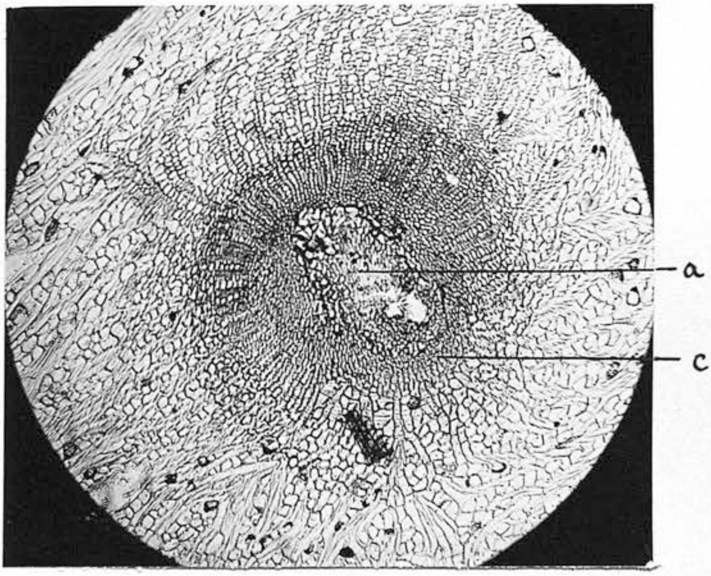


Fig. 2.

Plate 33.

Fig. 1. Globular shoot with core of compressed and lignified cells of latent bud. [redacted]. Occluded wound area present. Trans. sect. x 25.

Fig. 2. Globular shoot with core of compressed and lignified cells of latent bud. [redacted]. Trans. sect. x 70.

Fig. 3. Core similar to preceding. Taken from an old leaf scar. Trans. sect. x 225.

(a) Core.
(b) Occluded wound area.
(c) Wood tissue.

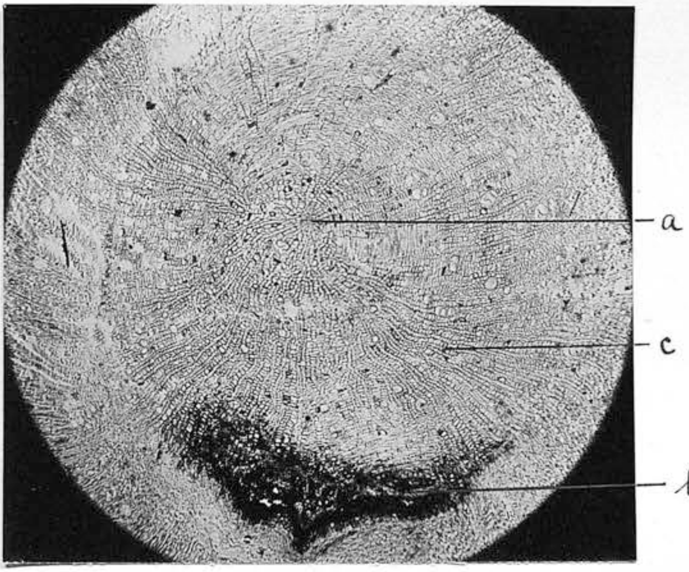


Fig. 1.

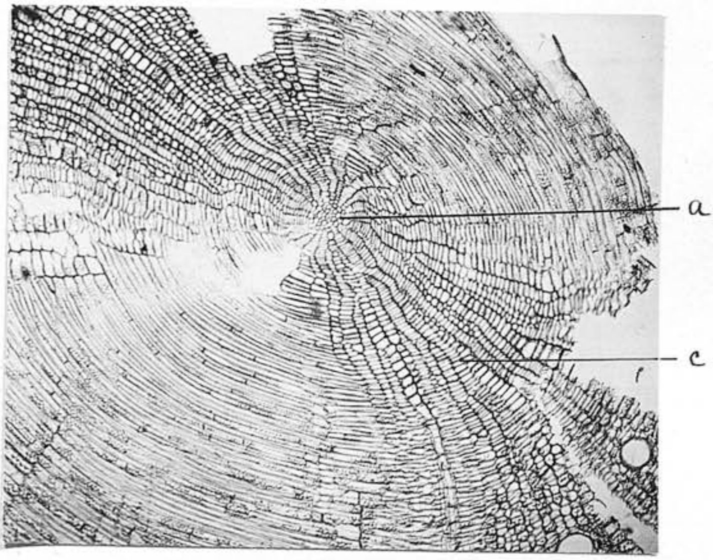


Fig. 2.

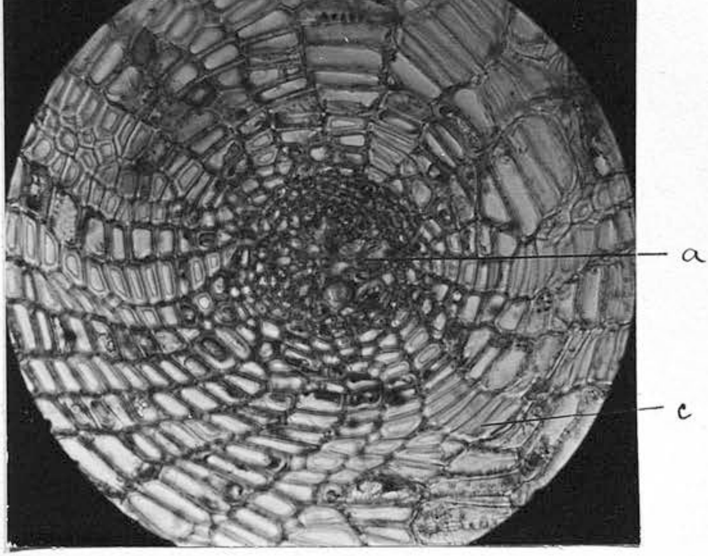


Fig. 3.

Plate 34.

Fig. 1. Globular shoot with rudimentary vegetative point, completely enclosed in stem cortex. Long. sect. x 50.

Fig. 2. Globular shoot with rudimentary vegetative point, completely enclosed in stem cortex. Long. sect. x 30.

Fig. 3. Globular shoot with rudimentary vegetative point, completely enclosed in stem cortex. Primordia of lateral shoots in overlying cortex. Long. sect. x 20.

(a) Primordia of organs.
(b) Cortex.
(c) Wood tissue of globular shoot.
(d) Primordia of lateral shoots.

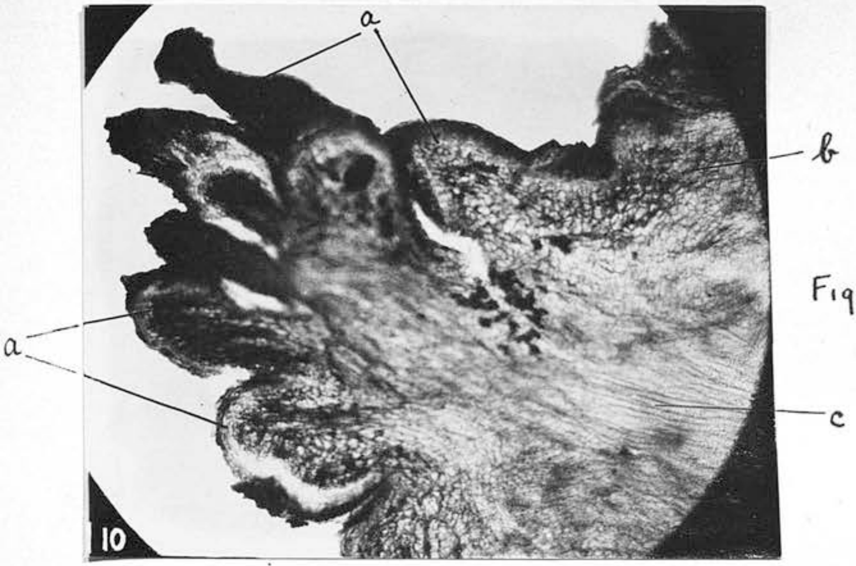


Fig. 1.

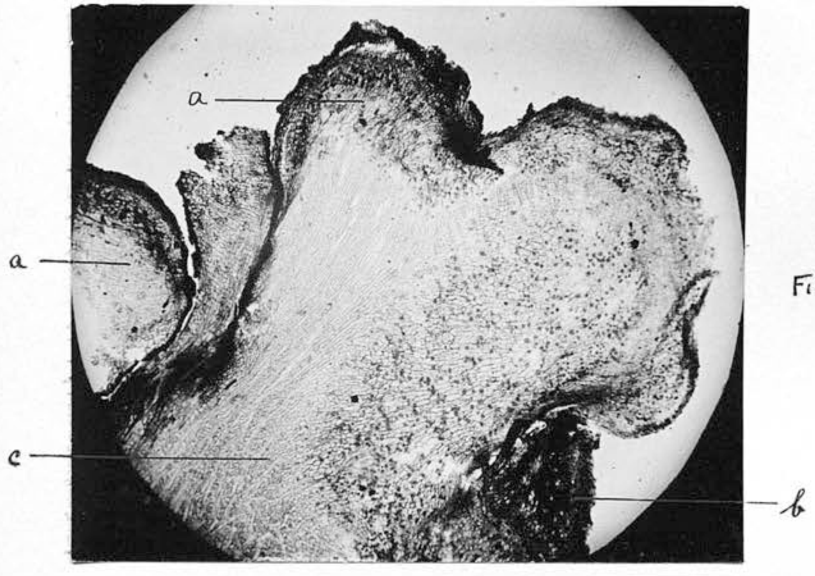


Fig. 2.

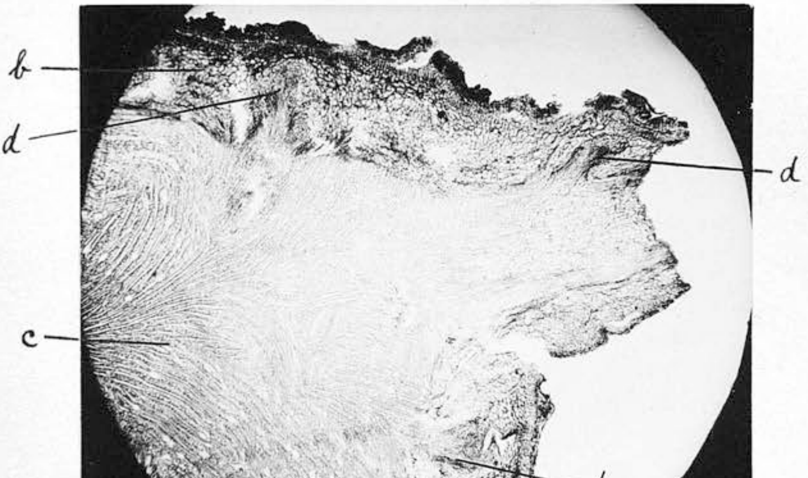


Fig. 3.

Plate 35.

Globular shoot with rudiments of vegetative point enclosed in stem cortex. x 30.

(a) Primordia of organs.

(b) Cortex.

(c) Wood tissue.

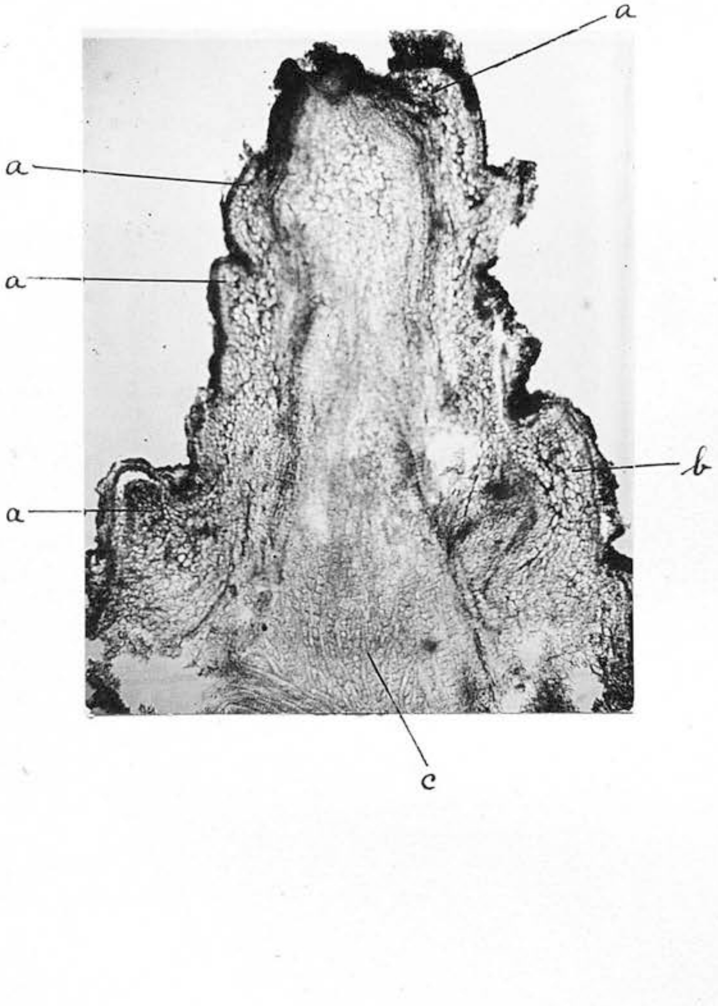

a
a
a
a
b
c

Plate 36.

Fig. 1. Globular shoot with bud trace occluded by the developing wood tissue. Trans. sect. x 40.

Fig. 2. Globular shoot with two vascular projections. Trans. sect. x 20.

Fig. 3. Globular shoot with vascular projection occluded by wood tissue. Trans. sect. x 20.

(a) Vascular connecting strand occluded by subsequent growth of wood tissue.

(b) Vascular connections.

(c) Occluded wound area.

(d) Wood tissue.

PLATE 36.

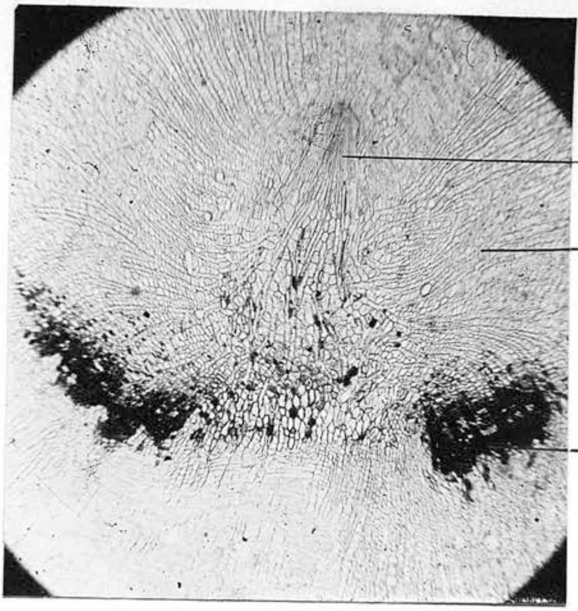


Fig. 1.

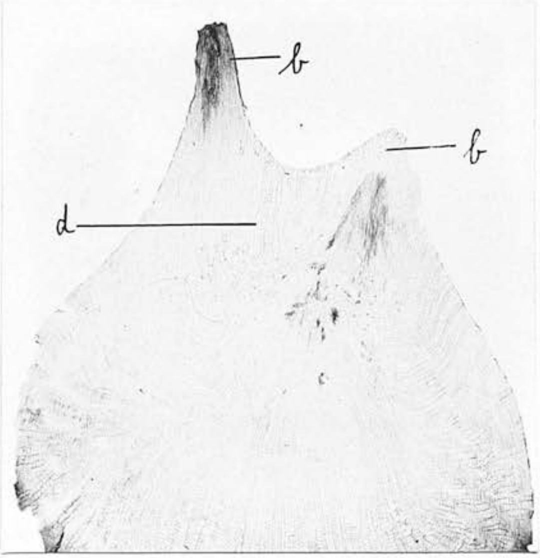


Fig. 2.

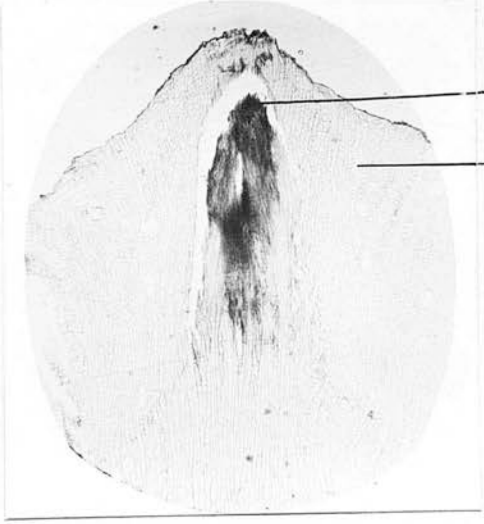


Fig. 3.

Plate 37.

Fig. 1. Globular shoot. Core of cells of latent bud [redacted] compressed and lignified. Wood tissue containing cells with tannin content. Trans. sect. x 35.

Fig. 2. Compound globular shoot formed by fusion of two adjacent developing shoots. Trans. sect. x 20.

Fig. 3. Compound globular shoot similar to preceding. Trans. sect. x 50.

(a) Core.
(b) Wood tissue.
(c) Tannin cells.

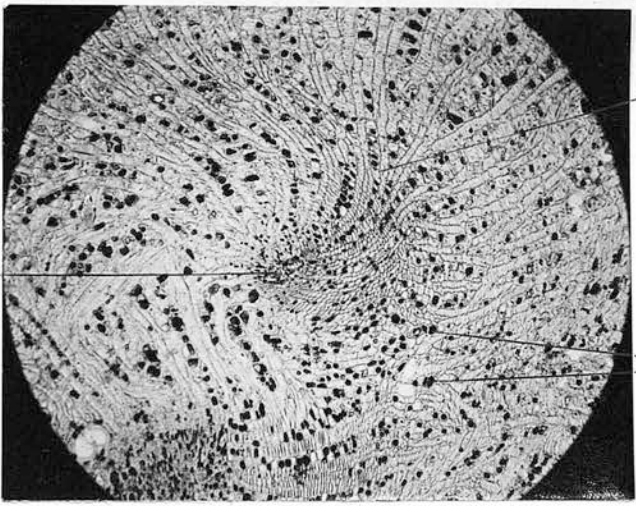


Fig. 1.

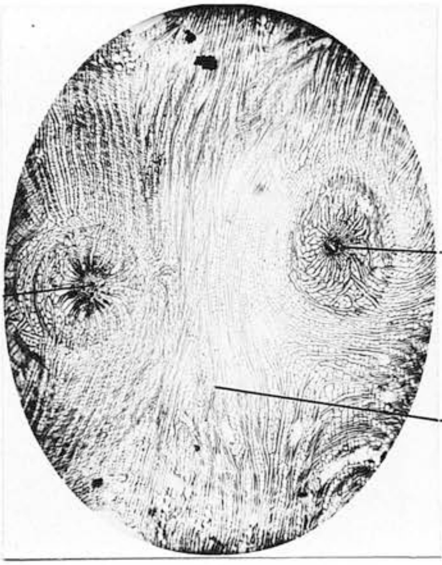


Fig. 2.

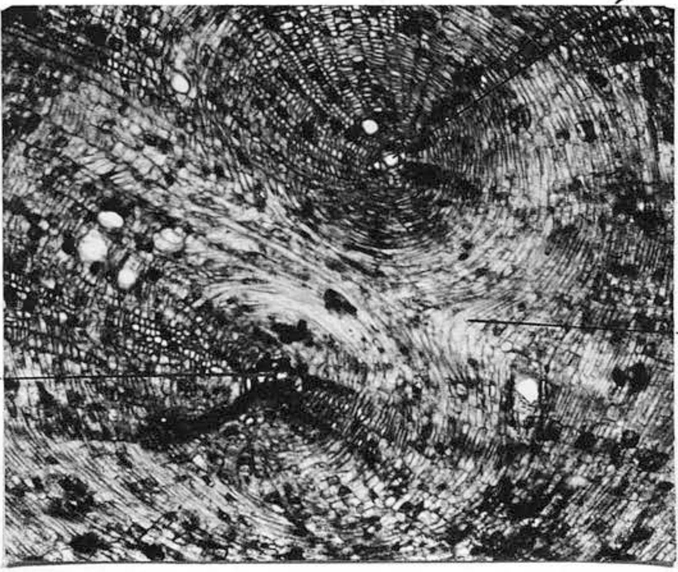


Fig. 3.

latent bud tissue

Plate 38.

Fig. 1. Globular shoot with core derived from [redacted]; bud trace present. Occluded wound area. Trans. sect. x 25.

Fig. 2. Globular shoot core derived from undifferentiated meristematic tissue. Trans. sect. x 30.

Fig. 3. Globular shoot core derived from lignified meristematic tissue. Occluded wound area present. Trans. sect. x 40.

(a) Core.
(b) Bud trace.
(c) Occluded wound area.
(d) Wood tissue.

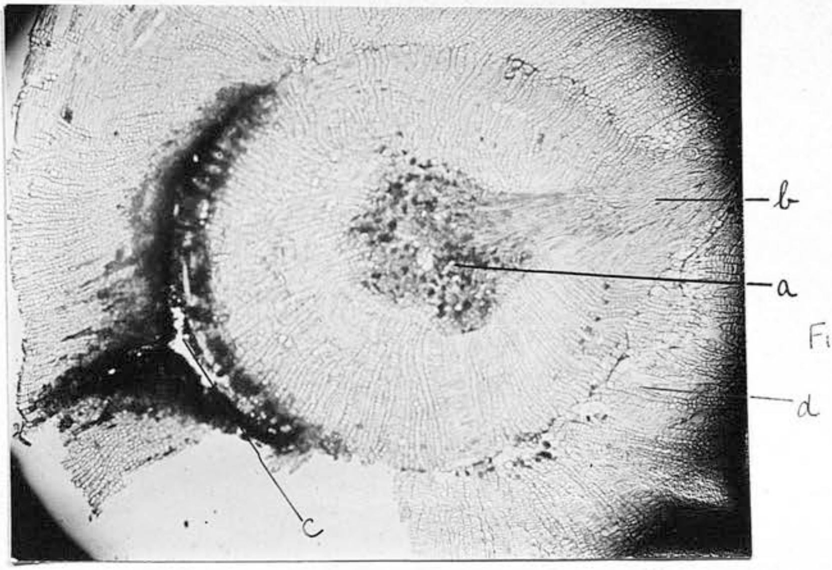


Fig. 1.

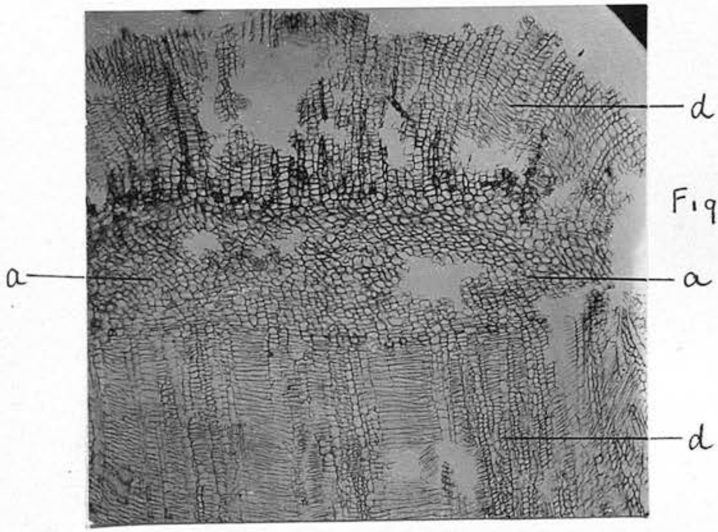


Fig. 2.

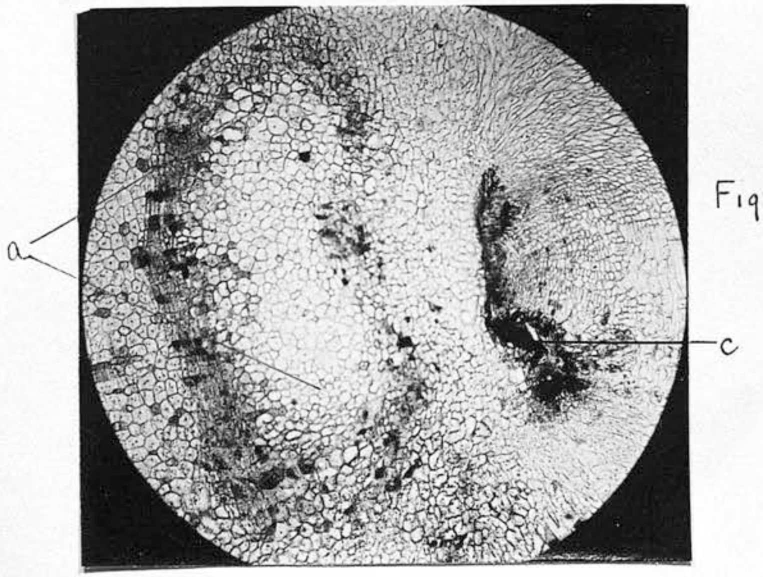


Fig. 3

Plate 39.

Fig. 1. Globular shoot with core derived from undifferentiated meristematic tissue containing many tannin cells. Trans. sect. x 25.

Fig. 2. Globular shoot with occluded wound areas. Trans. sect. x 10.

Fig. 3. Globular shoot with occluded wound areas. Trans. sect. 10.

(a) Core.
(b) Tannin cells.
(c) Wood tissue.
(d) Wound areas.

PLATE 39.

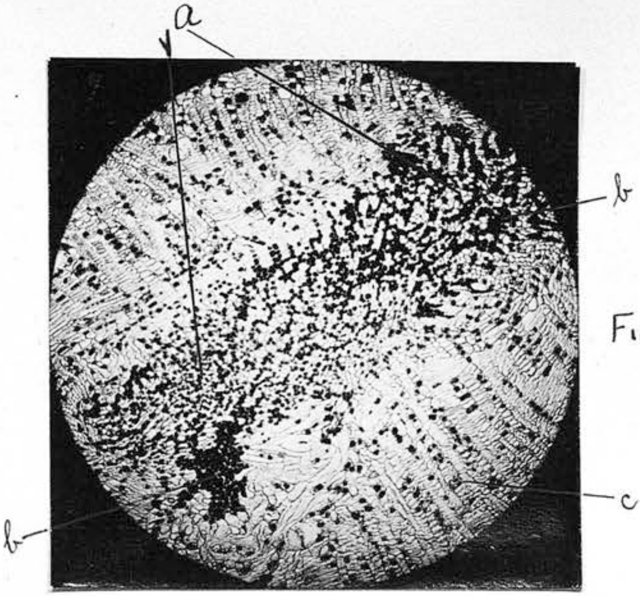


Fig. 1.

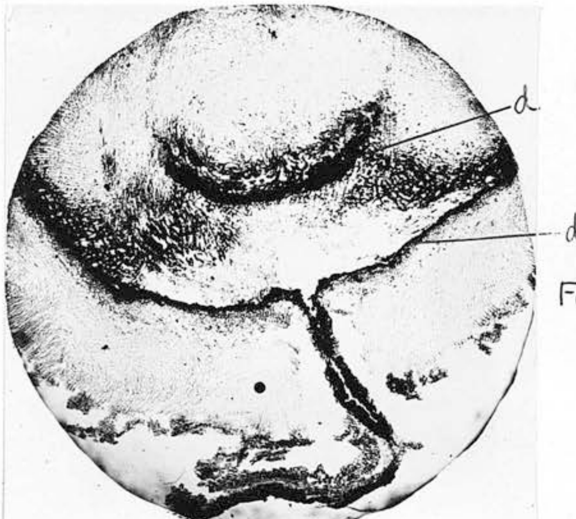


Fig. 2.

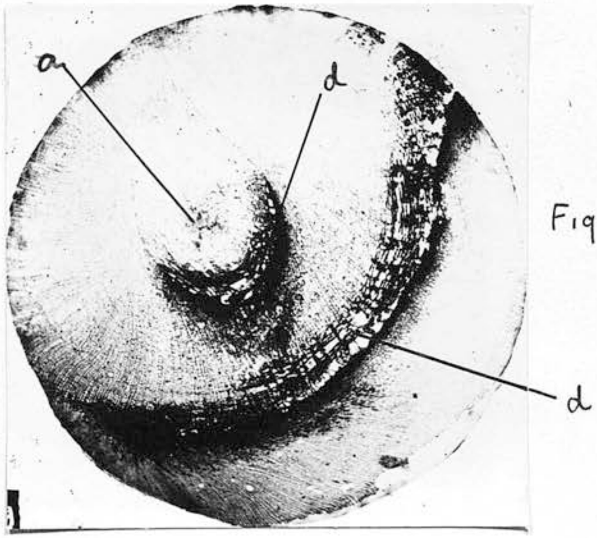


Fig. 3.

Plate 40.

Fig. 1. Globular shoot with wound area not occluded. Taken from an old leaf scar on stem. Trans. sect. x 10.

Fig. 2. Globular shoot with areas of tannin cells indicating wound areas. Trans. sect. x 10.

Fig. 3. Globular shoot with wound area in process of occlusion. Trans. sect. x 25.

(a) Wound area.
(b) Tannin cells.
(c) Wound callus.
(d) Cortex.

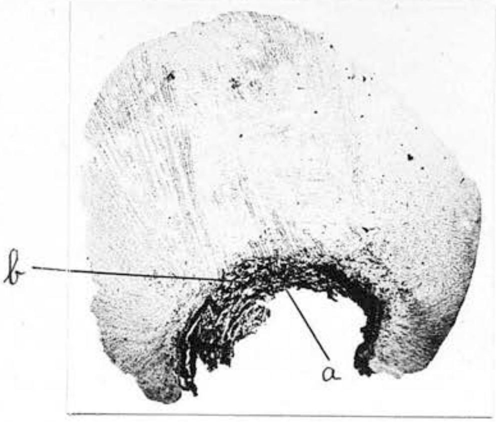


Fig. 1.

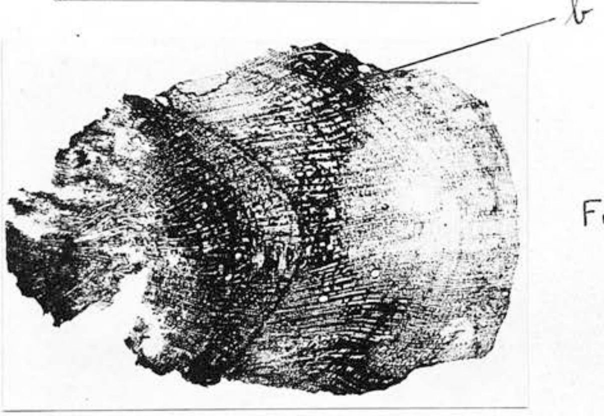


Fig. 2.

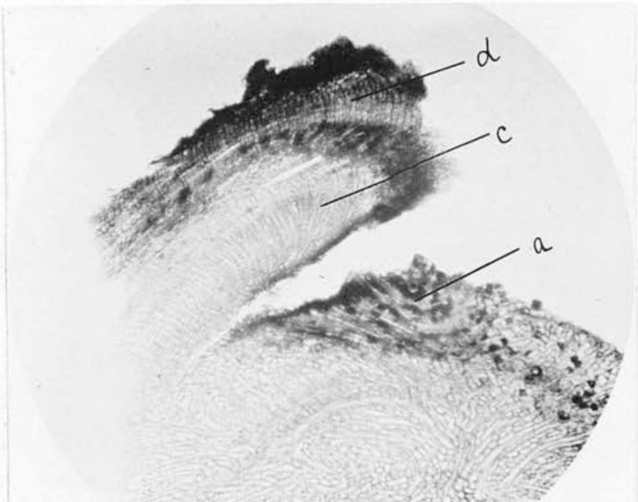


Fig. 3

Plate 41.

Fig. 1. Cortex overlying globular shoot with primordium of lateral shoot from the globular shoot. Trans. Sect. x 25.

Fig. 2. Cortex overlying globular shoot with vascular strand and rudimentary vegetative point traversing cortex towards the exterior. Trans. sect. x 50.

Fig. 3. Cortex overlying globular shoot with vascular strand and rudimentary vegetative point traversing cortex towards the exterior. Trans. sect. x 25.

(a) Cortex of stem.
(b) Primordium of lateral shoot.
(c) Exterior side.
(d) Interior side.

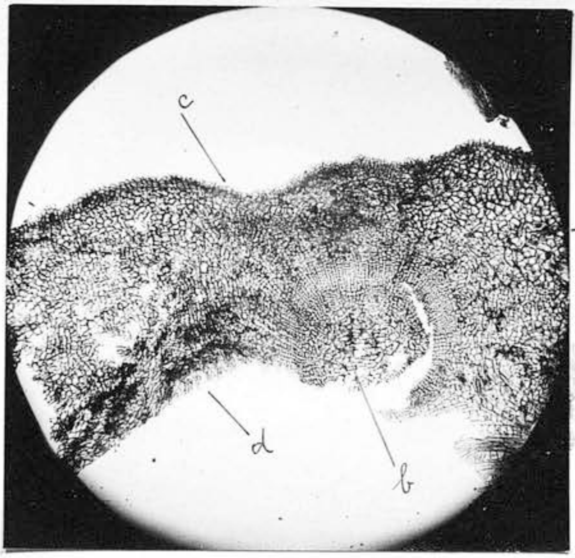


Fig. 1.

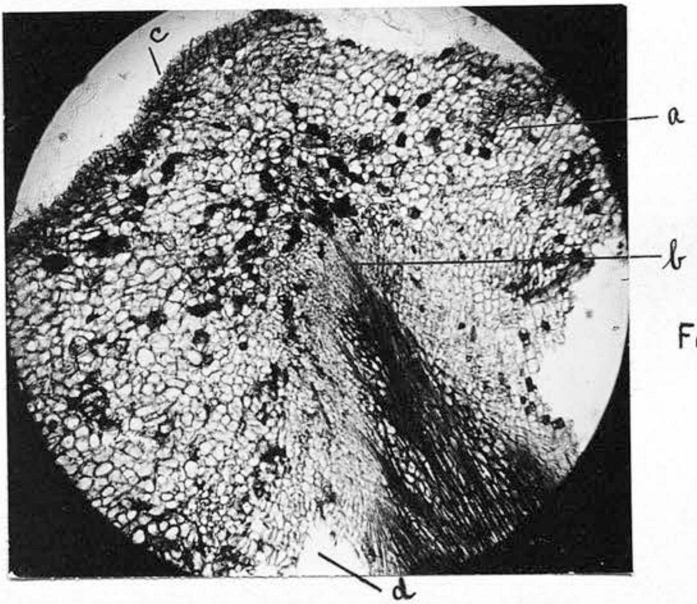


Fig. 2.

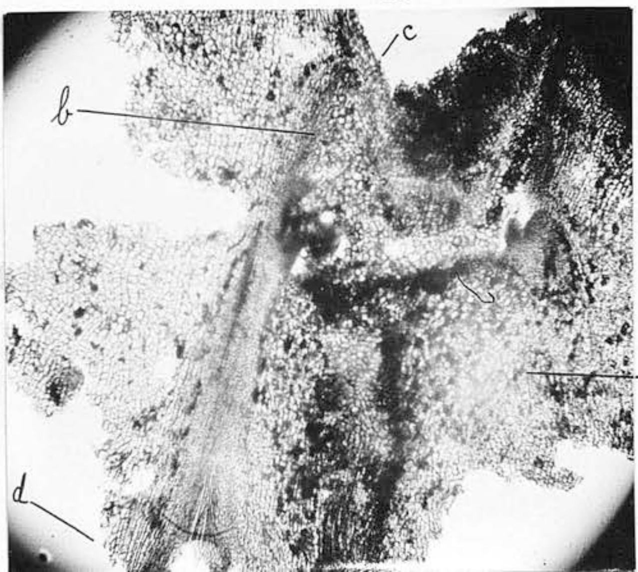
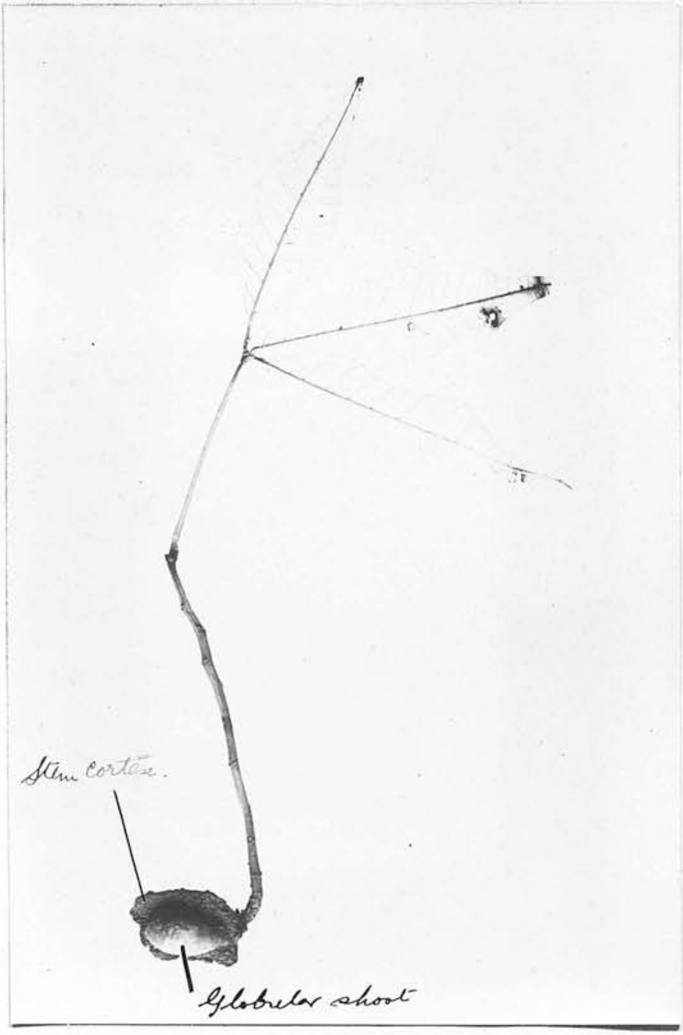


Fig. 3



Globular shoot with leafy shoot sprouting from it. No vascular connection with the stem wood.