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ANATOMY OF THE AXIS OF THE BANANA[1]

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(WITH TEN FIGURES)

Introduction

Although the development and anatomy of the inflorescence, the root, and the leaf of the banana have recently been the subject of studies by WHITE (14), ACQUARONE (1), and the writer (10, 11, 12), no detailed investigation appears ever to have been made of the anatomy of the axis. Numerous incidental references to the rhizome of the banana may be found in the literature, however, to the more important of which allusion will be made in due course. In the present paper the term "axis" is employed in its widest sense, to include the rhizome or bulb, the aerial stem, and the rhachis of the inflorescence. This study was begun late in 1928 at the Research Station of the United Fruit Company near Almirante, Panama, where only a preliminary survey of the subject was attempted, and was completed during 1930 at the Lancetilla Experiment Station of the Tela Railroad Company, near Tela, Honduras. In Panama a seeded banana known as "Martini," a variety of *Musa sapientum* sub. *seminifera*, was used; while in Honduras, since this type was not available, I employed the well known Gros Michel variety, the chief banana of commerce. No important anatomical difference between the bulbs of the two varieties was observed.

[1] Botanical contribution from the Johns Hopkins University no. 115. The work reported in this paper was begun while the writer held a Johnston Scholarship of this University, and completed under a Fellowship of the National Research Council of Washington.

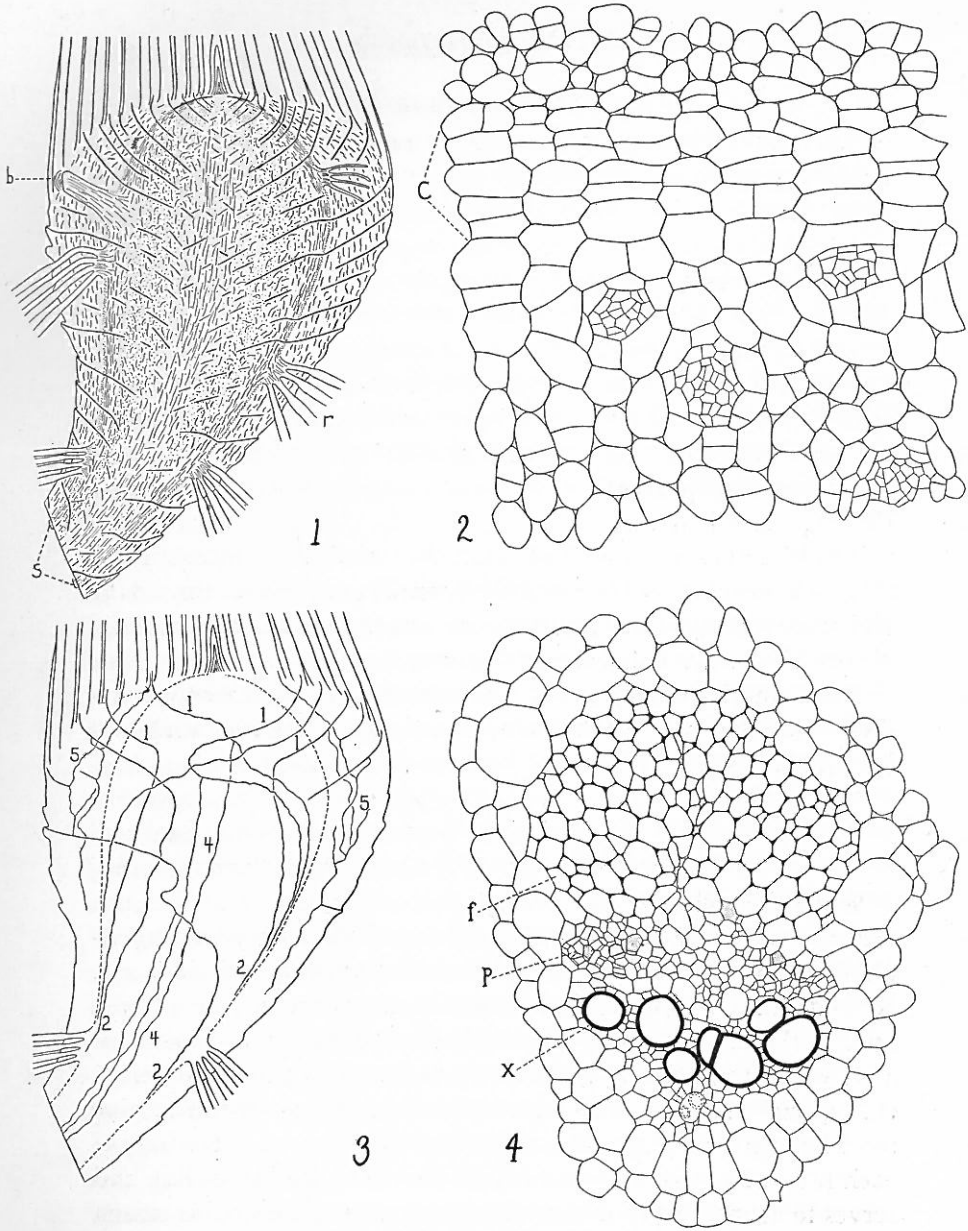
General features

The banana plant has a thick, many branched rhizome, each short branch of which expands rapidly toward its apex and is known by planters as a "bulb." From the upper surface of the bulb arises a rosette of leaves with elongated leaf sheaths closely overlapping to form a tall false-stem. The sides and older portions of the bulb are covered with the close-set circular scars left by the detachment of former leaves. Ultimately the axis elongates, pushes up through the center of the false-stem, and emerges from its upper extremity to bear the flowers and fruit. As in other herbaceous plants, the life of this particular shoot ends with its production of fruit, but the bulb at its base sends forth branches which develop into new flowering shoots.

The lateral buds of the bulb are rather unusual in their position. They are situated, not in the axils of the leaves, but on the side of the stem opposite these, between the two free margins of the leaf sheath (10, figs. 1, 2). This circumstance suggests that the rhizome of the banana is in reality a sympodium; that the apparently lateral bud is in reality a terminal bud of arrested development which has been pushed to one side by the development of the true lateral bud, originally situated between it and the axil of the leaf. Although this view of the situation would bring the banana into morphological conformity with the majority of plants, there appears to be nothing beyond the peculiar position of the buds to support it.

The lateral buds are unable to develop until the leaf sheaths covering them die and decay away. At first they grow horizontally outward and produce large, thick scales representing the leaf sheaths alone. After they reach a certain size, the leaf sheaths become sensitive to gravity and bend upward, erecting the still rudimentary false-stem (SKUTCH 13). The rhizome more slowly alters the direction of its growth until the growing point faces upward, and increases in thickness until a bulb is formed. In the Gros Michel variety this bulb attains a diameter of more than 30 cm. and a height of 35 cm. or more.

The massive central cylinder is readily distinguished from the thick cortex, in either a longitudinal or transverse section of the bulb, by the plexus of large bundles of generally horizontal course which



FIGS. 1–4.—Fig. 1, median longitudinal section through bulb of large sucker, showing diagrammatically the distribution of vascular bundles. Portions of bundles in plane of section represented by lines, bundles cut transversely by dots; cambium (near apex) indicated by heavy line; very young root rudiments by large black spots: *b*, lateral bud; *r*, lateral root; *s*, secondary zone. ×0.3. Fig. 2, cross-section through cambium (*c*) in region where its derivatives are forming longitudinal bundles, showing four bundles in various stages of differentiation. Camera lucida, ×190. Fig. 3, diagram showing courses of various types of vascular bundles in bulb. Broken line indicates boundary between cortex and central cylinder. The numbers are those under which each type is described in text (cf. fig. 1). ×0.3. Fig. 4, cross-section of leaf-trace bundle just after entering central cylinder of bulb: *f*, fibers; *p*, phloem; *x*, xylem. ×76.

occupies the outer region of the former (fig. 1). Just within the horizontal bundles is a narrow zone where all the bundles, although flexuous, run in a generally longitudinal direction. Both longitudinal and horizontal bundles are distinguished from all others found anywhere in the axis or leaves by their amphiphloic structure. Since they arise from a cambium-like meristem, they are designated as "secondary bundles." The bundles in the primary portion of the central cylinder present a bewildering disarray, especially in longitudinal section; for it is only the upper portions of the leaf-trace bundles which follow a straight course for any considerable distance, and short lengths of the other bundles are encountered running in every direction apparently at random. In a cross-section of the bulb, the secondary longitudinal bundles may be distinguished from the primary bundles of the central cylinder by their more even spacing and the absence of bundles with a tangential or oblique course in the region they occupy. They are, of course, interrupted by the radially directed leaf-trace bundles entering from the cortex.

The adventive roots arise, as in the rhizomes of other monocotyledons, from the surface of the central cylinder, almost invariably in longitudinal groups of four.

Rhizome

Origin of secondary bundles and adventive roots

While the collateral primary bundles differentiate directly from the massive tissues produced by the apical meristem, the amphiphloic bundles of the secondary zone arise from a special meristem. A cambium-like layer is of wide-spread occurrence just behind the apex of the rhizomes of a number of monocotyledons, and is associated with the production of adventive roots. Mangin (4) recognized this special meristem, which gives rise, not only to the adventive roots but also to a plexus of bundles which centers about the base of each root, or each group of them where they arise in a series, and serves to connect them with the leaf-trace bundles. For this reason he designated the meristem as the "couche dictyogène," and the plexus of bundles to which it gives rise as the "réseau radicifère." Unlike the more enduring cambium of such arborescent monocotyledons as *Dracaena* and *Yucca*, it is associated only with the produc-

tion of the roots, and does not occur on portions of the stem or rhizome where roots are not formed. Thus in the rhizome of *Iris florentina*, which creeps along the surface of the ground and bears roots on its lower side only, it is only on this side that the "réseau radicifère" appears. Later PETERSEN (5) described the same phenomenon, and discovered the fugacious cambium near the apex of the rhizome in a number of families of monocotyledons which he examined, with the exception of the Orchidaceae. He concluded that, "There exists among the monocotyledons a series of transitions from stems in which there is no localized meristem—here we do not refer to the growing point—to those where there arises a secondary meristem producing cells in radial series which effects an unlimited growth in thickness." MANGIN had come practically to the same conclusion ten years earlier.

In time of origin the cambium[2] of the banana rhizome differs from that generally encountered in dicotyledonous shoots in not being separated from the apical meristem by a considerable length of stem in which no tangential divisions of the procambial cells take place. In the banana the cambium may already be distinguished at about 5 mm. behind the rounded apex of the bulb, in a region which seems still a part of the growing point, for the surrounding cells are immature and divide rapidly. Thus the cambium is closely related to the primary growing point, and possibly should be considered merely as a special development of it: that here at the outer surface of the central cylinder it remains active longer than elsewhere and assumes a special function. The length of the short cambium cells hardly exceeds their width. The number of tangential divisions which each undergoes is limited; six cells are frequently encountered in a radial series, more rarely seven or eight. Everywhere the cambium is interrupted at frequent intervals by the radial leaf-trace bundles, which

[2] I have doubted the propriety of calling this meristem a cambium, since it differs in so many important respects from the true cambium of gymnosperms and dicotyledons. The bundle-forming meristem of the arborescent Liliiflorae, etc., which has much more in common with the meristem of the banana than with the dicotyledonous meristem, is also designated by this term, which in a loose way is applied to any meristem which undergoes many divisions all in the same plane. Hence for want of a better word it seems best to retain this in the present case. Perhaps a strict terminology would demand a special designation for the type of meristem exemplified in *Dracaena*, *Musa*, etc.

differentiate early. It reaches its greatest activity between 1 and 2 cm. from the apex, where numerous vascular bundles are differentiated from its daughter cells, entirely toward the interior, for it adds nothing to the thickness of the cortex. An entire longitudinal segment of a bundle, including all the various elements of xylem and phloem, is derived from the divisions of a single cell, as in the arborescent Liliiflorae (fig. 2). The first dividing wall may be either tangential or radial in position, apparently more commonly the latter. Thence walls are formed rapidly in all planes, and the small cells which result enlarge and differentiate to form the amphiphloic vascular bundle.

At about 2.5 cm. from the apex the last longitudinal bundle is formed, and horizontal bundles begin to differentiate from the daughter cells of the cambium. These are cut out from a single cell in much the same way as the longitudinal bundles, save that the walls now formed are horizontal instead of vertical. The change from the production of longitudinal to horizontal bundles is abrupt, the plane of division of the mother cells being, so to speak, rotated through 90° without any significant alteration in the shape of the cambium cells. The first rudiments of the horizontal bundles are encountered beneath a root primordium. In the region where horizontal bundles are produced the cambium becomes rather irregular, and at about 3.5 cm. from the apex, where the last bundles begin to differentiate, it dies out altogether. Thus its entire activity extends over an arc hardly more than 3 cm. in length; in the first 2 cm. it produces longitudinal bundles, in the last centimeter, horizontal bundles.

As has been stated, the lateral roots are also initiated by the cambium. At the points where these arise, the cambium becomes very active and divides repeatedly in all planes, forming a common primordium in the shape of a little mound of tissue from which are developed, in acropetal succession, the growing points of the four adventive roots which almost invariably arise together, always in a linear series. Thus there is direct continuity of meristematic tissue from the apical growing point of the bulb to the growing point of the root. MANGIN (4) states that in *Convallaria*, *Sisyrinchium*, *Ruscus*, and *Zea* the body of the root is alone formed from the cambium, while the root cap is produced by the innermost cortical cells. Refer-

ence to his plate 10, fig. 18, of *Ruscus aculeatus*, shows that it is extremely difficult to follow, in the very young root primordium, any clear line of demarcation between cells of cortical and cambial origin. Moreover, as described later, the cambium itself is constantly renewed from the inner cells of the cortex. In the banana it appears that the growing point of the root is derived in its entirety from the cambium. The cortical cells immediately in front of it are soon crushed by its rapid development, and hence further meristematic activity on their part is impossible. The common primordia of the groups of four roots are first clearly visible to the naked eye at about 1.5 cm. behind the apex, and the growing point of the lowest root, the most advanced of the group, is already distinguishable under the microscope at this point.

Since the number of times each cambial cell divides is strictly limited, it is necessary that the cambium be renewed from some source. This is provided by the innermost cells of the cortex, which remain undifferentiated longer than the primary tissues in other regions. As the cambium cells exhaust their possibilities of division, these cortical cells just outside of them begin to divide by tangential walls and take their places in the cambium. At the same time other cells in the cortex differentiate into the innermost cortical bundles. As in the secondary bundles of the central cylinder, each segment of the length of these cortical bundles is derived from a single mother cell.

The cambium in the banana accordingly differs in an important respect from the true cambium of dicotyledons, in which there is an initial cell for each radial row which divides tangentially an indefinite number of times. The former type of meristem is more characteristic of the monocotyledons than a true cambium. RÖSELER (7) pointed out that the cambium of the arborescent Liliiflorae divides according to different laws from that of conifers and dicotyledons, and demonstrated the absence of initial cells. SCHOUTE (8) found that in the stem of *Cordyline rubra* and other arborescent Liliaceae the cambium during the earlier stages of secondary thickening is of the irregular type just described, for which he proposed the term "Etagencambium" or "storied" cambium; but at a later period the meristematic cells continue to divide indefinitely and so a true initial

cambium arises. LINDINGER (3) states that in the roots of *Dracaena draco* and *D. fragrans* the early storied cambium is also succeeded by an initial cambium as the root becomes older. SCHOUTE (8), and later PHILIPP (6), investigated the origin of cork in monocotyledons and found that in the great majority of cases this is produced almost exclusively by an "Etagencambium," that is, each cork-producing cell exhausts its meristematic potentialities after producing a limited number of cork cells, when its place is taken by another cell lying on its inner side. Only exceptionally, as in some species of Araceae, is cork in monocotyledons produced by a true initial cambium.

The tracheids in the secondary bundles of the banana rhizome elongate by sliding growth. Examination of a longitudinal section of a mature bundle shows that the numerous sieve tubes are all approximately of the same length; and the transverse sieve plates, with few exceptions, fall into definite groups very nearly in a plane. These groups evidently represent the positions of the end walls of the mother cell from which a segment of the bundle was derived. All the phloem cells between successive groups are evidently the products of the same mother cell. Only occasionally is an isolated sieve plate found between the groups in which the great majority of them lie, indicating that a transverse division has taken place in a sieve tube in the length of a single mother cell. The distance between the groups of sieve plates varies from 288 μ to 576 μ. Although the exact length of the tracheids in the secondary bundles has not been determined, they are very much longer than this. Hence it appears that the tracheids have elongated more than their sister cells, the sieve tubes, pushing into segments of the vascular bundle derived from other mother cells. SCOTT and BREBNER (9) conclude, from studies more especially directed to this point, that the tracheids of *Dracaena*, *Yucca*, and *Aristea* elongate by sliding growth.

In the obliquely downward course which they follow, the adventive roots may have to penetrate the solid parenchymatous tissue of the cortex, in the thicker portion of the rhizome, for a distance of 6–7 cm. before they reach the surface. The tips of roots at all stages in their progress through the cortex were examined, both in hand sections of fresh material and in solid blocks of tissue, cut so as to expose the growing point, and viewed under the binocular microscope,

and it can definitely be stated that a "digestive pocket," in the sense of a cavity in the tissue filled with fluid, is not present. The root cap touches on all sides the thin-walled parenchyma cells through which it pushes its way, and the cells directly before it are always somewhat crushed. They are, however, prepared for the penetration of the root by some digestive action, probably by enzymes secreted from the cells of the already massive root cap. The tissue immediately in front of the root tip, to the distance of about 1 mm., feels distinctly softer when touched with the point of a needle than elsewhere in the cortex, and collapses at the slightest pressure. The walls of cells not yet touched by the root cap are already distorted and show signs of breaking down. The amount of actually crushed tissue directly in front of the growing point is very slight, less than one would expect if no digestive action took place; and moreover the cells of the root cap themselves, in their rounded form, give no evidence of being subjected to pressure.

The amount of crushed tissue between the sides of the mature root and the surrounding cortical cells is variable. In some places there is practically no débris of collapsed walls, while elsewhere there may be considerable. On the whole, the absence of the walls of crushed cortical cells from large areas along the length of the root indicates that they have been dissolved by some enzymatic action which, however, is not complete. To summarize, the advance of the root through the tissues of the cortex is facilitated through the softening of the cells which oppose it, but this is accomplished by a digestive action which does not act with sufficient rapidity to dissolve their walls in advance of the root and form a free space or digestive pocket for its reception. The process of digestion, however, is continued until much of the débris of cell walls disappears. Normal living cells are not crushed by the root cap.

When it arrives within a few millimeters of the surface of the rhizome, the root tip broadens abruptly. It may in a distance of a few millimeters increase its diameter from 1.5 to 3 mm.

Courses and composition of vascular bundles

In order to follow the courses of the vascular bundles it was found necessary to differentiate them from the surrounding parenchyma by staining. To accomplish this, large suckers with broad leaves, and

bulbs in about the stage of that reproduced in figure 1, were selected and dug up in the early morning while the dew was still heavy on the leaves and the tracheids flooded with water. With a stout machete, the bulb of the sucker was first severed from the parent plant, and the roots were cut through in the soil at a distance of about 8 or 10 inches from the bulb. Then the bulb was dug up, leaving about the remaining length of the roots a ball of earth, which was later washed away under running water. After the bulb had been carefully cleansed, the sucker was tied upright against a support and the ends of a number of the best roots cut off again under water and at once inserted into test-tubes filled with the stain. Eosin and trypan blue, in 1 per cent aqueous solution, were both employed. Trypan blue, because it is strongly absorbed by the walls of the tracheids and diffuses hardly at all into the surrounding parenchyma, gives a much more precise differentiation of the bundle than does eosin. When neighboring roots of the same plant are placed one in eosin and the other in trypan blue, the eosin rises through the bundles much more rapidly, apparently because the other is so quickly removed from solution by the walls of the tracheids through which it passes that the water flowing upward soon becomes colorless.

After the roots had been about five hours in the stains, on a bright day a sufficient number of bundles was usually found to be colored. Attempts to trace the course of the leaf-trace bundles in longitudinally halved bulbs were invariably failures, since the bundles which enter the center of the bulb rarely complete their courses on one side. It was found necessary to begin at the top of an entire bulb and dissect downward, a laborious procedure. The course of a bundle was frequently so tortuous that a portion of it was inadvertently cut away while clearing a nearby length upon which it doubled back, and so its continuation was irretrievably lost. Only a single bundle could be followed in one bulb, since in tracing this bundle it was necessary to pare away much of the surrounding tissue.

The following types of bundles may be recognized. The general course of each may be seen by referring to the corresponding number in figure 3.

1. PRINCIPAL LEAF-TRACE BUNDLES.—These are the large vascular bundles, containing protoxylem elements, which are found in the

longitudinal septa of the leaf sheaths (10). Upon entering the bulb they follow an almost straight radial course through the cortex, penetrate the secondary zone (and the cambium in the case of the younger bundles), and proceed toward the center of the central cylinder. As they near the center their course becomes irregular and tortuous, with many baffling twistings and turnings. Some pass, in this indirect manner, across the bulb and finally lead to roots on the side opposite their point of entry; others, when they reach the center, turn to the right or left; and still others double back and connect with roots on the side from which they entered. In any case, as they again near the secondary zone they gradually turn downward and slowly converge with the secondary bundles. Finally, entering the secondary zone, they continue downward as secondary bundles, until they at length form connections with the roots.

The composition of these bundles changes greatly from one end to the other of their course through the bulb. As they enter it from the leaf sheath they are collateral. The xylem of each bundle contains several small protoxylem elements which are early disrupted and their lumina occluded by the ingrowth of the neighboring parenchyma cells, as described in an earlier paper (10), and by several metaxylem cells of medium size with spirally thickened, unlignified walls. The phloem with its occluded early sieve tubes is surrounded by a heavy sheath of fibers with very thick but unlignified walls, while a few thin-walled fibers occur around the xylem portion. Many sterigmata lie along the outside of the sheath of fibers. As the bundle passes inward through the cortex, the walls of the fibers become thinner, with the thickening restricted to the corners of the cells, and have larger lumina. By the time it enters the secondary zone the tracheids, which were previously arranged in a triangle, have spread out into a crescent, the thickening of the fibers is distinctly collenchymatous, and the sterigmata have disappeared (fig. 4). In the center of the rhizome the fibers accompanying each bundle are still further reduced in number and the thickening at the corners becomes very slight. The protoxylem is reduced to one or two elements usually not occluded. The metaxylem tracheids in this region are thickened by numerous, low-pitched spiral bands. Lignified elements are entirely absent.

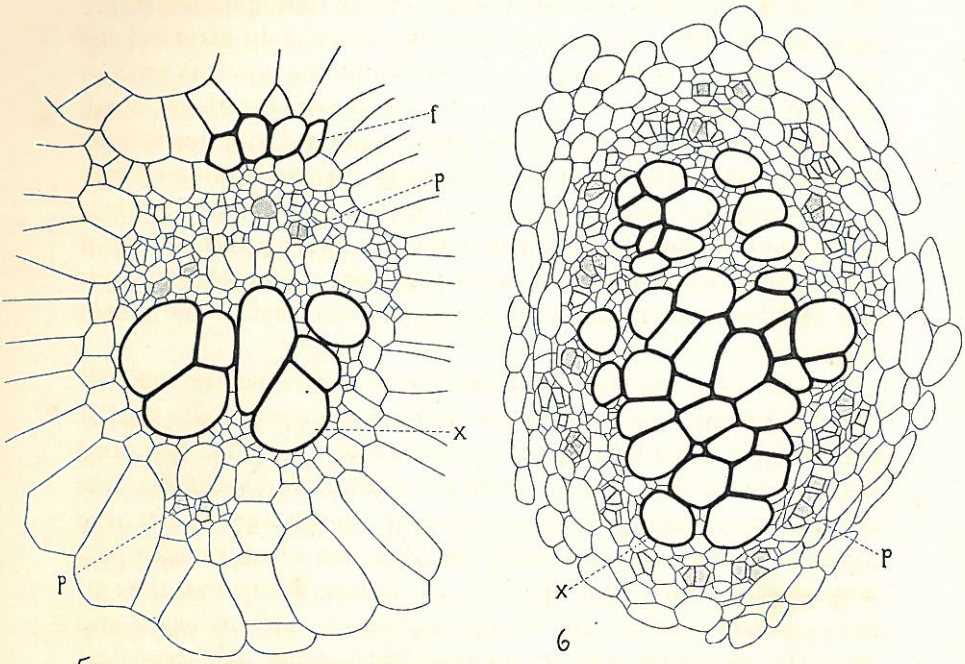
As the bundle passes downward and outward to meet the secondary zone, the protoxylem elements completely disappear and there is still further reduction in the number of fibers. As the bundle approaches the secondary zone, it acquires a few sieve tubes on its inner side, but still retains a few fibers (fig. 5). Upon entering the secondary zone, the phloem cells increase until they completely surround the xylem, while the fibers drop out of the bundle (fig. 6). The walls of the sieve tubes here as elsewhere are slightly thickened by broad, reticulated bars. Thus a collateral bundle equipped with protoxylem elements, fibers, and sterigmata gradually changes into an amphiphloic bundle devoid of any of these elements. The bundles differentiated from the cambium are merely the downward prolongations of the leaf-trace bundles, serving to form the connection between them and the adventive roots. They finally become part of the plexus about the base of a group of four roots.

Not all of the leaf-trace bundles which enter the central cylinder progress inward as far as its center. A large number (usually smaller bundles with fewer protoxylem elements than those just described or else none at all), after proceeding a greater or less distance into the central cylinder, bend rather abruptly to the right or left (the direction seems to be indifferent) and run for some distance in a tangential direction, girdling the bulb at the same time that they incline gradually downward. Finally they turn outward again and enter the secondary zone as amphiphloic bundles like those last mentioned. The tangential courses of these bundles cause them to be cut transversely in a longitudinal section of the bulb, such as figure 1, and the presence of the very numerous bundles encountered in cross-section in the intermediate zone of the central cylinder is at first sight a most confusing feature in the anatomy of the rhizome.

2. LONGITUDINAL SECONDARY BUNDLES.—These, as just explained, are the downward prolongations of the leaf-trace bundles. They are very large amphiphloic bundles of the type illustrated in figure 6. Together they form a zone at the outside of the central cylinder 3–6 mm. thick, in which the bundles occur three or four deep.

3. HORIZONTAL SECONDARY BUNDLES.—These, like the longitudinal secondary bundles, are very large and amphiphloic, often much larger and more complex than the longitudinal bundle chosen for

illustration (fig. 6). They form a plexus centering about the insertion of each group of four roots and anastomose with the longitudinal bundles, thus conducting water from the roots to the leaf traces. Since they form a system completely girdling the bulb, water enter-



FIGS. 5, 6.—Fig. 5, cross-section of leaf-trace bundle in lower portion of its course through bulb, on inner edge of secondary zone, showing transformation from collateral to amphiphloic bundle (note appearance of sieve tubes on inner side and great reduction in number of fibers). Fig. 6, cross-section of amphiphloic longitudinal secondary bundle. ×76.

ing through any one root can in case of need be distributed to the leaf-trace bundles ending on any side of the bulb. These bundles occupy a zone just outside the longitudinal bundles and more narrow than theirs, in which only one or two but occasionally three may be found on a radial line.

4. CENTRAL BUNDLES.—Connecting with the lower side of those leaf-trace bundles which penetrate to the center of the rhizome are certain slender bundles, devoid of protoxylem and prosenchyma ele-

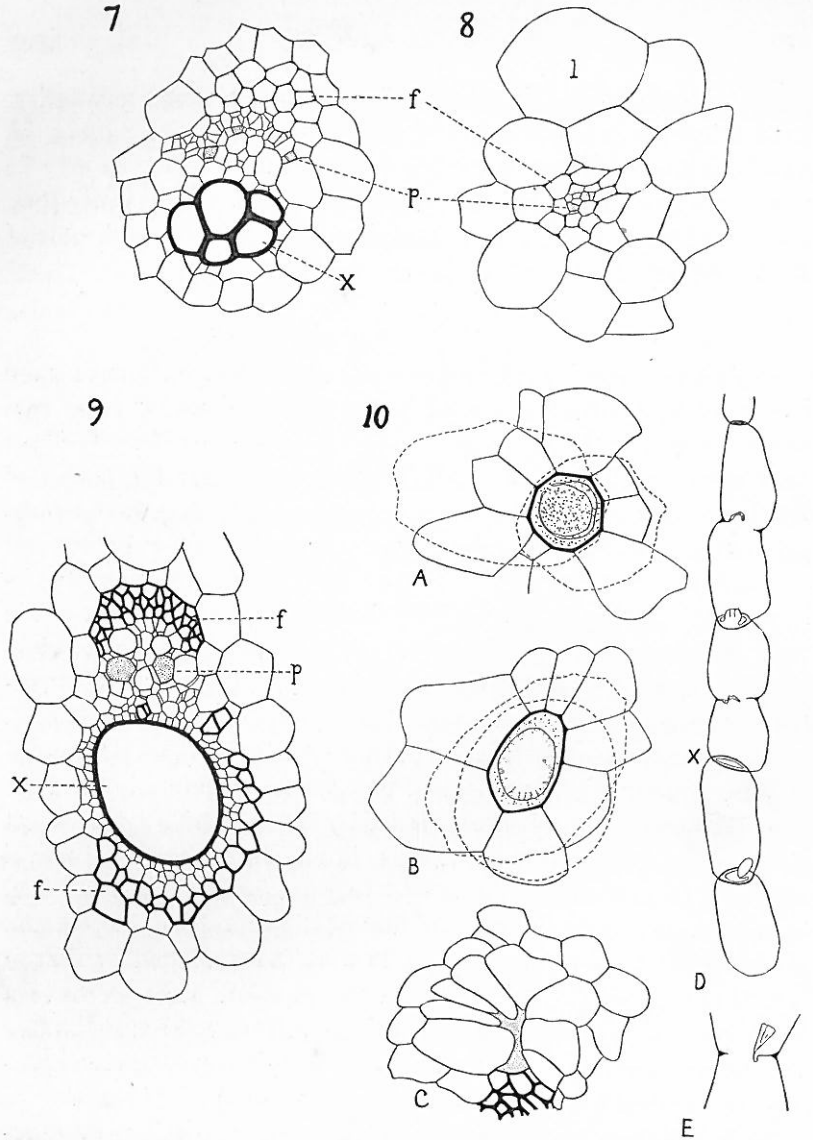
ments, and containing a few large tracheids, which run downward in an axial position but follow a rather flexuous course. Some at least continue until they enter the parent bulb.

5. CORTICAL LEAF-TRACE BUNDLES.—In the cortex there occur, in addition to the radially directed principal leaf-trace bundles, tortuous branching bundles whose general course is longitudinal. These vary in size from rather large bundles containing many tracheids, sieve tubes, and fibers (fig. 7 is a rather small but complete bundle) to very small bundles consisting of a few sieve tubes and thin-walled fibers, entirely devoid of tracheids (fig. 8). They finally enter the leaf sheaths, and hence form a second type of leaf-trace bundle. Their only communication with the roots is indirect and through the connections they form with the principal leaf-trace bundles as they pass radially through the cortex (fig. 3).

ENDODERMIS

As already mentioned, the short-lived cambium ceases its activity and its cells mature at a distance of between 3 and 4 cm. from the apex. At a later period an endodermis of an irregular type develops in the position previously occupied by it, between the horizontal secondary bundles and the cortex. The endodermal cells occur in an irregular series, interrupted by large gaps where the leaf-trace bundles penetrate it. They are nearly isodiametric, and do not differ greatly in shape from the cells of the ground parenchyma of the cortex and central cylinder, except that they are somewhat flattened tangentially. They are distinguished by the absence of starch grains (which are numerous in the surrounding parenchyma) and by the lignification of the middle lamella of the radial walls. This lignified strip differs from the usual Caspary band in the absence of the transverse corrugations so characteristic of the latter.

In the basal portion of the rhizome, far below the bases of the lowest living sheaths, the inner tangential and the radial walls of some of these cells become prominently thickened, lignified, and penetrated by numerous small, irregular pits. The thickening is always greatest on the inside wall (but here very variable even in cells close together) and tapers off on the radial walls in the manner typical of the endodermis of many monocotyledons. The occurrence of these



FIGS. 7–10.—Fig. 7, cortical leaf-trace bundle of medium size. ×84. Fig. 8, very small cortical leaf-trace bundle, destitute of xylem: *l*, latex vessel. ×120. Fig. 9, cross-section of vascular bundle from outer portion of central cylinder of aerial stem. ×76. Fig. 10, latex vessels: *A*, end wall between two component cells of latex vessel, showing central portion of wall remaining attached by narrow neck at one side; *B*, end wall between two cells, showing less usual case where central portion has broken away entirely (broken lines give outlines of central portions of two adjoining cells), ×166; *C*, latex vessel from older portion of rhizome, showing lumen almost occluded by ingrowth of surrounding parenchyma cells; *D*, portion of latex vessel: at *X* the end wall between the cells has completely disappeared while elsewhere it remains attached at one side, ×68; *E*, diagram showing end wall between two latex cells.

cells is extremely irregular: in places they form a continuous series; in others they are interrupted by endodermal cells with merely the middle lamella lignified; elsewhere in the same section they may lie singly between the thin-walled endodermal cells. Occasionally they are radially two or three deep, and in places they surround some of the outermost secondary bundles.

EPIDERMIS, CORK, AND LEAF SCARS

In the upper portion of a young rhizome the surface, except for the leaf scars, has a smooth, varnished appearance, and is of a deep cherry or mahogany color, variegated in spots with waxy yellow. The heavily cutinized epidermis persists until after the period of fruiting, although with increasing age numerous longitudinal fissures arise in it. The slow increase in diameter of the bulb stretches and flattens the epidermal cells until the lumen is almost or entirely obliterated. Their walls become irregularly lignified. The walls of the three or four outer layers of cells of the cortex become slightly thickened and impregnated with a brownish substance, apparently suberin, which renders them resistant to concentrated sulphuric acid.

The formation of cork is initiated beneath the cracks to which reference has just been made, and thence extends laterally until the older portions of the bulb are encircled by it. The cork originates just beneath the suberized cortical cells, in the fourth or fifth cortical layer from the exterior. The cork cells are not formed by a true initial meristem, but the activity of the first phellogen cells is limited, and after the cessation of its divisions its work is superseded by that of the next cortical cell lying toward the interior. Thus we have a "storied" cork or "Etagencork" such as SCHOUTE (8) and PHILIPP (6) found to be characteristic of the monocotyledons. The total production of cork cells is at best slight, except at the leaf scars.

In each of the lowest lacunae of the older leaf sheaths is an accumulation of a hard, white substance, in part attached to the bottom and sides, and in part in small granules lying loose in the lacuna, the whole having a rather mealy appearance. This is composed of small, roundish cells freely proliferated from the bottom of the chamber. In the older living sheaths these cells are already suberized and resistant to the action of concentrated sulphuric acid. When the sheath

dies and decays, these masses of small cells continue to cover the portions of the scar which represent the bottoms of the lowest lacunae, and cork is not formed in these places. Elsewhere the outer cells of the scar are first suberized and later cork is formed beneath them. This is likewise a "storied" cork, but as many as 19 cells have been counted in a series derived from a single parent cell.

The lumina of the tracheids in the leaf-trace bundles beneath the scar are completely plugged by the ingrowth of the neighboring parenchyma cells in the form of tyloses. The tracheids in the most recent leaf scar are already occluded in this manner, and the entrance of fungi from the soil is thereby blocked.

Aerial stem

General features

As each shoot of the banana plant approaches maturity, the axis becomes more slender and produces longer internodes, pushing up through the center of the false-stem. Eventually it emerges from its upper extremity, when it is bent downward by the weight of the massive flower bud and so produces the pendent inflorescence and later the heavy bunch of fruit. Unlike the aerial stems of the majority of herbs, that of the banana is entirely too weak to hold itself erect (to say nothing of the fruit it bears) without the support of the numerous leaf sheaths which inclose it; for although of considerable thickness, it is almost entirely devoid of lignified fibers to impart the requisite strength. Removed from between the leaf sheaths it has a columnar appearance and is pure white outside and inside when fresh. On its lower half are inserted the largest leaves produced by the plant (**10**, table I). The internodes become increasingly long toward the top, and range from a few millimeters at the base, where there is gradual transition from the close-set nodes of the bulb, to about 90 cm. in length at the apex. In diameter the internodes range from about 5 to 8 cm. in the aerial stem proper. Each is thickest at its upper end, just below the insertion of a leaf.

In the aerial stem the central cylinder occupies practically the entire cross-section, while the narrow cortex is only 1–3 mm. thick. The ground tissue throughout is composed of thin-walled, practically isodiametric parenchyma cells, their walls penetrated by obscure,

fine, roundish or elliptical, simple pits, and rich in starch grains. In the central cylinder are many lacunae, which are most numerous in its central part, where they are narrow and long, attaining a length of 1 cm. or more.

No amphiphloic or secondary bundles are produced in the aerial stem, for these are found only in association with the adventive roots, and the last of them occur with the highest of these roots, at the point where the bulb narrows into the aerial stem. Neither does an endodermis arise in the aerial stem, but the boundary between the central cylinder and the cortex is marked by the presence of numerous crowded collateral bundles of the type represented in figure 9. Exterior to this ring of large bundles the cortical bundles are abruptly smaller. Passing outward in the narrow cortex, they show a gradual reduction in the already sparse xylem and phloem until strands composed of fibers alone lie near the epidermis.

Courses of vascular bundles

The courses of the vascular bundles in the aerial stem were determined, as in the case of the bulb, by placing the cut end of a stem, still surrounded by the leaf sheaths necessary to support it, in a 1 per cent solution of trypan blue. After the 24 hours or longer necessary to obtain good coloring of the bundles, the stem was removed from the stain and cut in halves lengthwise, and the bundles exposed by the use of a scalpel. Since the bundles follow a smooth and even course, this was an easier task than in the case of the bulb. Some of the bundles penetrate to the center of the stem. These may then continue across to the opposite side, or may again bend outward toward the side from which they entered. These two cases, it will be remembered, are also found in the bulb. Both the inward and outward courses are very gently inclined, and because of the great length of stem traversed by each bundle, it was not found possible to trace any one down to its connection with the roots, or until it reached the outer limit of the central cylinder the second time. Other leaf-trace bundles penetrate but a short distance into the central cylinder before again inclining outward toward the cortex. The courses of the bundles are not essentially different from those of the bulb, except for the great tortuosity of the latter, which appears to result from the abbreviation of the internodes.

As a vascular bundle enters the stem from a leaf, there is a considerable but temporary multiplication of the number of tracheids it contains, together with a marked reduction in their diameter. A typical case of a single bundle taken at various levels in the leaf sheath and stem will serve to illustrate the situation. At *A* (10, fig. 18), a point in the leaf sheath 8 mm. above its insertion, there was a single large functional tracheid and the overlapping ends of two narrow metaxylem tracheids. In addition there appeared the occluded lumen of a protoxylem element, and doubtless there were one or two smaller and earlier ones so completely obliterated that none of their widely separated bands of thickening appeared in the section. This bundle was here typical of the larger bundles throughout the leaf sheath. At *B* (the same bundle in the stem about 6 mm. below the insertion of the leaf), 14 distinct functional tracheids, large and small, were counted. The overlapping ends of two tracheids in the same longitudinal series are always counted as one, for were the bundle followed a short distance upward or downward, one or the other would fail to appear. The single large tracheid at *A* had about 2.7 times the cross-sectional area of the widest tracheid at *B*. At *C*, 5 cm. below *B*, the number of large tracheids was reduced to two, both much broader than the widest at *B*, and there were only four distinct functional small tracheids. At *D*, 38 cm. below the leaf insertion, there was a single very wide tracheid and a single narrow one (fig. 9), a condition again approaching that found in the leaf sheath.

Length of tracheids

A number of futile attempts to determine the length of the tracheids were made before a satisfactory procedure was found. Because of their great length, it is well nigh impossible to orient a longitudinal section with sufficient accuracy to include their entire extent. To isolate them by maceration is not practicable, because the extremely delicate membranes break down in the process and the spiral bands of thickening unravel. Cut stems were set into dilute suspensions of Higgins' American India ink, with the idea that as the water was drawn up into the tracheids by transpiration from the leaves above, the particles of carbon would be held back by the first end wall they encountered and so indicate its position; but these parti-

cles, which are invisible under the oil-immersion lens, proved so fine that they readily penetrated the walls and rose to a height of 60 cm. Finally the following method was successfully employed. A thin suspension of cornstarch in water was prepared, and the starch grains deeply colored by the addition of a solution of iodine in potassium iodide. A section of freshly cut stem was taken, cut in half longitudinally so that one end could be held between the lips while the other was immersed in the suspension, the stem being held as nearly horizontal as practicable. Upon sucking at the upper end the water was drawn into the broad tracheids, carrying along with it the starch grains, which accumulated at the upper end of those tracheids whose lower ends had been exposed by the cut. Upon uncovering the bundles by scraping away the surrounding parenchyma with a scalpel, and measuring the distance of the black mass of starch grains from the end, it was possible to determine the length of the tracheid. Of course, in only a small percentage of cases will the true length be obtained; for the tracheids will have been severed at all distances from their upper ends but only a small proportion will have just enough of the lower end cut away to permit entry of the starch grains, and these alone will reveal their full length. Accordingly only the maximum measurements of a series obtained by this method are significant.

A serious disadvantage of this procedure is that the starch grains burst through the end wall of a tracheid and enter the next above. If suction is continued longer, they accumulate in the upper extremity of the second tracheid until they finally burst through and enter the third, etc., and this in spite of the fact that the maximum pressure which could be exerted on these walls by suction is one atmosphere, while the actual pressure was undoubtedly very much less. No matter how light the suction, the starch grains broke through. The end walls of the tracheids are very oblique, and the spiral bands of thickening of the two tracheids separated by this wall are crossed, forming a grating with very fine meshes closed by the delicate cell membrane. The wall as a whole apparently was not broken down, but the starch grains appeared to have been forced through the meshes, tearing the membrane. This seemed to occur only after there was a considerable accumulation of grains, clogging the wall and building up a pressure.

lap of two superposed tracheids in the same longitudinal series amounts to 5–10 mm. This broad overlap adds greatly to their water-conducting efficiency, for the greater the area of the membrane the less the resistance experienced by the water passing through it, at a given rate of flow in the tracheids.

The segments of the sieve tubes in the aerial stem are much shorter than the tracheids, and the longest encountered was only 1.2 mm. in length. Except at the top of the stem, where the light penetrates the leaf sheaths, the fibers surrounding the vascular bundles are thin-walled and unlignified, with the result that the stem, despite its considerable thickness, is weak and brittle.

Latex vessels

Since the latex vessels are a prominent feature of the anatomy of all parts of the axis, it seems most convenient to devote a separate section to them. Although varying greatly in degree of development in different regions, they are everywhere of the same type. They consist of cells joined end to end to form long vessels which occasionally branch (fig. 10 *D*). A single circular perforation, occupying almost the whole of the end wall between contiguous cells, gives free communication from one to another. The membrane which originally closed this orifice is not dissolved away, but rather the central portion is torn bodily from the edges. Usually it remains attached for a short distance at one side, and is folded back, more or less crumpled, into one or another of the two adjacent cells (fig. 10 *A*, *E*). Less frequently the wall is torn completely around and the central portion has entirely vanished, leaving only a narrow rim surrounding the wide perforation (fig. 10 *B*). Rarely an entire end wall remains between two cells in the longitudinal series. Both the circular flap, where this remains, and the persistent rim are perforated by numerous exceedingly fine pits. In a long series of cells making up a vessel, as a rule all the flaps are turned back the same way, suggesting that they have been forced in this direction by a common pressure.

In the bulb these latex vessels are found in both the cortex and the central cylinder, including both its primary and secondary regions. A cloudy fluid, which on exposure to the air becomes gummy, oozes slowly from them when the bulb is severed; and a steel knife used to

cut the bulb is soon blackened by the tannin they contain. A wide latex vessel lies on the exterior side of about half the longitudinal bundles of the secondary zone, but it may occur anywhere, and some bundles have two latex vessels associated with them. The chains of cells forming the vessels are here rather irregular (fig. 10 *D*) and the individual cells very large, ranging from 176 to 384 μ in length, by 64–144 μ in greatest diameter. In those latex vessels which follow the large leaf-trace bundles, the component cells are much elongated. In the cortex they attain 864 μ in length by 96 μ in diameter; in the secondary zone 1056×128 μ; in the primary region of the central cylinder 624×144 μ. In the older portion of the rhizome the lumina of the latex vessels are more or less occluded by the neighboring parenchyma cells, which stretch radially and push into them (fig. 10 *C*). Their content hardens to a firm, brownish substance which fills the remaining lumen.

In the aerial stem the latex vessels are of far less importance than in other regions of the axis. The exudation from them is scarcely noticeable when the stem is severed, and the knife employed neither turns black nor becomes fouled with a gummy substance, as in the case of the bulb. The tissue of the aerial stem contains so little tannin that it actually tastes slightly sweet. The latex vessels which occur throughout the cortex and central cylinder are rather narrow, being from 36 to 120 μ in diameter; but the component cells are long, attaining from 1.5 to 2.3 mm. in length. The proportions are accordingly significantly different from those of the segments of the latex vessels in the rhizome. It is of interest that the longest cells of the latex vessels of the aerial stem are about the same length as the longest segments of the sieve tubes.

It is in the rhachis of the inflorescence that the latex vessels reach their greatest prominence. If the rhachis is severed, the latex exudes in a steady trickle of cloudy drops, which on contact with the air soon become gummy. The rhachis of the male flowers is the only part of the plant where the latex vessels are as wide and prominent as the tracheids. Here their diameter reaches from 140 to 176 μ.

The fresh latex of the banana is a slightly cloudy or turbid liquid. The most prominent feature of its contents is the many sizable oil globules, which stain bright red in an alcoholic extract from the al-

kanna root. There are also many minute crystals which appear cubical but are so small that one cannot make certain of their shape, and extremely slender, rod-shaped crystals. The latex is immediately coagulated by a solution of ferric chloride, which imparts a black color because of the tannin it contains.

Summary

1. Close behind the apex of the bulb of the banana there develops a cambium-like meristem of limited duration, whose chief function is the origination of the adventive roots and the vascular bundles which link them with the leaf-trace bundles.

2. The number of tangential divisions which each cambium cell undergoes is rarely greater than seven, but the meristem is constantly regenerated from the adjacent undifferentiated cells of the inner cortex.

3. A single daughter cell of the cambium gives rise to an entire segment of a vascular bundle, as in the arborescent Liliiflorae.

4. The cambium gives rise first to longitudinal amphiphloic bundles, then to horizontal amphiphloic bundles and to the primordia of the adventive roots, which arise always in longitudinal rows of four. After initiating the horizontal bundles the meristem loses its activity, at about 3.5 cm. from the apex. The region of its activity extends for about 3 cm. in all.

5. The parenchymatous cells which stand in the way of the adventive roots pushing out through the cortex are softened by an enzyme secreted from the tip of the root, but a "digestive pocket" appears never to be present.

6. The strongest leaf-trace bundles penetrate to the center of the bulb. Thence they may pass outward toward the cortex in any direction, either by continuing across to the side opposite their point of entry, by doubling back to the side from which they entered, or by bending to right or left. As they approach the secondary zone on their outward course they incline downward and finally enter it. Their course through the central cylinder is everywhere extremely tortuous.

7. The longitudinal secondary bundles, formed from the cambium, are merely the downward prolongations of the leaf-trace bundles.

The same bundle which in the upper portion of its course is collateral becomes amphiphloic at its lower extremity.

8. The horizontal secondary bundles radiate from the bases of the roots and form a system girdling the bulb. Through their anastomoses with the longitudinal bundles they conduct water to the leaves.

9. The courses of the vascular bundles of the aerial stem do not differ essentially from those of the bulb, save that they are straight and regular.

10. The tracheids of both aerial stem and leaf sheath attain a maximum length of 8 cm. Those between 4 and 6 cm. long are numerous.

11. The latex vessels are formed of chains of large cells joined by a wide perforation occupying almost the entire end wall. The central region of the end wall is torn away from the narrow peripheral region, but usually remains attached at one side, forming a loose flap.

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