

ON THE DEVELOPMENT AND MORPHOLOGY OF THE LEAF OF THE BANANA (*MUSA SAPIENTUM* L.)¹

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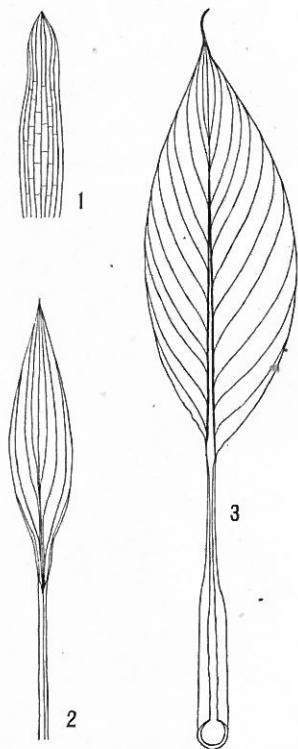
In a previous publication (18), I described the anatomy of the mature leaf of the banana. The process of development was considered only in reference to a few isolated points, such as the disruption and occlusion of the protoxylem elements, and a discussion of the morphology of the leaf was avoided. Many details, however, connected with the process of unfurling and the acclimatization, so to speak, of the young leaf to its environment, are meaningless unless we understand the past history of the leaf and its development while it was still hidden away inside the massive false-stem. During a recent sojourn in Panama, on a plantation where an abundance of material of many species and varieties of bananas was available, I was able to follow the early stages in the formation of the leaf. As a result, certain points which had previously been obscure, such as the presence of the fugacious hyaline wing which borders the newly unfurled leaf, the tearing off of the apex of the right half of the lamina in unfurling, and the basal inequality of the lamina, are now full of significance. These points can be best interpreted in the light of the phyllode theory, propounded by Mrs. Arber (4), and the banana, in turn, deserves to stand as a strong support of that theory, and to offer further confirmation from developmental history of a view which at present rests largely upon anatomical evidence. I trust also that it may prove a stepping stone to a better understanding of the development of the leaves of palms, those most interesting and complex of all monocotyledonous leaves.

SEEDLING LEAVES

The seed and seedling of the banana have been described by Greve (11) and others. It is not my purpose to go into that history here, but merely to figure and describe the sequence of leaves produced by the young plant. Text figure 1 shows the first plumular leaf of a hybrid seedling of *Musa sapientum*. It will be noticed that the leaf is represented by sheath alone, that the veins are all parallel and run without converging almost or quite to the tip of the leaf and that horizontal anastomoses occur between them. Succeeding leaves show a differentiation into lamina and sheath, and at length a petiolar portion is intercalated between these parts. The lamina is at first devoid of a distinct midrib; later one appears at the base, and in succeeding leaves approaches nearer and nearer to the apex. The leaf shown

¹ Botanical Contribution from the Johns Hopkins University no. 108.

in text figure 2 has a midrib only at the base, and in its venation resembles the leaves of many of the Liliaceae—*Convallaria*, for example. Text figure 3 represents a later leaf which, in the termination of the midrib in the apical third, and the direction of the lateral veins, might pass for the lamina of *Strelitzia reginae* among the Musaceae. A small precursory appendage is already present. As in successively older leaves the midrib approaches

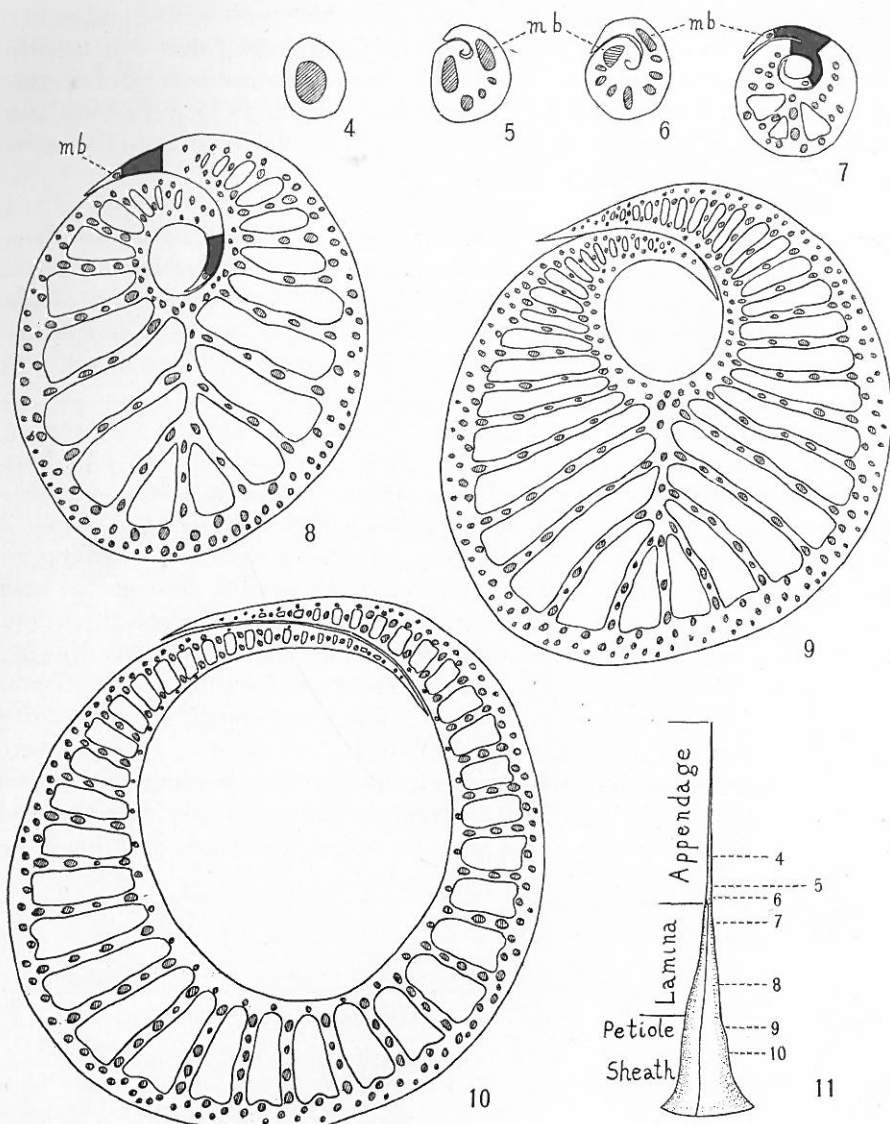


TEXT FIGS. 1-3. Leaves of seedling bananas (*M. sapientum* hybrid). 1. First plumular leaf, $\times 1\frac{1}{3}$. 2. A later leaf, $\times 1$. 3. Still later leaf from older seedling, $\times 1/3$.

nearer and nearer the apex, the veins diverge from it at greater and greater angles, until finally those in the central portion of the mature leaf stand at right angles to it, while at the base they are actually inclined backward (text fig. 17). This very gradual production of leaves of the mature type seems to indicate a long phylogenetic history, and its significance will be discussed in a later portion of this paper.

DEVELOPMENT OF THE MATURE LEAF

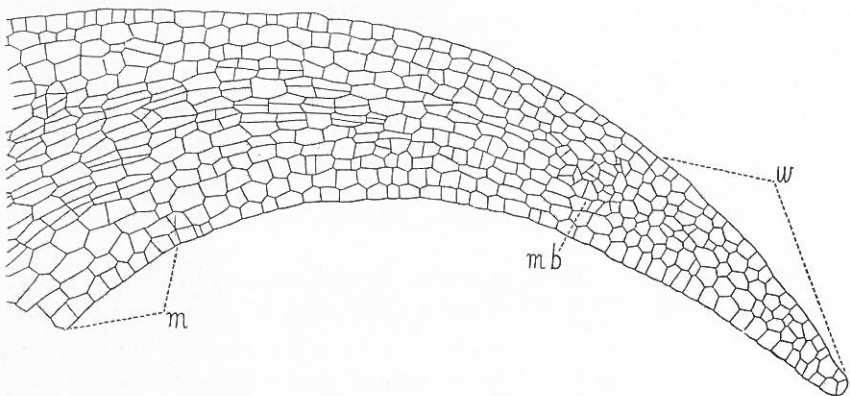
In the mature leaf four portions may be distinguished (18); these are: (1) The sheath, crescentic in cross-section, which, closely embracing and in turn embraced by its neighbors, helps form the peculiar false-stem of the



TEXT FIGS. 4-11. Figures 4-10 are diagrammatic cross-sections based on camera lucida drawings through the 52-mm.-long leaf rudiment shown in figure 11, at the levels indicated there. They are intended to show the degree of differentiation of tissues which is evident at this stage. The young lamina-halves (FIGS. 7 and 8) are indicated in solid black, the incipient vascular bundles by shading; the large unshaded spaces in the figures are the regions of the developing lacunae. *mb*, marginal vascular bundle. FIGS. 4-8 $\times 18$; FIGS. 9-10 $\times 12$; FIG. 11 $\times 1$. In these sections, which are represented with the acroscopic surface upward, the right lamina-half appears to cover the left. The leaf is, however, rolled in the normal direction, with the left half outermost.

banana plant; (2) the massive petiole; (3) the lamina; and (4) the precursory appendage or forerunner tip, a temporary organ which dies and usually breaks off shortly after the unfurling of the lamina (see text figs. 14-17). As I have already pointed out, these divisions are purely topographical, are useful merely for convenience in reference, and are valueless from the point of view of comparative morphology.

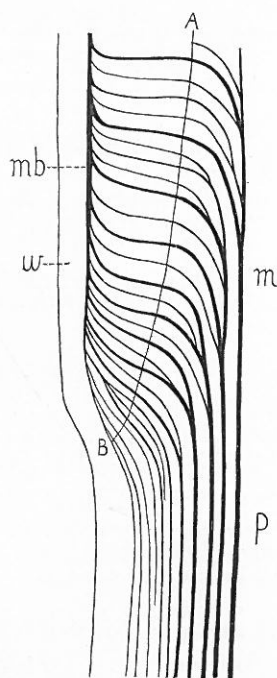
The leaves arise from the depressed growing point at the apex of the massive, bulbous rhizome. In order to reach the young rudiments, it is necessary first to strip away all of the sheaths of the mature leaves, which collectively form the false-stem, and then carefully cut away each of the immature leaves in order to expose the next younger, which is completely enclosed by it. As smaller and smaller leaf rudiments are uncovered, it is found that the precursory appendage occupies a larger and larger proportion of its length, until in the very young rudiments surrounding the growing point it accounts for about half the length of the leaf (table 1). Text figures 4-10 represent a series of cross-sections through a leaf rudiment 5.2 cm. long, taken from a large sucker which had not yet begun to "shoot," or produce flower-buds. The rudiment tapers so rapidly from base to apex that it was found necessary to reproduce the sections through the base on a smaller scale than that employed for the sections in the apical portion. The levels at which the hand-sections were cut are indicated in the drawing of the whole rudiment (text fig. 11). In all of what we may call the axial portion of this rudiment—sheath, petiole, midrib, and appendage—the entire ground plan of the mature organ is already laid down. Thus, in text figures 4-10, one may see the incipient vascular bundles, and the regions where the lacunae are beginning to form are already clearly differentiated from the surrounding walls and septa. In text figures 7 and 8, through the



TEXT FIG. 12. Cross-section through the left lamina-half of a leaf-rudiment 37 mm. in total length. *M*, midrib; *mb*, marginal vascular bundle; *w*, hyaline wing. The portion between the midrib and the marginal bundle is the young lamina-half. Camera lucida sketch $\times 220$.

region of the future lamina, however, it will be observed that the lamina-halves, which are indicated here in solid black, occupy an altogether insignificant portion of the whole cross-section, while in leaves which are just appearing from the top of the false-stem, and are already full grown, the left or outer half makes 4-5 turns about the midrib, and the right half 12 or more turns coiled in the concavity of its upper surface (text fig. 18).

Examined under a higher power of the microscope, the cells in the regions indicated by solid black in text figures 7 and 8 are found to be smaller and more deeply staining, in other words more highly meristematic, than those in the remaining portions of the cross-section. This region of young and very actively dividing cells does not extend quite to the margin of the



TEXT FIG. 13. Basal end of the left lamina-half of a rudiment 37 cm. long, cleared in xylol. *A-B*, boundary between midrib (*M*) and lamina-half; *Mb*, marginal vascular bundle; *p*, petiole; *w*, hyaline wing. Camera lucida sketch $\times 11$.

organ, but is bordered on the exterior by a region of cells which contain a less dense protoplasm and give evidence of greater maturity. This is the future hyaline wing of the lamina. Separating the wing from the lamina-half is the rudiment of the future marginal bundle of the lamina (*mb*, text figs. 7, 8, 12, and 13). In studying sections such as these, one is drawn to the conclusion that the lamina-halves are younger than the remaining portions of the leaf, and are intercalated between the midrib on the one hand, and the marginal bundle and wing on the other. In rudiments somewhat younger

than that chosen for illustration the lamina-halves are not evident, and the midrib tapers gradually to a thin margin which has already begun to become membranaceous. Here it may be seen that the marginal bundle of the lamina is merely the outermost bundle of the midrib, a continuation of the outermost bundle of the sheath, and completely homologous with the other bundles of midrib and sheath. The actual size of the rudiment when the lamina-halves first become evident varies somewhat with the size of the plant from which it is taken. Thus, the rudiment from which text figure 12 was drawn was only 37 mm. in total length, and already shows the origin of the lamina, while in a 44-mm. rudiment from a larger plant with a false-stem 3.1 m. high (table 1) the lamina could not be distinguished.

TABLE 1. *Measurements of the Immature Leaves of a Plant of Musa sapientum Subspecies seminiifera with a False-stem 310 cm. High, with Four Mature Leaves for Comparison*

Leaf No.	Condition	Total Length cm.	L. of Appendage cm.	L. of Lamina cm.	L. of Petiole cm.	L. of Sheath cm.	Breadth of Left Lamina-Half † cm.	Ratio, L. of Lamina: B. of Left Half
1	Mature	503*+	Withered	165	58	280	32.0	5.2
2	"	542+	"	177	68	297	31.4	5.6
3	"	544+	"	177	57	310	33.2	5.3
4	"	561+	"	192	62	307	32.0	6.0
5	Just emerging	383+	Curled					
6	Immature	177	13+	197	173		33.2	5.9
7	"	85	19	95	63		15.9	6.0
8	"	38.8	18	42.5	24.5		2.9	14.6
9	"	19.2	10.8	18.5	9.5		0.4	46.3
10	"	9.2	9.1	5.9	4.2		0.09	65.6
11	"	4.4	4.9	2.1	2.2		0.05	42.0
12	"	2.4	2.2	1.1	1.1		0.00	
			1.1		1.3		0.00	

* Does not allow for the withered appendage.

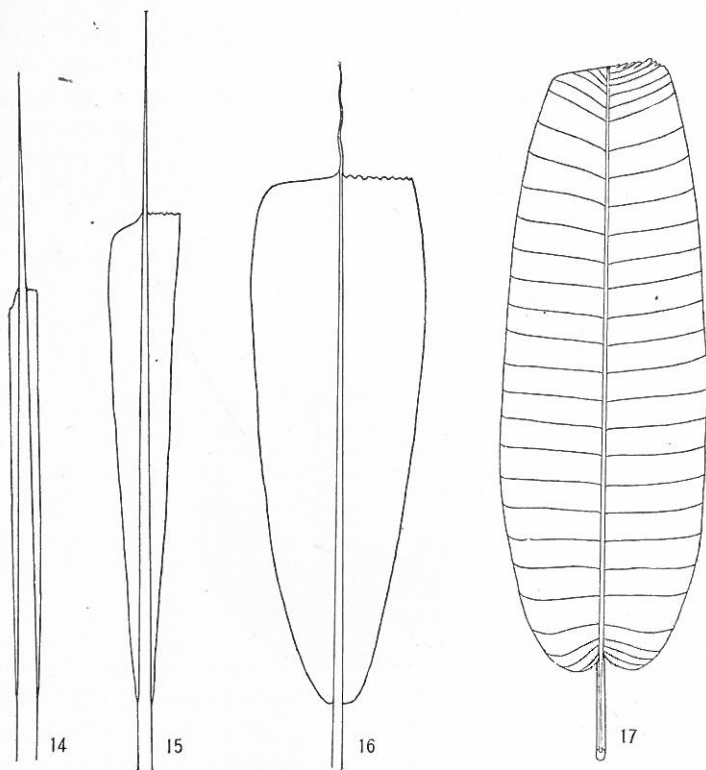
† The two sides of the lamina are very nearly equal.

The condition of tissues at the base of the lamina confirms the view derived from the study of cross-sections. Text figure 13 gives the appearance of the region at the base of the left² or outer lamina-half of a rudiment 37 cm. long, which has been cleared in xylol and is viewed as a transparent object. The broad, membranaceous wing *W* is continuous from the petiole to the lamina, but has been pushed out above the point marked *B* by the intercalation of the lamina-half between it and the midrib to the right of the line *A-B*. As the leaf grows in breadth and the basal lobes begin to push downward (cf. text fig. 17), transverse wrinkles will appear at *B*, indicating that the development of this wing is not harmonious with that of the lamina-half. The marginal bundle is also continuous from the petiole to the lamina, but becomes stronger as it advances toward the apex, and is

² As reckoned by an observer standing at the petiole and looking toward the apex of the leaf in its normal orientation.

augmented by the distal ends of the veins of the lamina. The course of these is sufficiently evident from the figure, where it will be seen that the more distal portions of the lamina are supplied by the more central, and older, bundles of the midrib.

As the lamina-halves grow in breadth, they begin to assume the well-known convolute form of veneration. The left or outer half coils around the midrib and the right half, making finally 4-5 turns about them. How the thin, soft lamina-half manages to push between the midrib and the inner surface of the next older leaf, which fits tightly against it, without becoming



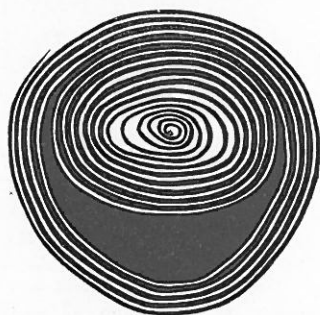
TEXT FIGS. 14-17. FIG. 14, lamina and appendage of Leaf 8 (see table 1) drawn to scale $\times 4/15$. FIG. 15, Leaf 7 $\times 2/15$. FIG. 16, Leaf 6 $\times 1/15$. FIG. 17, a mature leaf $\times 1/30$.

crumpled, without even the extremely delicate wing becoming folded back upon itself, remains a mystery to me. The outer surfaces of all the organs are covered by a smooth cuticula at a very early age, which eases, but does not remove, the difficulty of picturing the mechanics of the process. The inner half becomes coiled into the concavity of the upper surface of the midrib, making as many as 18 turns in the broadest portion of very large

leaves. Here it grows into a free space created by the enlargement of the midrib.

The intercalation of the lamina between the midrib and the wing begins at the apex and proceeds basally. As a result the laminae of young leaves are broader at the apex than at the base. Text figures 14-17, drawn to different scales so as to make all of approximately the same size, show this progressive change of shape. The earlier figures (14-16) must be considered as merely diagrammatic, since the shape of the midrib is such that it is impossible to spread the young lamina out in a plane. The lamina-halves at this stage are so thin and brittle that it is impossible to unroll them individually without first killing the cells and destroying their turgor by immersion in boiling water. As the leaf increases in breadth, the outer portions of each lamina-half grow more in length (that is, in the direction parallel to the margin), than the inner portion, the longitudinal growth of which is controlled by the midrib to which it is attached. This results in the pushing backward of the basal veins and in giving the lamina a more or less cordate base.

Not only is the apex of the lamina older than the base, but the differentiation of the marginal portions precedes that of the regions nearer the midrib. The order of the differentiation of the vascular bundles in the



TEXT FIG. 18. Diagrammatic cross-section of the lamina of a large leaf just before unrolling, to show the form of veneration.

various regions of the lamina was determined by injecting the leaf with eosin, since only those veins capable of conduction would show the stain. A whole plant was dug up in the early morning, while the dew was still heavy on it, all but the upper portion of the rhizome to which the leaves were attached was pared away under water, and this submerged in a vessel of 1-percent aqueous eosin solution. The solution rose into the completely enclosed leaves in response to the growth-requirements of their tissues. The plant was left in the solution for 6 to 22 hours, the object of the long periods being to allow the injection of all the vessels capable of conduction. In very young rudiments, only 6 cm. in length, in which the lamina was in the earliest stages of development, the tracheids of the precursory appendage

were stained densely to the apex, thus confirming the conclusions of Genter (9) and Raciborski (16) on the early maturity of this portion of the leaf. Only the most apical veins of the youngest leaves in which the lamina-halves were discernible indicated by taking the stain that they were functional in conduction. The marginal bundles became stained from the apex downward, and generally showed staining for a short distance below the most basal of the stained veins, indicating the basal flow of the solution in them. Many of the veins, especially those of the subordinate type, became stained for a greater or less distance inward from the marginal bundle, but not as far as the midrib. At the time the full-grown lamina begins to appear at the apex of the false stem, many of the subordinate veins still show the same inward course of water in their vessels.

Thus the marginal bundles are of importance in supplying water to the tissues of the growing lamina-halves, although they are apparently of little or no value to the leaf after it unfolds and transpiration begins. In the very young rudiment, the water enters these bundles through the precocious precursory appendage. As I have shown in a previous paper (18) and as is evident from text figures 4-8, the marginal bundles become the principal vascular supply of this appendage, while in its distal portion all of its bundles fuse together, so that here the marginal bundles are united with the central bundles which lead the water up from the rhizome through the sheath and midrib. Flowing backward from the apex in the marginal bundles, the water enters the more mature marginal extremities of the transverse veins in the lamina-halves, and proceeds inward along these. The tissues supplied by these veins accordingly receive their moisture in a very indirect manner. As soon as one of the veins has become capable of conduction throughout its length, it forms a short cut by which water can enter the marginal bundles by a more direct path than by way of the appendage, and this happens at a very early age, when the entire leaf-rudiment is only about 13 cm. long, and the lamina-halves still only a few millimeters broad.

In its basipetal direction of differentiation, the leaf of the banana agrees with those of most palms (7, 19), with the exception of *Chamaedorea*. In these the folding or invagination of the lamina to form the future pinnae usually proceeds from the apex downward.

At the time of its first appearance at the apex of the false-stem the lamina is full grown. It is still tightly rolled, and is quickly pushed upward and outward by the elongation of the sheath at its base, which up to this time has lagged behind it in growth, but is destined to exceed it in final length (see table 1). When it has emerged to practically its full height, the lamina begins to unroll. I shall discuss in two subsequent papers the emergence of the lamina and the mechanics of its unfurling. Suffice it to state here that the unrolling is effected by the growth of the cells of the upper water tissue lying above and beside the principal veins, and along either side of the midrib. By the activity of the former cells the principal

veins are pushed above the general surface of the lamina-halves, and these, which up to this time have been perfectly smooth, acquire their characteristic ribbed appearance. Without the formation of these ribs, the broad, thin lamina-halves would lack the strength to hold themselves in a horizontal position. Thus we have the formation of a device essential to the proper functioning of the leaf postponed to the last possible moment, a fact in harmony with the relatively late appearance of the lamina-halves themselves. These statements will acquire greater significance when, in a later paragraph, we come to compare the banana with the palms.

The lamina-halves have been intercalated between the midrib and the marginal bundle. At the apex of the leaf, where the marginal bundles join with those of the midrib to form the vascular supply of the precursory appendage, we may well expect difficulty in adjustment if the lamina becomes broad and blunt in this region, as it does in the large, mature leaves of all varieties of *Musa sapientum* with which I am familiar. The left or outer half of the lamina is rolled about a rod, so to speak, and since it is closely pressed by the sheath of the next older leaf which encloses it, it is of mechanical necessity rolled flat. The marginal bundle has been forced to accommodate the growth of the blade. In consequence of this, this side experiences no difficulty in unfurling. On the right side, however, the lamina grows into a free space prepared for it by the enlargement of the midrib. Even here, it is true, there is not much wasted room, but the folds are not so tightly packed as on the opposite side. Here the marginal bundle does not keep pace with the growth of the apical portion of the lamina-half, which as a result becomes hooded or invaginated. When the pressure of the unfurling leaf loosens the coils of this lamina-half, forming a hollow cylinder, this hood enlarges to become a dome closing off the coils (see Skutch, 18, fig. 11). But the tissues are now too mature to yield further, and the entire cap is torn off as the leaf finally spreads out. Thus the right half of the lamina is terminated by a torn margin, in large leaves 12 cm. across. Some of the strain of mechanical adjustment at the apex may be inferred from the fact that the veins, as they are about to join the marginal bundle are on both lamina-halves turned sharply back through about 140°. Then they apply themselves to the inner face of this bundle and run up into the precursory appendage.

Whether or not the apex of the lamina is torn in unfolding depends entirely on its size and shape. In the narrow leaves of sword-suckers, and even in the smaller of the broad leaves subsequently produced by these, the right side is able to flatten out without becoming lacerated.

Meanwhile the hyaline wing, now often tinged with red, has expanded until in large leaves it is 2.5 mm. or more wide. The fact that it never develops chlorophyll also suggests that this tissue is quite-distinct from the lamina-half proper. The first sunny day suffices to shrivel it as far as the marginal bundle. In the abacá or Manila hemp plant (*Musa textilis*)

the marginal wing on the left side usually adheres so strongly to the surface of the coil lying adjacent to it in veneration that, when the leaf unfurls, it pulls away from the marginal bundle and remains attached to the lower surface of the lamina, as a straight, narrow, brown line, running almost parallel to the left margin. Although not every leaf of the abacá shows this mark (its failure to appear is perhaps a result of the atmospheric conditions prevailing at the time of the emergence and unfurling of the leaf), I do not remember a single large plant which failed to show it on at least some of its leaves; so, if the plant as a whole is considered, it is a good specific character. At the same time, the precursory appendage, which varies a good deal in texture in various species of *Musa*, shrivels up and falls away, if indeed it was not already torn off along with the dome on the apex of the right lamina-half.

Another late development in the life of the lamina is the enlargement of the cells along the lower side of the pulvinar band to form the motor tissue which allows the lamina-halves to fold downward beneath the midrib in the middle of a dry day, and raises them again in the afternoon. The final act in the adjustment of the leaf is the tearing of the lamina-halves into narrow strips by the wind. I am almost inclined to consider this a belated act in its development since, although it is a perfectly passive laceration, the leaf is not entirely adjusted to its environment on the plantation until it becomes, in this manner, falsely pinnate. In the abacá, the first tears across the lamina-halves are actually made during the emergence of the leaf from the top of the false-stem. Very soon after the appearance of any particular length of the lamina, it begins to unroll. The portions immediately basal to it are still held within the false-stem, and of course are not able to follow, but the forces acting to bring about the unfurling of the outer lamina-half are sufficiently strong to create transverse tears reaching to the midrib, and these permit the expansion to proceed by steps.

Every banana leaf I have ever examined closely was rolled in the same way, the right half covered by the left. This constant form of veneration is associated with the invariable direction of the spiral of phyllotaxy, which rises from the right to the left of an observer facing the stem. These statements are true not only of the numerous varieties of *Musa sapientum*, but also of *M. rosacea*, *M. malaccensis*, *M. tomentosa*, *M. sanguinea*, and *M. textilis*, which constitute all of the species I have been able to examine. The direction of development is a character which is constant for whole species, possibly even for the whole genus *Musa*.

AN INTERPRETATION OF THE DEVELOPMENT OF THE LAMINA IN THE LIGHT OF THE PHYLLODE THEORY

In attempting an interpretation of the morphology of the leaf of the banana, we are faced with a two-fold problem. In the first place, it is necessary to define the relation of the lamina-halves to the remainder of

the leaf. Secondly, it is desirable to determine the morphological value of the midrib itself, whether we are to regard it as the equivalent of the sheath, petiole, or midrib of the normal dicotyledonous leaf. Since the development of the lamina proceeds in two distinct steps, (1) the formation of the midrib and (2) the outgrowth of the lamina-halves from it, the two questions which we have proposed are in a measure independent of each other. The first, which seems to me the more important, is fortunately the easier of solution, and the validity of our conclusions will not be seriously affected by the morphological value we ascribe to the midrib.

A considerable amount of evidence points to the conclusion that the lamina-halves of the banana are a secondary development, and not homologous with the expanded portion of dicotyledonous leaves. A comparative view of the thin, expanded portion of the lamina, variously called the "wing" or "blade," as distinct from the rhachis or midrib, in different stages in the series of vascular plants, lends weight to this view. In the Hymenophyllaceae, Polypodiaceae, and other leptosporangiate ferns, the wing is formed on the sides of the rhachis by the activity of a series of marginal cells or initials, which are formed, in some cases at least, from the very earliest segments of the terminal growing point of the frond (Bower, 5, Pl. XXI, fig. 30). In the more bulky fronds of the Osmundaceae and Marattiaceae, definite marginal cells can not be recognized, although the wings are still formed on the sides of the originally terete rhachis by marginal growth. In the leaves of many dicotyledons, the future midrib (or rhachis) is the first portion to develop, and the wings first appear as paired outgrowths from its sides. This circumstance was already known to Trécul (19) who did not, however, devote much attention to the point. It is evident from his descriptions and figures that this is the mode of origin of the wings of *Liriodendron* (Pl. 21, fig. 47), *Citrus* (Pl. 22, fig. 24), and *Rumex* (Pl. 25, fig. 168), but in other cases their development in this manner is not so clear. Mrs. Arber (3) found that the wings of the lamina of a number of species which she studied develop as marginal outgrowths from the future midrib. In *Trifolium* the wings of the leaflets arise in much the same way from the ventral faces of their respective midribs. In *Syringa*, however, "the petiole passes almost insensibly into the lamina." Foster (8) observed that the wings of the leaflets of *Aesculus* originate from meristematic ridges along the ventral faces of their future midribs, much as Mrs. Arber described for *Trifolium*.

For a description of the exact manner in which this outgrowth of the wings occurs, and the meristematic layers involved, we must turn to the researches of Noack (15) and Krumbholz (13) (see also Schüepf, 17). The former found that the wings of the leaf of *Pelargonium* are produced by a marginal meristem in which the histogenetic layers behave very much as in the terminal growing point of the leaf, or even in the growing point of the stem. The hypodermal layer of the meristem is responsible for the origin

of all of the mesophyll, while the epidermis is formed by an independent dermatogen. In *Oenothera*, according to Krumbholz, the rôles played by the various meristematic layers in the formation of the wing are somewhat different but (and this is what concerns us in particular) the expansion of the wing is the result of a process which very much resembles apical growth.

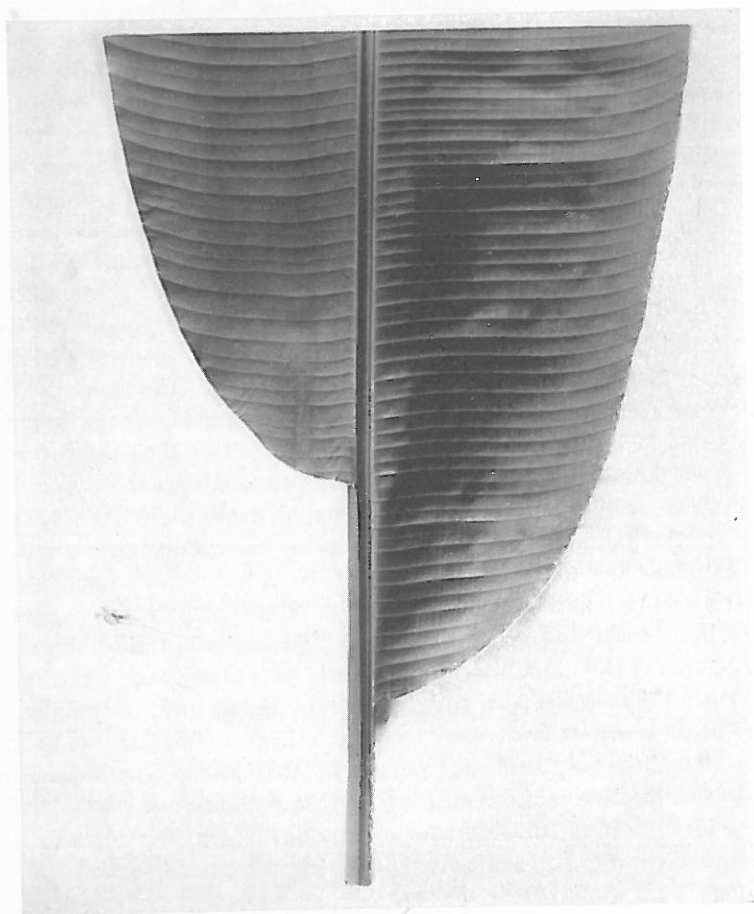
Mrs. Arber (3) has already called attention to the fact that the wings of a number of monocotyledonous leaves, including *Sagittaria*, *Aponogeton*, and *Potamogeton* in the Helobiae, *Calla* and *Arum* in the Araceae, and *Smilax* in the Liliaceae, originate as lateral outgrowths of the midrib. In so far as the primary fact of the formation of its lamina by the "winging" of its midrib is concerned, these monocotyledons essentially resemble numerous dicotyledons, but in certain of them an additional process, not known to occur in the latter group, plays a subordinate part in the development of the lamina. This process is invagination, which Mrs. Arber has demonstrated to be of major or subordinate importance in the development of a large number of monocotyledonous leaves, and considers one of the mainstays of the phyllode theory.

The banana agrees with the ferns, a large number of dicotyledons, and many other monocotyledons in the formation of the lamina by the "winging" of the rhachis or midrib, nor is it distinguished from them by the participation of invagination in its development. But the point of origin of the meristem from which the wing is developed is different (so far as I am aware) in *Musa*, and other Scitamineae, from all other plants, with the single exception of the palms. In ferns and dicotyledons, the wings originate at an early age before the marginal tissues of the midrib (or rhachis) have lost their meristematic character; in ferns from cells which from the very first are specialized for this function. But in *Musa* the lamina-halves do not commence to develop until a comparatively late date, when the marginal cells of the midrib have lost their meristematic nature, and have differentiated into a scarious border; hence their initiation is relegated to deeper, less specialized tissues, and the margin of the developing lamina-half is occupied by a hyaline wing, instead of by the formative meristem itself, as in *Pelargonium*. It is for this reason, among others, that I consider the lamina-halves of the banana a secondary development, and in no sense homologous with those of the dicotyledonous leaf.

The production of marginal outgrowths is not restricted to that portion of the leaf which is morphologically lamina, but may occur in manifold forms in organs of different morphological value. Foster (8) has described the broadening of the inner bud scales of *Aesculus*, which he has demonstrated to be developments of the leaf-base, by wing-like outgrowths from their sides (l.c. Pl. L, fig. 30). This production of a pseudo-lamina by a leaf-base in a dicotyledon is of particular interest, in view of the theory which I shall presently advance, that the leaf of the banana bears just such a pseudo-

lamina. The venation of the wings of the bud scale of the horse-chestnut is irregularly dichotomous, not parallel as in monocotyledons, which should indicate that the form of venation alone is of little value as an indication of the homology of the lamina.

As the result of the activity of two entirely independent meristems, one lamina-half of the banana frequently extends farther down the petiole than the other. In certain varieties of *Musa textilis* the right half usually



TEXT FIG. 19. Base of the lamina of a leaf of *Musa textilis*, showing the unequal basal extension of the two halves of the lamina.

extends far below the left, and in one case an inequality of 17 cm. was measured (text fig. 19). There is no general rule as to which side is produced the farthest basally. In *Musa tomentosa* and *M. sapientum* variety Gros Michel, for example, the left side extends below the right, while in *M. sanguinea* and many varieties of *M. sapientum* the two lamina-halves meet

the petiole at approximately the same level. The nature of this basal inequality is entirely different from the obliquity or basal asymmetry of many dicotyledonous leaves, which is caused merely by the unequal outgrowth of the basal lobes, and these may nevertheless meet the petiole at the same level. In some species of dicotyledons whose leaves possess a distinct, marginless petiole, it is possible to find numerous examples in which the lamina-halves meet the petiole at different levels, just as in *Musa textilis*, but from the smaller size of the laminae the inequality is much less conspicuous. *Cornus florida* and *Quercus palustris* furnish many leaves of this character. In one case as in the other, the basal inequality of the lamina-halves is lasting testimony of the fact that they are of independent origin.

The very late appearance of the lamina-halves, compared with the other portions of the leaf, also points to a phylogenetically later origin. It is almost a truism in embryology that the characters or organs more recently acquired by the ancestral line make their appearance in the developing individual at a relatively late date; the ontogeny repeats the phylogeny. While it must be admitted that ecological requirements sometimes obscure this law, its general validity is supported by the vast majority of cases. The delayed appearance of the lamina-halves, while perfectly evident from text figures 4-11 and the description which accompanies them, is further supported by measurements of leaf rudiments in various stages. Table 1 gives the dimensions of successive leaves of the same plant. Reading the table from below upward, it is seen that the lamina-halves do not appear until the future lamina (that is, the midrib which will support it) exceeds 1.1 cm. in length. In the next older rudiment, the lamina half on the left side (the only one it is possible to measure with accuracy in very young rudiments) is only one forty-second the length of the lamina. If I have erred in determining the breadth of the lamina-half at this stage, it is on the side of generosity, for in the succeeding rudiment the ratio of breadth to length is 1 to 66, whence there is a regular increase until the mature proportions of 1 to 5 or 6 are attained (cf. also text figs. 14-17). In every case, the lamina-half was measured at its broadest point.

In dicotyledonous leaves the petiole is a relatively late development, intercalated between the lamina and leaf base after the former is well advanced (Trécul, 19; Deinema, 6). In the banana the condition is just the reverse. The petiole is easily distinguishable in rudiments where the lamina-halves are in their earliest stages. Because of the gradual transition from the sheath to the petiole (see Skutch, 18, p. 361) it is not possible to place the limit between them in very young rudiments with sufficient accuracy, and it was found desirable to measure them together in making table 1, but none-the-less, a distinct petiolar portion may be discerned at a very early stage, and in cross-sections it is easy to distinguish it from the sheath by the arrangement of the longitudinal septa.

The length of the future midrib is to a certain extent determined before

the lamina-halves are initiated, or at least while they are still quite young, and their outgrowth from the sides of the former is more or less independent of its size. An interesting result of this is the great variation in the *proportions* of the various leaves produced during the course of the life of a single plant. The first leaves formed by a young sucker are of the "sword" type, long and narrow, practically linear in outline. As the sucker matures, the relative breadth of the lamina increases until the oblong leaves of the mature type are formed. The change in the proportions of the leaves is quite as striking as their change in absolute size. If one cuts between a young sucker and the parent rhizome with a sharp machete, thereby severing the organic connection between the two without destroying the root system of the former, the leaves of the former which unfold after the operation, while increasing considerably in length, show a very much greater increase in breadth, showing that the two formative processes have been influenced to different degrees.

The evidence presented seems to favor the conclusion that the lamina-halves, the essential assimilating portion of the leaf, are a secondary development, acquired late in the history of the species and in no wise homologous with the lamina of a dicotyledonous plant. This circumstance points to the fact either that the remote ancestors of the present-day bananas were devoid of true laminae, or that they lost them at the same time that these substitute laminae, or phyllodes, were acquired. Our knowledge of the phylogeny of the Musaceae is too slight even to hazard a conjecture as to the exact mode by which the present type of leaf was developed.

The second point which we are called upon to settle is the morphological nature of the midrib. Mrs. Arber (1) has pointed out that the more or less radial arrangement of the vascular bundles in the precursory appendage strongly resembles the disposition of the bundles in the petiole of many dicotyledonous leaves. She has compared this appendage to the corset of the sepals of *Clematis*, *Passiflora incarnata*, and certain other dicotyledonous flowers. These sepals are developments of the leaf-base or sheath, while the corset is the vestige of the petiole. Many bud scales, too, as in *Fatsia japonica*, are modified leaf bases, and are surmounted by a small appendage which shows a radial disposition of the vascular bundles and represents the reduced petiole. Hence, she considers the precursory appendage in the banana to be the vestige of the tip of the petiole, while the lamina is a pseudo-lamina formed by the expansion of the distal portion of the petiole, but not involving the very apex.

The effort to explain the precursory appendage in the banana on morphological rather than on physiological grounds (cf. Genter, 9) seems a step in the proper direction. The purely mechanical function of the appendage in forming a passage for the portions of the leaf which follow it up the compact false-stem is obvious, but although this may account for the retention, or even the exaggeration, of a structure already present, it does not suffice to

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explain its origin. I regard its physiological importance as negligible, for leaves with the appendage cut off as soon as it appears from the false-stem developed normally and grew as rapidly as others on which it was allowed to remain until it withered, which was usually long before the leaf had completely emerged.

But while I am entirely in accord with Mrs. Arber in regarding the appendage as a vestige of the petiole, and the blade as a pseudo-lamina or phyllode, I cannot join her in considering the appendage as the vestige of merely the apical extremity of the petiole, or the lamina the expansion of its distal portion. Neither the (apparent) petiole nor the midrib of the banana leaf shows any of those anatomical characters from which Mrs. Arber deduces the petiolar nature of the precursory appendage, or of the leaves of the Iridaceae and many other monocotyledons. The bundles are all normal in their orientation. All of the changes which occur in passing from the sheath to the petiole, which in its distal portion presents almost exactly the same cross-section as the greater portion of the midrib, show clearly that the development of the abaxial side has been favored at the expense of the adaxial, and this has resulted in pushing back the central lacunae from the upper surface (cf. Skutch 18, figs. 23 and 24). The process is similar to that by which Goebel (10, p. 278) explains the origin of the unifacial leaves of species of *Iris* and *Allium*, etc. It is true that the same process, carried a step farther, would account for the structure of the precursory appendage itself, but it would not explain the presence of this in the first place.

It seems most logical, therefore, to consider the entire leaf, upward to the base of the precursory appendage, as morphologically leaf-sheath. Another mode of viewing the problem leads to the same conclusion. The almost longitudinal veins converging at the apex, characteristic of the entire surface of the laminae of very early seedling leaves (text fig. 2) are found only nearer and nearer the apex in progressively later leaves. In leaves of the fully mature type, such an approximately parallel and longitudinal arrangement of bundles is found only in the base of the appendage, before it becomes a solid organ (cf. text fig. 6). It seems, then, that the process by which the lamina halves are formed encroaches lower and lower in the leaf rudiment, while that portion which represents the seedling leaf is represented only at the very apex of the lamina of the mature leaf. The seedling leaf itself is of the liliaceous type, which Mrs. Arber (4) considers to be a leaf-base phyllode.

The complex history of the development of the leaves of palms has induced many to follow its course. The view of Naumann that the layers of the plicate leaf arise by the splitting of an originally solid rudiment has been effectively refuted by Hirmer (12), who is in accord with all other of the more recent investigators (6, 7), that they arise by the folding, or more properly (2), the invagination, of the lamina. The young rudiment of the leaf of a feather palm shows, in addition to the basal sheath, a comparatively very massive rhachis, bordered by a relatively narrow and in-

significant marginal tissue which is the rudiment of all the pinnae. This marginal tissue soon begins to form the folds so characteristic of the palm leaf. The invagination or folding of the tissue does not, however, extend to the very edge, but is restricted to an at first narrow zone, while a peripheral band remains unfolded. This binds together the tips of the pinnae and is torn away from them when the leaf finally expands. Only in *Chamaedorea*, among all the species which have been investigated, do the folds extend practically to the edge of the rudiment, and an extremely narrow border, which soon disappears, is left over.

In the production of a very evident rhachis before there is any trace of a lamina, the presence of a marginal wing which does not constitute a portion of the mature leaf, and the intercalation of the future lamina between the rhachis and the wing, the palm agrees closely with the banana. While I have not been able to find any definite statement that the unfolded margin of the palm leaf is older than the portion which forms the folds, I infer, from a statement by Hirmer that the cells of the former have early lost their meristematic character, that this is the case. In referring to the folded portion, I have used the word lamina advisedly, for the pinnae of a feather palm leaf constitute merely a split-up lamina, its divisions separated by the intercalary growth of the midrib, which thereby becomes a rhachis. If we were to imagine the lamina-halves of the rudiment shown in text figure 14 to grow more rapidly in a longitudinal direction than the midrib, they must inevitably be thrown into folds, since the wing could not, and the midrib does not, keep pace with them. If these folds were then to become separated by the death of the tissue at the upper or lower creases, we would have something like a feather palm.

I have restricted my discussion to the feather palms because of their closer resemblances to the banana leaf, but it would apply to the fan palms equally well for, according to Eichler, the only fundamental difference between the two types is the originally shorter rhachis of the latter, and its failure subsequently to elongate.

The two largest and most striking types of monocotyledonous leaves, exemplified by the Palmae and Musaceae, are not so fundamentally different in their mode of development as would appear at first sight, great as the differences undoubtedly are. One further point seems worthy of mention, and that is the much earlier development of the lamina in the palms. Thus in a rudiment of *Phoenix spinosa* only 0.5 cm. long, the process of disorganization of the upper creases, which results in the separation of the pinnae, had already begun (7). In a leaf-rudiment of the banana of the same size, the lamina has not yet begun to form, and when the leaf emerges, the lamina is still entire. As a result of the very early separation of the pinnae of the palms, while their tissues are still embryonic, they are in some cases (*Cocos*, *Chamaerops*) able to regenerate an epidermis to close off the wound, but the splitting of the banana leaf into "false-pinnae" is accom-

plished by outside agencies after the leaf is mature, and the wound is closed merely by the suberization of those cells which happen to border it, as is the case in many palms. An attempt to throw the banana leaf into the folds necessary for its mechanical support, resulting in the formation of ribs, occurs at the time of unfurling, instead of very early in the bud. The palms certainly possess a more highly developed type of leaf than the Musaceae, despite the fact that taxonomic works generally place them lower in the scale.

SUMMARY

1. In the rudiment of the banana leaf the lamina-halves arise at a relatively very late period. In the future sheath, petiole, midrib, and precursory appendage, the lacunar regions are clearly differentiated from the outer walls and septa, and in these the principal vascular bundles are laid down, before the lamina-halves appear.

2. The lamina-halves arise from the edges of the midrib, but interior to the hyaline margin and the outermost vascular bundle of each side of the former. This margin, which early loses its meristematic condition, becomes the evanescent membranaceous wing which borders the newly unfurled lamina, and the vascular bundle becomes the marginal bundle of the lamina.

3. The lamina-halves differentiate in a centripetal and basipetal direction. The apex of each half precedes the base in differentiation, and the marginal region that near the midrib.

4. The right and left halves of the lamina originate at the same time, but entirely independently of each other. In some species of *Musa*, one half may extend down the petiole many centimeters beyond the other.

5. The varying proportions of the leaves indicate that the outgrowth of the lamina-halves is in a measure independent of the length of the midrib, and is determined at a later period than this.

6. The lamina of the banana leaf is a secondary development, and its morphological value is entirely different from that of typical dicotyledonous leaves. Its midrib is morphologically a portion of the leaf-base or sheath, while the precursory appendage is probably a vestigial petiole.

7. The present study is in accord with the phyllode theory of the monocotyledonous leaf as propounded by Mrs. Arber.

8. In the early development of the midrib or rhachis, and the intercalation of the lamina between this and a marginal wing which does not form a portion of the mature lamina, the banana shows points of agreement with published descriptions of the origin of palm leaves.

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