VOLUME LXXXIV NUMBER 4

THE

BOTANICAL GAZETTE

December 1927

ANATOMY OF LEAF OF BANANA, MUSA SAPIENTUM L. VAR. HORT. GROS MICHEL[1]

ALEXANDER F. SKUTCH

(WITH FORTY-FOUR FIGURES)

I. External features

1. DISTRIBUTION OF LEAVES ALONG STEM; PSEUDOSTEM

Until a certain stage in the development of the plant, the entire aerial portion of the banana is made up of leaves alone. To a superficial observer, the banana of this age appears to consist of an erect, unbranched stem surmounted by a crown of enormous leaves, to be, in fact, a "tree," as it is often loosely designated, with a "trunk" 3–4 m. high and 15 cm. or more in diameter. If, however, the "trunk" is cut across at any level above the base, it is found to be a pseudostem composed of the overlapping, close-fitting leaf sheaths alone, and containing no axial member at all. As the plant approaches maturity, the condensed stem at its base begins to elongate and to push upward in the center of the pseudostem, finally emerging at its upper extremity, where it bends downward and produces the pendent inflorescence. The leaf insertions, which previously were in contact on a stem condensed into a bulb, are more and more widely separated along the lengthening axis, and internodes of increasing length appear.

[1] Botanical contribution from the Johns Hopkins University, no. 88. This investigation was made and its results are published with the aid of a grant from the Department of Agricultural Research of the United Fruit Company.

Whether or not the banana has a true aerial stem is a question more of academic than of practical importance. As SCHUMANN (20) observes, the phyllotaxy, whether distichous and alternate or spiral with a smaller divergence, is of more importance in determining the appearance of a genus of the Musaceae than the degree of development of the axis. However, since the theoretical interpretation is apt so to color the mere statement of the actual situation that if it is a mistaken one a false impression will be left in the mind of the reader, it seems desirable to re-examine the facts. Most brief accounts of the structure of the banana plant, particularly the more or less popular ones (4, 18, etc.), place so much stress upon the peculiar pseudostem, contrasting it with the "true" stem or bulb at its base, and with the floral axis which pushes its way upward through the former toward the light, that an erroneous picture of the aerial stem is very naturally formed. One might well expect, after reading these accounts, to find the inflorescence borne on the end of a gigantic, leafless scape, naked except for the bracts just beneath the flowers. Accordingly, the writer was considerably surprised, when he made his first longitudinal section of an entire plant, slicing it up the center with a long cutlass, to find the stem leafy almost to the summit (table I). WITTMACK (22) gives a clear statement of the facts, but the writer was unable to obtain this article until later. The other accounts just referred to contain no actual misstatement of the case, but are at fault rather from lack of completeness, and in particular from false emphasis.

Table I gives the sizes and heights of insertion of all of the leaves present on two fruiting plants. In these plants, respectively 396 and 422 cm. high, the largest leaves were inserted 30–150 cm. above the ground, and the absolutely largest at 69 and 67 cm. respectively, while the stems bore true foliage leaves to about 3 m. above the base. In other words, more than the basal three-quarters of that portion of the stem within the leaf sheaths was leafy. WITTMACK records the heights of insertion of the leaves of a specimen of *M. ensete*, which resembles *M. sapientum* in the distribution of leaves along almost the entire inclosed portion of the stem. The sizes of the leaves are not recorded in his table, but the largest leaf scar, and presumably the largest leaf, occurred at 49 cm. from the ground. On the

other hand, the stem which bears these leaves is totally incapable of supporting them without the aid of the inclosing sheaths. Whether or not the elongated portion of the axis which bears the largest leaves is to be considered a true stem, as well as the condensed basal portion which bears most of the leaves, is a question of definitions. Morphologically it is certainly stem, whatever we may choose to

TABLE I

SIZE AND DISTRIBUTION ALONG STEM OF INTACT LEAVES OF TWO FRUITING PLANTS

Number of leaf	Plant I* Pseudostem = 396 cm. high			Plant II† Pseudostem = 422 cm. high		
	Height of insertion	Length of leaf	Greatest width	Height of insertion	Length of leaf	Greatest width
1	Basal	262 cm.	79 cm.	19 cm.	274cm.	79 cm.
2	Basal	178+‡	86	22	274	86
3	8 cm.	279	84	24	282	Withered
4	9	292	84	28	277	89
5	14	284+‡	89	29	300	89
6	18	239+‡	86	36	310	91
7	25	302	97	43	323	91
8	32	305	94	53	315	91
9	43	330	99	67	328	84
10	69	330	97	98	318	84
11	109	320	99	146	300	84
12	180	305	86	224	272	75
13	277	226	74	318	178	56
14	363	Dead§	Dead§	387	Dead§	Dead§

* 15 sheaths, totally or partially alive, the laminae belonging to which had fallen away, were removed from the outside of the pseudostem.

† 16 sheaths were removed.

‡ End of lamina torn off.

§ "Protecting leaf."

call it in regard to function. The banana may well be likened to any of our familiar perennial herbs of field or garden, which during the first year form a basal rosette of leaves at the crown of the rhizome, and in the succeeding season produce a leafy, aerial, flowering stem; only in the banana, a tropical plant, there is no resting season, and the circumstance that the leaves of the rosette are erected into a pseudostem which conceals and supports the true aerial stem is apt to be confusing. Even the pseudostem is not without representatives among temperate plants. The leek furnishes a good but diminutive example, although here the flowering shoot is lateral and not cen-

tral, as in the banana. The celery plant forms a larger but rather loose pseudostem.[2]

2. Phyllotaxy

The phyllotaxy is not constant throughout the life of the plant, but the angle of separation between successive leaves increases with the age and size of the individual. The fraction expressing the spiral of phyllotaxy was determined both by counting the number of leaves and of turns between two superposed leaves on the pseudostem, and by studying the arrangement of the sheaths of cross-sectioned pseudostems. Consistent results were obtained by the two methods, except in the case of very young suckers, where, probably as a result of a slight torsion of the pseudostem, the leaves often show a divergence very close to 1/3, although the angular separation as determined by the sheaths is nearer 2/5. The actual separation of the sword leaves of a young "ratoon," 50 cm. high or less, is often very slightly over 1/3. Somewhat larger ratoons show very clearly a phyllotaxy of 2/5, both of the blades and of the sheaths. At a somewhat later stage the spiral becomes clearly 3/7, both in the blades and sheaths. The size of the plant when the transition occurs depends largely upon its situation. A ratoon growing up at the base of a large plant, where it is shaded and produces sword leaves for a long time, may retain the 2/5 arrangement until it is over 120 cm. high, while an isolated sucker planted in the open, where it soon forms broad leaves, may show a 3/7 phyllotaxy at less than half that height. The two arrangements may often be seen in the same plant, the divergence between the older (lower) leaves being 2/5, that between the younger (upper) 3/7. Mature plants always have a phyllotaxy of 4/9, which may occur in plants 2 m. high, and is very clearly maintained in plants bearing full bunches of fruit, the presence of the bent-over stem causing no confusing distortion of the spiral.

The angular separation of the leaves of a very young ratoon, then, is slightly more than 120°. At a somewhat later stage, the age and size of the plant depending upon the environment, it becomes 144°

[2] *Veratrum album*, among temperate monocotyledons, provides an excellent example of the pseudostem. See Mrs. Arber's *Monocotyledons*, fig. xxxiii (Cambridge, 1925).

(in the ideal case). Still later it increases to 154°, and in full grown plants and those bearing fruit, the angular divergence is 160°.

WITTMACK gives the phyllotaxy of *M. ensete* as 3/7. GREVE (8) repeats this statement, and adds that it is true for all species of *Musa*. In young seedlings he found the phyllotaxy to be 1/2. SCHUMANN (20) records the 3/7 spiral as general for the Musoideae. In addition to examining numerous examples of the Gros Michel variety on the plantation, the writer had the opportunity to inspect the varieties Apple, China, Honey, Ramkelat, Robusta, and White House, as well as "*Musa kewensis*," in Hope Gardens, Jamaica. Mature fruiting plants of all of these showed a divergence of 4/9, younger plants 3/7 or less, according to their age. A single fruiting plant of the slender-stemmed *M. kewensis* maintained the 3/7 divergence of its leaves to the last.

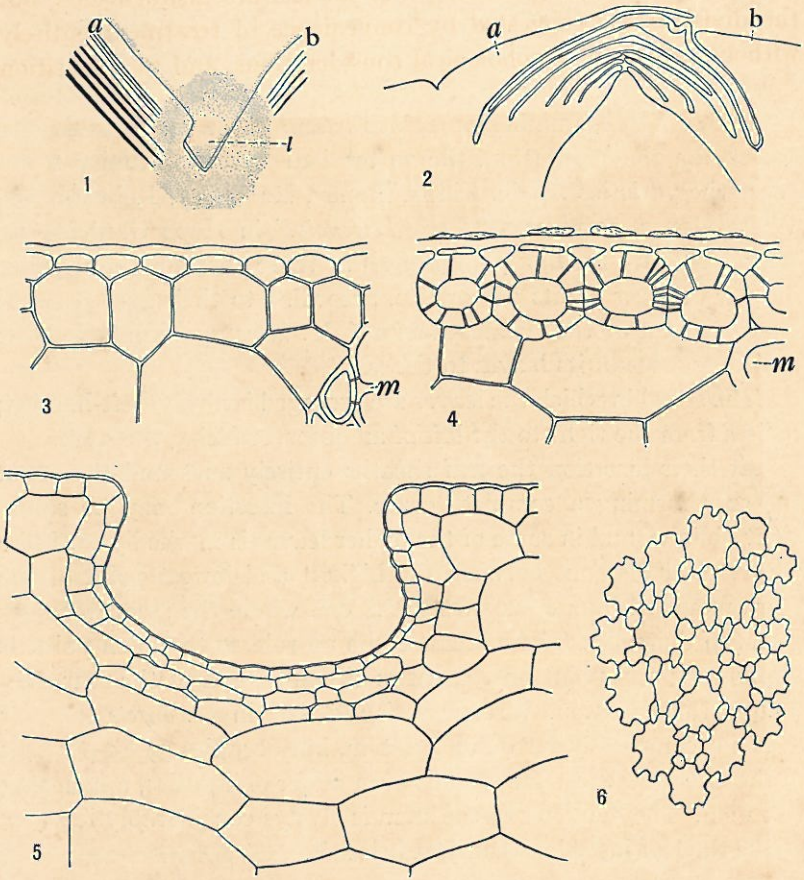
The spiral in which the leaves are arranged is always left-handed; it rises from the right to the left of an observer facing the stem.

At their insertion the leaf sheaths entirely surround the stem, the scar forming a complete circle. The insertion may be somewhat oblique, and in some of the higher leaves is markedly so. Here the vertical distance between the highest and lowest point of the scar amounted in one instance to 8.8 cm. where the stem was only 5 cm. in diameter. There seems to be no rule as to which point is uppermost; any point on the entire circumference of the scar may occupy that position. WITTMACK found that in *M. ensete* the scar does not completely surround the stem, but occupies 59–80 per cent of the circumference. He records even larger obliquities, amounting to 22 cm. The diameter of the stem is always considerably less just above the leaf insertion than just below it.

3. LATERAL BUDS

The lateral buds do not occur in the axils, as stated by SCHUMANN, but are situated opposite them. They regularly appear in the angle of the V formed by the two margins of the sheath as they converge to the point of insertion (fig. 1). The scarious margins overlie the outermost scales of the bud (fig. 2). Buds occur regularly at the insertion of each of the basal leaves of the plant, but not of those situated in the region of elongated internodes, that is, the

aerial stem. The position of the buds suggests that possibly the stem is a sympodium, but the point has not been investigated anatomi-



FIGS. 1–6.—Fig. 1, lateral bud (*L*) in surface view; *A*, *B*, margins of sheath of about 16th leaf from center of pseudostem; ×1. Fig. 2, horizontal section through similar bud; ×10. Fig. 3, outer epidermis and subjacent cells from a sheath near inside of pseudostem; *M*, portion of fibrous strand; ×400. Fig. 4, same but from exposed sheath of same plant; ×400. Fig. 5, pit from inner surface of sheath, in horizontal section; ×150. Fig. 6, stellate cells from transverse septum of sheath; ×36.

cally. In the related *Ravenala madagascariensis* the buds are truly axillary.

4. Leaf parts

Four regions along the length of the leaf are distinguished, but the divisions are suggested by convenience of treatment entirely without regard to morphological considerations, and the transition

Fig. 7.—A "protecting leaf" which hangs over a bunch of immature fruit

from one region to another is gradual and not sharp. These are, from the apex downward: the precursory appendage,[3] the lamina, the petiole, and the sheath. The appendage is a temporary organ, and has already withered when the leaf reaches maturity. The lamina contains a strong midrib which is flanked on either side by a pulvinar band. This is followed by a broad blade, bordered in the

[3] So I translate the *Vorläuferspitze* of German authors.

young leaf by a scarious margin which soon withers away. The petiole is a region of transition from the sheath to the midrib, in the larger leaves reaching 30 cm. or more in length. The sheath may be defined as that portion of the leaf which participates in the formation of the pseudostem.

5. Size and form of lamina

The lamina of the banana, in its pristine state as it emerges from the pseudostem, represents one of the largest unbroken expanses of photosynthetic tissue in the entire plant kingdom. In the largest leaves of the Gros Michel it attains a length of about 4 m. and a maximum breadth of over 1 m. It is exceeded in size notably by the enormous leaves of another member of the Musaceae, *Ravenala madagascariensis*, which are stated to attain 6 m. in length, by the floating leaves of *Victoria regia*, the largest of which reach 4 m. in diameter, and by the blades of certain kelps, such as *Laminaria longicruris*, attaining 6 m. in length and 1 m. in breadth. They are approached and perhaps equaled in area by the leaves of certain species of *Gunnera*. Of course, many tree ferns and palms have leaves of greater dimensions, but these are all compound, and not directly comparable with those of the banana. It is a significant fact, the bearing of which will be evident when we consider the splitting of the lamina by the wind, that the banana and its relatives bear perhaps the largest undivided aerial leaves to be found anywhere. Reliable data on the size of leaves are difficult to obtain.

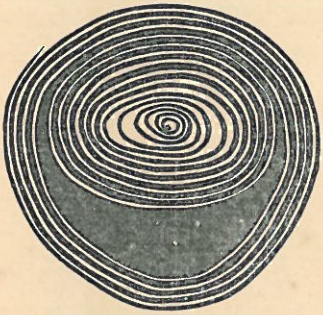


Fig. 8.—Transverse section of leaf as rolled inside pseudostem, showing form of vernation; ×3.

The ovate-oblong leaves of the mature form are the last of a long series, the first of which are strikingly different in both size and shape. The first leaves arising from the subterranean bud, which grows out from the bulb to form the replacement shoot or ratoon, are reduced scale leaves, in which the portion that represents the sheath alone is prominent. In the succeeding leaves the lamina

becomes more and more conspicuous, first in the form of the long narrow "sword leaves" characteristic of the young ratoon, and as the plant grows older, gradually increasing in size and relative

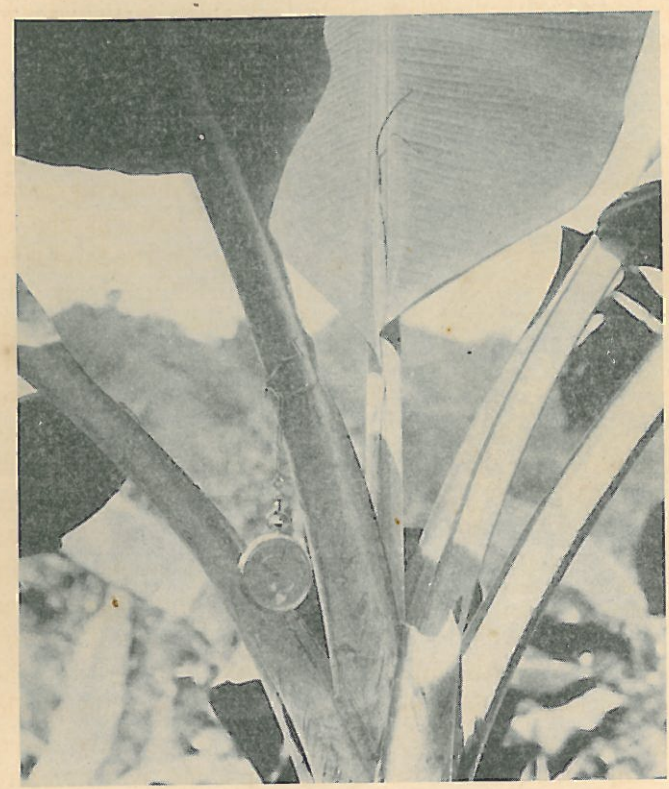


FIG. 9.—Young leaf just emerging from pseudostem; note long precursory appendage.

breadth until the mature proportions are attained.[4] The rapidity of change depends upon environmental conditions, of which light is probably the principal. Isolated suckers form broad leaves much

[4] According to COOK (3), there are two kinds of suckers, which differ in the character of their early leaves. The "broad-leafed" suckers originate from buds situated near or above the surface of the ground, and produce broad leaves from the first; the "sword" suckers arise from more deeply buried buds, and produce the characteristic linear leaves. For many excellent illustrations of leaves of both forms, and of the plant as a whole, see REYNOLDS (19).

earlier than those still attached to the parent plant. The fruiting plant retains about 11–14 intact leaves, together with about 12–16 sheaths which are still in part or entirely succulent and aid in the support of the stem, and perhaps serve as storage organs, although their blades have withered and fallen.

FIG. 10.—Leaf which has emerged from pseudostem to almost full length of lamina, but which has not yet begun to uncoil, at top of figure near middle.

6. "PROTECTING LEAF"

The last of the series of green vegetative leaves differs considerably from those just below it, and is distinguished as the "protecting leaf." In comparison with the other leaves it is very much reduced in length, but about equally broad (fig. 7). The broad flat

petiole retains a sheathlike structure, and clasps the inflorescence axis as it emerges from the top of the pseudostem, preventing more or less completely the penetration of rain water between the innermost sheaths and the stem. It is incapable of supporting the lamina, which bends forward and usually hangs for a time over the inflorescence, affording it temporarily a certain degree of protection from sun and rain. This leaf is inserted very near the top of the pseudostem, in the plants measured 30–40 cm. from its apex. It is short-lived, and droops and withers before the fruit is mature.

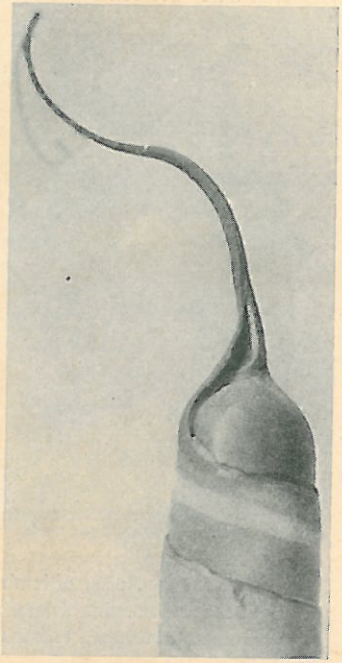


FIG. 11.—Dome which caps lamina just before it begins to uncoil, surmounted by partially withered precursory appendage.

7. VERNATION

In vernation the leaf is convolute. The rolled right[5] half of the lamina, making about 18 turns at its broadest portion, fits neatly into the concavity of the upper side of the midrib, and the whole is surrounded by the 4–5 turns of the left half (fig. 8). Preceded by the precursory appendage, the coiled leaf pushes upward from the center of the sheath of the one next in age (fig. 9), and emerges to practically the full length of the lamina as a straight, stiff, green rod (fig. 10). Then the coils begin to loosen, and the leaf first expands at the apex. The hollow cylinder which is formed just before the leaf spreads out terminates in a dome or cupola which is surmounted by the precursory appendage (fig. 11). The right half of the lamina alone participates in the formation of this dome, while the left half, rolled about the outside of the cylinder, may readily uncoil and spread out. Since the tissues of the dome undergo no

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

further expansion, mechanical considerations make it at once evident that the right half cannot unroll without tearing away the permanently curved portions. The rupture of tissues occurs principally along the veins, and the dome is removed more or less intact. Usually the dome with the appendage remains at the end of the midrib, but sometimes they are torn from the latter and carried to

FIG. 12

FIG. 13

FIGS. 12, 13.—Apices of lamina of two leaves which have just uncoiled, showing torn right end and remains of dome and precursory appendage; in fig. 12 tear is straight and dome intact, in fig. 13 tear is more irregular.

the right side of the leaf. The line of separation is evident throughout the life of the leaf, and is more or less regular, according to whether the tear follows a single vein (fig. 12) or strikes across the lacunae from one vein to another (fig. 13).

II. Anatomy

A. SHEATH

8. GROSS STRUCTURE

The sheaths innermost at any particular stage of growth extend for practically the entire height of the pseudostem. Exception must be made, of course, for the leaves inserted along the late-appearing

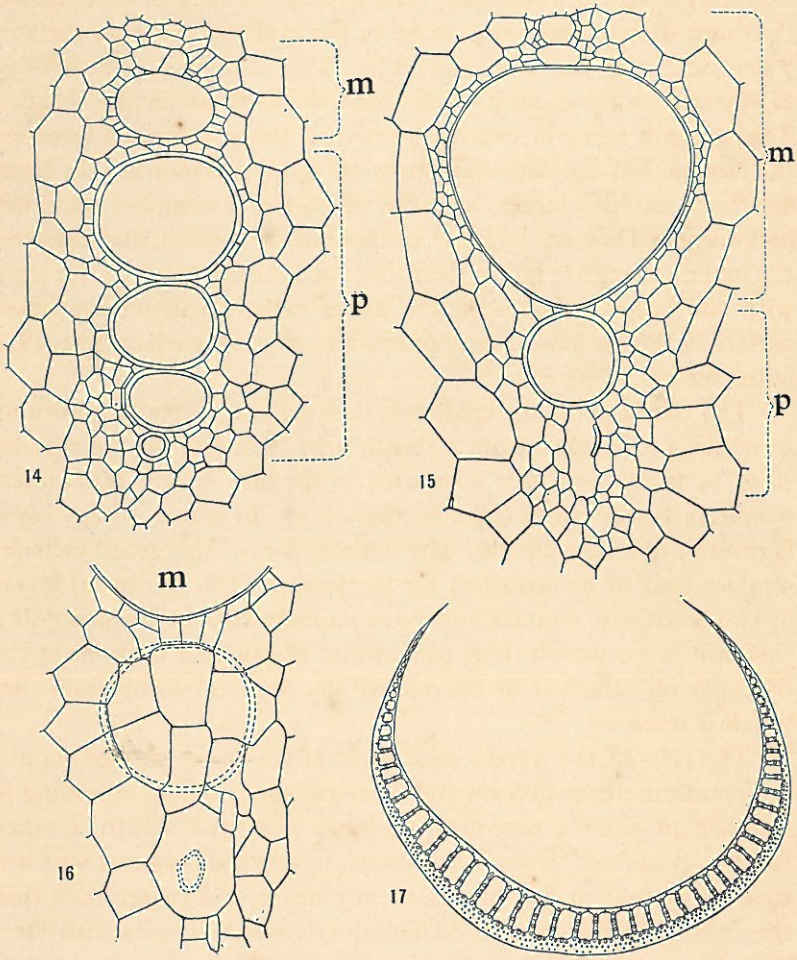
aerial shoot. Although the margins of the young sheath overlap and the sheath forms a hollow cylinder, the older, more exterior sheaths are typically crescentic in cross-section (fig. 17). The thickest point is near the center, whence the cross-section tapers to a thin transparent wing, which contracts at the margin to the thickness of two extremely narrow cells (about 9 μ). At the base the maximum thickness of the sheath is about 14–17 mm., at the top, about 10 mm. At its insertion on the stem the sheath completely surrounds it. It narrows abruptly to about half the initial breadth at a point 30 cm. higher up, whence it contracts gradually to the petiole. At their bases, old sheaths are penetrated while still alive by roots arising from that portion of the stem inclosed by them.

Between a thick outer and a thinner inner wall is situated a series of lacunae which occupy the bulk of the volume of the sheath. A series of radial septa runs the entire length of the sheath and divides the cavity between the walls into longitudinal canals. These are interrupted at frequent intervals by thin horizontal septa, with the result that a series of rectangular air chambers is formed. In the widest portion of large sheaths the lacunae are about 5–8 mm. wide (tangential dimension), 8–11 mm. deep (dimension normal to surface of sheath), and 2–6 mm. from top to bottom. At the base of the pseudostem the inner wall of the sheaths is often strongly corrugated, and the horizontal septa strikingly folded. This condition is reminiscent of the wavy grain of the wood at the base of large trees, and is a result of the same mechanical stresses in tissues of the same function but very different homology.

9. Dermal system

The epidermis is composed of straight-walled cells, rectangular in surface view, with their long axes parallel to the length of the sheath. Beneath the epidermis is a hypodermal layer of cells having their long axes parallel to those of the epidermis in the case of the outer surface, but perpendicular to them in the inner surface. Stomata occur on both the outer and inner surfaces of the sheath throughout its length, as well as on the inclosed portion of the stem even to its base. On the inner surface of all the sheaths and on the stem the stomata are not exposed to the atmosphere, since the

sheaths fit very tightly together. On the outer surface of some sheaths they are after a long period exposed, but here also on many



FIGS. 14–17.—Fig. 14, xylem portion of vascular bundle of sheath of leaf just emerging from pseudostem, section cut at about 5 mm. above insertion of sheath; protoxylem elements (*P*) still intact, metaxylem (*M*) immature; ×160. Fig. 15, bundle from sheath of about same age, section at 24 cm. above insertion of sheath; earliest protoxylem elements disrupted, and large metaxylem element almost mature; ×160. Fig. 16, portion of mature bundle, showing site of occluded protoxylem elements; annular thickening and turn of spiral band, slightly below plane of drawing, indicated by broken lines; ×285. Fig. 17, transverse section of sheath from fruiting plant, position of principal vascular bundles indicated by circles; ×about 0.5.

sheaths they are never brought into contact with the air. The presence of these stomata seems a result of phyletic inertia rather than physiological advantage. The average density of stomata on the outer surface was found to be 11 per $\overline{mm.}^2$ on the inner surface, 7 per $\overline{mm.}^2$ near the base, and 12 per $\overline{mm.}^2$ at the top. The density of stomata on the stem itself is about the same as on the sheaths. The stomata agree in general form with those described later for the lamina, but the cuticular ridges are more pronounced, the front and back cavities larger, and the substomatal chamber narrower and deeper. They are larger than those of the lamina, and those on the inner surface are larger than those of the outer surface, agreeing with the larger stomata on the upper rather than on the lower surface of the lamina. Length of stomata on inner surface is 34–38 μ, outer surface 27–34 μ.

The character of the epidermis does not vary greatly according to whether it is taken from a sheath near the center of the pseudostem, or from one which is exposed to the air. A very thin cuticle overlies a thick wall of cellulose (figs. 3, 4). In places a waxy layer is present over the cuticle. The cutinization of the guard cells resembles that to be described for the lamina. The epidermal layers of two sheaths in contact adhere so strongly that in stripping off a sheath it is a common thing to find that the thinner portions at the edge remain attached to the one within, and tear away from that which is removed.

The cells of the hypodermal layer of the outer surface show a profound difference in form and chemical composition, according to whether an outer exposed, or an inner protected sheath is taken (cf. figs. 3 and 4). If an inner sheath is selected, say one which is covered by four or five others, or any nearer the center than this, the hypodermal layer will be found to consist of cells with large clear lumina, and thin walls of unaltered cellulose; they show no trace of suberization. An entirely different picture is presented by the hypodermal cells of the outermost living sheath. The walls are much thickened, having attained 4–13 μ in thickness where in the inner sheath they are less than 1 μ. They are penetrated by prominent radial pits and are distinctly laminate in places. The lumina are very much reduced. Microchemical tests show that these thick

walls are lignified. The anticlinal and inner walls of the epidermal cells are thickened and lignified, while the outer walls and the cuticle are apparently unaltered. Occasionally the walls of the cells of the layer next beneath the hypodermal layer are somewhat thickened and suberized.

The alteration of the hypodermal cells begins when the sheath, which is pushed from the interior toward the exterior of the pseudostem by the dying off of the old sheaths on the outside and the pushing up of new ones within, is fourth or fifth from the surface. The walls thicken gradually and become suberized,[6] lignification not occurring until a later stage, when the sheath is covered by only two or three of those exterior to it. The hypodermal cells bordering the substomatal chambers behave differently from the others, which alone are referred to in this description, in that their walls thicken and become lignified at an earlier period. Thus, for example, in the fourth sheath from the exterior they were found to be greatly thickened (as much as the other cells in the second or even the exterior sheath) and lignified, while the surrounding cells were very slightly thickened, and the chemical alteration had proceeded only as far as a faint suberization.

Since the alteration of the hypodermal cells commences in sheaths still tightly covered by those exterior to them, it is obviously not caused by their proximity to a transpiring surface. The penetration of sunlight is probably the stimulus initiating the changes in a given sheath. The first indications of the thickening and suberization of the walls (except of the cells bordering the substomatal chambers) are usually to be found in that sheath which is the innermost containing visible traces of chlorophyll, and there is at least a roughly quantitative correlation between the greenness of a sheath and the thickness of its hypodermal walls.

The hypodermal stratum of the inner surface of even an outer-

[6] That is, they show a strong retention of GRÜBLER's cyanin, stain yellow to brown with chloroiodide of zinc (with or without previous treatment in javelle water), are insoluble in conc. H_2SO_4, and do not stain in a solution of phloroglucin and HCl. Membranes are said to be lignified when they are insoluble in conc. H_2SO_4 and give a positive reaction with phloroglucin. They usually stain some shade of orange or brown in the chloro-iodide reagent. The same significance is attached to these terms throughout the remainder of this article.

most sheath is not greatly different from that of the inner sheaths. The walls of the former are faintly suberized, but not noticeably thickened, and never lignified. In this surface occur numerous small depressions or pits (fig. 5). These are circular to elliptical in outline, and vary greatly in size, the largest being 500 μ in diameter and 160 μ in depth. Their frequency is roughly 20–30 per $\overline{\text{cm.}}^2$ Both the epidermal and hypodermal cells beneath the pits are shallower than elsewhere, and small intercellular spaces containing air occur among the latter. The pit is lined with a cuticle perhaps slightly thicker than that found on the surrounding surface. When a section of the sheath, the cut ends coated with vaseline, is immersed in an aqueous solution of safranin or methylene blue, the stain penetrates and colors the whole inner surface, with the exception of the pits, which are impervious to it and remain white. The function of these pits, if any, remains problematical.

10. Vascular and mechanical systems

The ground tissue of the walls which border the lacunae of the sheath at their outer and inner ends and of the longitudinal septa is a thin-walled parenchyma, in which are distributed the vascular bundles and the strands of prosenchyma (fig. 17). The most prominent vascular bundles are those situated in the longitudinal septa. In the thicker portions of the sheath there are 2–4 large bundles in each septum, in addition to very few small ones, and occasional fibrous strands. A large bundle is situated in the outer wall opposite the center of each lacuna, and another where each septum joins this wall. Alternating with these is a series of smaller bundles, somewhat nearer the outer surface, and still a third series alternates with and is external to the second. Exterior to these are numerous small bundles, in which the vascular tissue is very much reduced or lacking, and the outermost bundles are reduced to mere strands of fibers. In the inner wall there are usually 1–3 small bundles opposite each lacuna, but the number may increase to 8 or 9 near the base of the sheath.

The development of the xylem, and in particular the fate of the protoxylem, present features of special interest and were studied in some detail. The course of the ascending sap in leaves of various

ages was traced by injecting the bundles with trypan blue in 1 per cent solution, as recommended by Miss BUCHHOLZ (2). Whole plants were cut from the bulb and set in the solution in a sunny place, where they were allowed to remain for six hours. In this period there was considerable upward movement of the dye, even through leaves still inclosed within the sheath and hence not transpiring, probably largely in response to the requirements of the tissues for growth.

The bundles at the inner edges of the longitudinal septa are those which show the largest series of protoxylem elements. The earliest and narrowest protoxylem elements have annular thickenings. Following upon these are tracheids in which annular thickenings may alternate with spiral bands. Next follow ducts thickened by a single spiral band, which in places may be doubled by splitting. Each of the successive protoxylem elements, of which there are 3–6 in the larger bundles, according to the bundle and the level of the cross-section, is of greater diameter than the last, until the single large metaxylem tracheid is reached. This tracheid is strengthened by 10–14 low-pitched spiral bands which divide and reunite, so that even in a single tracheid their number is not constant. This large element is succeeded toward the phloem by several narrow, spirally thickened tracheids which may briefly be designated the commissural connectives, since it is to them that the commissural tracheids are joined. The writer has distinguished as protoxylem all elements of temporary duration, and as metaxylem all which are permanently functional.

The spiral bands of these tracheids, like those of the tracheids in the stem, pull out readily, and a cutlass used in cutting up the banana plant (especially if it is not very sharp) is soon enveloped in a thick wad of them. WITTMACK quotes PACTON (15) as stating that this material once was employed as tinder in the West Indies.

As is generally known, the sheath of the banana leaf elongates through the activity of an intercalary growing zone situated in the region of its insertion on the stem. The rate of elongation of the leaf is very rapid, and MAXWELL (13) has recorded a maximum rate of growth of 21 cm. per day (see also TRELEASE 21). A cross-section just above the base of a sheath which is still growing shows that

in each bundle the 3–5 earliest protoxylem elements are still intact and stained with the trypan blue, indicating that they are active in conduction (fig. 14); several more protoxylem elements are in process of formation, and the large metaxylem tracheid is still small and unthickened. At a higher level the rings of thickening of these earliest elements have become more widely separated, and the surrounding parenchyma cells have begun to bulge into their lumina. The commencement of the process of occlusion of the earliest elements may clearly be recognized at 1 cm. above the insertion of the leaf. The metaxylem is still immature and does not function, but the younger protoxylem has matured to take the place of the disrupted earlier elements. At a still higher level the metaxylem begins to stain, and one or two protoxylem elements still conduct (fig. 15). The lacunae left by the disruption of the protoxylem continue to stain for some time after their occlusion by parenchyma cells has begun, and apparently play some part in conduction, although they soon become filled with a mucilaginous substance which stains deeply with Delafield's haematoxylin. Finally the lumina of the protoxylem elements are completely occluded by the inward growth of the neighboring parenchyma, and the metaxylem alone is functional. The isolated rings or elongated spiral coils are visible closely imbedded in the parenchyma (fig. 16). One large cell may more than cover the site of the vanished lumen. A longitudinal section shows that the smallest rings are very widely separated, and the distance between the rings or turns of a spiral decreases as the element to which they belonged lay nearer the metaxylem (was of later origin). The level at which the metaxylem begins to conduct depends upon the age of the leaf. In a leaf just appearing above the pseudostem the metaxylem did not stain at all, although the solution rose through the entire length of the sheath in the protoxylem; in another, which had spread its lamina but was still elongating, the metaxylem stained at 3 cm. above the insertion of the sheath.

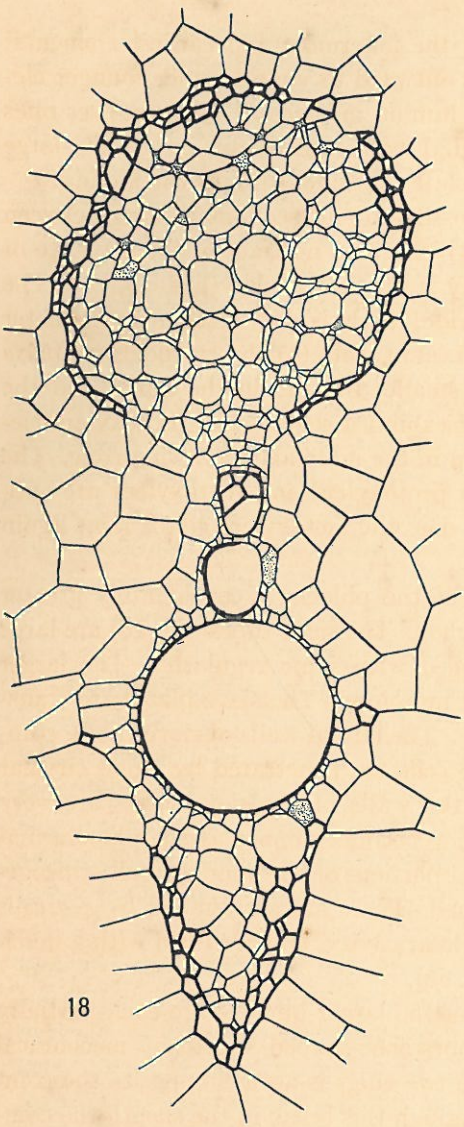
The sequence of events just outlined agrees essentially with that described for *Musa* by Miss Buchholz (2). *Musa* belongs in the third of the four classes of monocotyledons which she distinguishes on the basis of the fate of the protoxylem in organs with intercalary growth. If we trace the course of the ascending water current, we

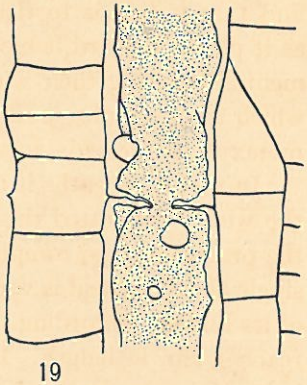
find that it begins to rise in the innermost and earliest elements; as it passes upward it moves outward to younger and younger elements, following their wider lumina in place of the narrower ones which are becoming occluded. Finally the stream enters the large metaxylem tracheids, in which it continues up into the lamina.

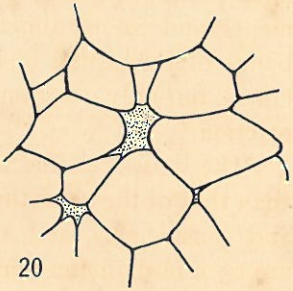
In mature sheaths it is possible to cut sections passing between the widely separated rings which show no trace of the presence of the protoxylem, so completely is the scar healed (figs. 16, 18). The single large tracheid is very wide, reaching 0.25 mm. in the diameter of its lumen. According to HABERLANDT (9) the tracheids of *Musa* reach 1 cm. in length. The smaller bundles in the septa, and the inner and outer walls, do not exhibit a sequence of protoxylem elements, and are not functional in the intercalary growing zone. The bands of thickening of both protoxylem and metaxylem are suberized, but only occasionally does the metaxylem give a faint lignin reaction.

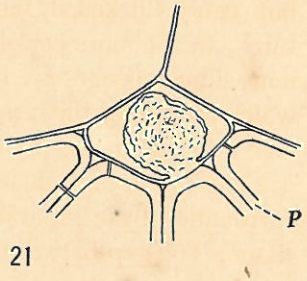
The cross-sectional area of the phloem is considerably greater than that of the persisting xylem. The sieve tubes (fig. 18) are large and conspicuous, and arranged with some regularity. The larger are 65 μ in diameter and 2.4 mm. long. The sieve plates are transverse or very slightly oblique. The lateral walls of sieve tubes, companion cells, and cambiform cells are penetrated by small circular pits. In immature bundles the walls of the sieve tubes are very noticeably thickened, but they become thinner as the phloem matures. In the more peripheral portions of the bundle small schizogenous slime passages are formed. These are surrounded by 4–7 cells which bulge into the intercellular cavity, and are filled with a mucilage which stains deeply (fig. 20).

The xylem and phloem of the larger bundles are each partially surrounded by a separate horseshoe-shaped sheath of mechanical tissue. The gap between the two rings is always opposite the commissural connectives, and through this break in the sheath the commissural bundles enter the longitudinal bundles (fig. 18). The thickness of the sheath depends upon the position of the bundle. In the large bundles in the longitudinal septa it is 1–3 cells thick. The relative development of prosenchyma increases in proportion as the bundle lies closer to the outer surface of the sheath. At the same time









FIGS. 18–21.—Fig. 18, vascular bundle from mature sheath; ×100. Fig. 19, immature mucilage vessel from petiole, showing perforation of end wall between two of cells composing vessel; ×345. Fig. 20, schizogenous mucilage passage from phloem of petiole; ×325. Fig. 21, stegma from bundle in sheath; *P*, prosenchyma; ×675.

the amount of conducting tissue is diminished, and the outermost bundles are mere strands of thick-walled fibers, without vascular tissue, which are largely responsible for the rigidity of the pseudostem. The sheath around the large interior bundles of the septa, especially its xylem portion, is often of rather thin-walled cells, and does not extend around the large tracheid. This is true especially at the base of the leaf sheath. Fig. 18 shows a sheath of moderately thin-walled cells incomplete around the large tracheid. The thinner fibrous sheaths are interrupted by gaps in which the cells are thin-walled, and serve as transfusion cells.

The composition of the walls of the fibers varies considerably in different leaves, and even in different portions of the same leaf sheath. The strands of fibers alone and the thick sheaths of greatly thickened cells in the outer wall of the leaf sheath are usually lignified. The thinner sheaths around the large inner bundles often give a distinct lignin reaction with phloroglucin, but in other places are suberized and not lignified.

FIG. 22.—Portion of tracheid from commissural bundle of sheath.

Accompanying the mechanical sheath on its outer face are groups of cells containing concretions of silica, the so-called stegmata. The stegmata are small cells with unthickened walls; they are short with blunt ends, and arranged in longitudinal rows. Each contains a roughly spherical mass of silica, apparently devoid of any organic basis (9), which almost completely fills the lumen, and is attached to the wall of the cell by a short stalk (fig. 21).[7]

Surrounding the bundles, outside the mechanical sheath, is a jacket of starch-filled parenchyma cells. This starch sheath persists even where it is separated from the vascular tissue by a sheath of 4–6 layers of heavily lignified fibers. The orientation of the principal bundles of the sheath, petiole, midrib, and lamina is always normal, the xylem toward the adaxial, the phloem toward the abaxial side.

[7] They may best be observed by following a modification of the method described by KÜSTER (11). Hand sections are dehydrated in alcohol and then mounted for observation in benzol, which gives the concretions a faint red tint. The cell walls may be stained in safranin, etc., while in the alcohol.

The curvature of a septum in the midrib may sometimes cause an easily detected physical reversal of morphologically normal orientation. In the longitudinal septa of sheath and midrib the axis of some of the smaller bundles without protoxylem is sometimes turned sideways, and occasionally the orientation is completely reversed.

The longitudinal bundles are connected at all levels by numerous commissural bundles, which lie in the plane of the horizontal dissepiments. However, only extremely rarely do these commissures strike across the dissepiment; normally their course is around its margin, where it joins the longitudinal walls of the lacuna. Here the commissural bundle may extend around two or three sides of the lacuna, sending out arms which connect with the small tracheids (commissural connectives) of the longitudinal bundles near its course. Other commissures occur in the outer wall. The commissural bundles consist of a small amount of phloem, and usually a single narrow tracheid, the thickening of which is reticulate and often of very intricate pattern (fig. 22).

11. Mucilage ducts and cells

External to the bundles but parallel to them are numerous mucilage ducts. These arise by the end-to-end union of a longitudinal series of parenchymatous cells, and correspond to the latex vessels of Haberlandt (9). Often several mucilage-bearing cells lie end-to-end, apparently without connection between them; at other times a large central pore penetrates the end walls separating the cells, and in some cases this wall almost completely disappears. A stage in the fusion of two mucilage cells to form a vessel in a young petiole is represented in fig. 19. Isolated cells having contents giving the same staining reactions as those of the mucilage ducts occur throughout the leaf, including the vascular bundles, and especially the phloem, where the cambiform cells may contain mucilage (fig. 18). In the lamina, sieve tubes which themselves contained a similar substance were discovered. The schizogenous passages in the phloem in all regions contain the same substance, and probably have a similar significance to the plant (fig. 20). The mucilage ducts are the *Milchsaft-Gefässe* of Wittmack. According to this author, their contents, in *M. ensete*, are rich in potassium chloride, potassium

oxalate, and tannins. The sheath of the Gros Michel is also rich in tannins.

12. Aerenchyma and air chambers

The lacunae arise by the tearing apart and destruction of the tissues of certain regions in the interior of the sheath; they are rhexigenetic in the sense of De Bary. A cross-section through a young sheath near its base shows regions of comparatively large cells, which have begun to round off, separated by smaller, closely packed cells. The former are in the lacunar region, the latter will become the longitunal septa. A longitudinal section through the lacunar region at a slightly higher level reveals transverse layers of intact cells separated by thicker layers of large, thin-walled cells devoid of much contents. The former give rise to the transverse septa, the latter are being pulled apart by the elongation of the sheath to form the lacunae. The disrupted tissue is evidently resorbed, since the mature lacunae are quite free from cell fragments. The dissepiments are of two kinds. Both contain the characteristic aerenchyma (fig. 6), made up of a reticulum of stellate cells. Morren (14) describes and figures the formation of the stellate cells. The septa of the first type are formed by 1–4 horizontal layers of this stellate aerenchyma alone. Those of the second type are composed of a single or several layers of small parenchyma cells situated between an upper and a lower stratum of the stellate cells, each of which may be one or two cells in thickness. The thick septa are more common in the sheath than in the midrib. Starch grains are numerous in both types of cells, and according to Greve (8) the transverse septa, particularly the central layer of parenchyma of the compound type, are a principal tissue for the storage of starch. The lacunae are usually filled with air, but in wet weather may become partially or almost completely filled with water, a circumstance noticed also by Baccarini (1, fide Greve).

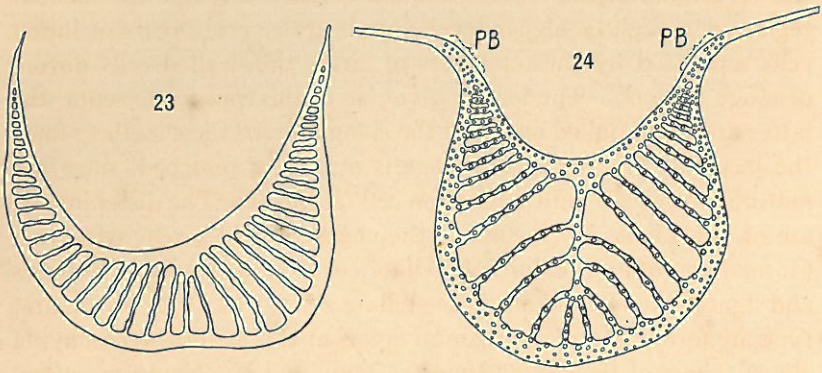
Lying free on the surface of the transverse septa are numerous large raphid cells filled with bundles of acicular crystals of calcium oxalate. These cells are furnished with processes resembling those of the star-shaped aerenchyma, and by these they are attached to the latter. They may attain the very great size of 322 μ in length and 81 μ in diameter. Raphid bundles are numerous in giant cells

imbedded in the tissues of all portions of the leaf, and isolated monoclinic crystals of calcium oxalate are abundant in the parenchyma everywhere.

B. PETIOLE AND MIDRIB

13. Gross structure

The petiole and midrib resemble each other in general structure so strongly that they may be described together, occasional differences being noted where necessary. At the top of the pseudostem each sheath begins to become narrower and thicker. The central



Figs. 23, 24.—Fig. 23, cross-section at about middle of petiole, showing transition from structure of sheath to that of midrib; ×0.5. Fig. 24, cross-section of midrib, near base of lamina of large leaf, position of principal vascular bundles indicated by circles; *PB*, pulvinar band; ×1.

lacunae contract toward the adaxial surface; they are crowded inward by those lateral to them, and these finally meet in the central line, overarching the central lacunae and pushing them away from the adaxial wall (fig. 23, and cf. figs. 17 and 24). This change from the typical structure of the sheath to that of the midrib occurs gradually in the proximal portion of the petiole, and the typical cross-section of the midrib is presented by its distal portion. This structure will be sufficiently clear from fig. 24. It is only necessary to add that the midrib, which near its base is very massive in large leaves, 4.5 cm. from side to side and 2.7 cm. from top to bottom along the median line, tapers gradually toward the apex, the lacunae becoming fewer and smaller. It does not, as in many monocotyledons

(for example, the related *Strelitzia reginae*), blend into the blade before the apex of the leaf is reached, but is distinct throughout the length of the latter (fig. 12).

14. Peripheral tissues

As in the sheath, the peripheral tissues on the two sides of the petiole and midrib differ markedly. Considering first the lower surface, the epidermal cells are of the same general type as those of the sheath, but shorter. A thick external wall of cellulose is covered

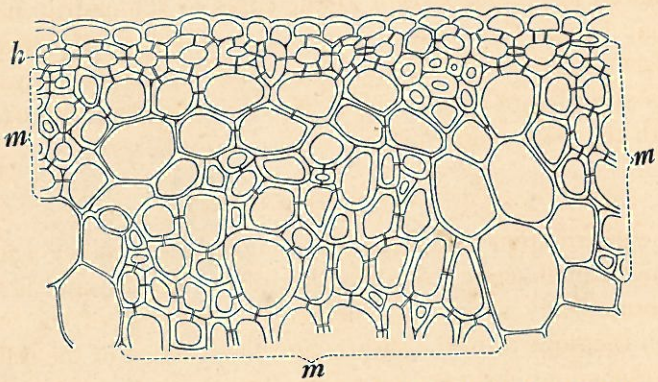


Fig. 25.—Peripheral region of lower side of midrib; *H*, lignified hypodermal layer; *M*, fibrous strands; ×350.

by a thin cuticle, which bears a very heavy waxy "bloom," similar to that of the lamina mentioned later. The hypodermal layer is made up of cells rectangular in surface view, their long axes coinciding with the length of the midrib. These cells are very thick-walled and lignified, and their walls are penetrated by prominent radial pits. Beneath this is a second layer of cells with walls slightly thinner, but also lignified and pitted. Within these are 2–3 layers with walls slightly thickened, and suberized rather than lignified (fig. 25). The lignification of the walls of the hypodermal cells becomes incomplete, and that of the second layer disappears near the distal extremity of the midrib. The continuity of all strata interior to the hypodermal layer is broken by numerous strands of lignified prosenchyma. These fibrous bundles are very abundant in this region, the outermost abutting on the hypodermal layer itself. They are of all

sizes, ranging from 5–6 to several dozens of cells in cross-section, and they lie so close together that usually not more than three cells of the ground tissue intervene between two adjacent strands (fig. 25).

The upper surface bears an epidermis covered with a moderately thick cuticle, reaching 2 μ in thickness. Beneath this are 2–3 layers of large colorless cells, elongated from side to side of the midrib, forming a hypodermal water tissue. Their general appearance in surface view resembles that of the corresponding cells of the lamina, reproduced in fig. 32. Except at the edges of the midrib, near the pulvinar bands, the walls of these cells are slightly thickened and suberized, but not lignified as in the case of the lower surface. The fibrous strands are not nearly so numerous beneath the upper as beneath the lower epidermis.

15. Internal anatomy

The distribution of the vascular bundles between the walls and the longitudinal septa resembles that of the sheath, and is shown diagrammatically in fig. 24. The general character of the bundles is much the same as in the sheath, and the reaction of the cell walls of corresponding elements is similar. The larger bundles show the same succession of occluded protoxylem elements, but the process of occlusion was not studied here. As hinted previously, the fibrous strands in both outer and inner walls, as well as in the septa, are more numerous than in the sheath. These strands are usually but not always lignified, but if not lignified at least they are suberized. The commissural bundles are of the same type as in the sheath, but more often pass directly across the transverse septum from side to side of the lacuna, instead of hugging the longitudinal walls. When the petiole and lower portion of the midrib are split in half longitudinally, and one side only placed in a solution of eosin, the solution readily crosses over in the commissural tracheids, and moves downward into the midrib and blade of the other half below the upper end of the cut (50 cm. below in one experiment which lasted 3 hr. 20 min.). The transverse septa are of the same type as in the sheath, but the thinner kind, composed of aerenchyma alone, without the small-celled central parenchyma, are relatively more numerous here.

It may be profitable to consider for a moment the mechanical features of the midrib and petiole, which must support in an almost horizontal position an enormous expanse of lamina. The lower surface, the term extended to include all of that portion beneath the pulvinar bands, is surrounded by a woody shell at least two cell layers thick, strengthened on the inner side by numerous longitudinal ribs, the fibrous strands. This woody shell with its supports, because of the curvature of its walls, is well qualified to resist buckling under the compressional stresses to which it is subjected. The prosenchymatous strands, both surrounding the vascular tissue and distinct from it, concentrated in the upper wings of the midrib and petiole, are adapted to support the tension to which their location exposes them, and are more efficacious here than an equal number would be if collected in the central portion of the upper wall, since in their actual position they are farther removed from the lower side.

16. Pulvinar bands

The diurnal movements of the lamina were described by Johow (10) and later by Trelease (20). In the early morning, or during a wet day, the two halves of the lamina stand out almost in a horizontal plane on either side of the midrib (fig. 27). During a bright day the lamina halves bend downward, bringing their lower surfaces together beneath the midrib (fig. 26). Where the lamina has been torn into strips, the individual segments move together synchronously, almost as though the lamina were intact. This movement occurs rapidly during the morning of a dry day, and undoubtedly is very effective in decreasing transpiration, since most of the stomata are on the lower surface, and the profile position assumed greatly diminishes the amount of radiant energy absorbed. The change in the appearance of the plant is very striking. The movement is not a passive drooping brought about by the wilting of the leaves, but is produced by the activity of the pulvinar bands, which bend downward along the sides of the midrib in response to changes in the turgor of their tissues.

The pulvinar bands lie along the edges of the midrib, flanking it for its entire length, and merge on the external side into the blade (fig. 24 *PB*). They differ from the tissues on either side of them in

that they contain no lacunae. Their thickness is between 1.2 and 1.8 mm. The ground tissue is of rounded parenchyma cells, resembling the motor tissue of the pulvini of dicotyledonous leaves. Beneath the epidermis is a water tissue composed of 4–6 layers of clear

FIG. 26.—Banana plant photographed at noon on a bright day; "false pinnae" hanging downward in profile position.

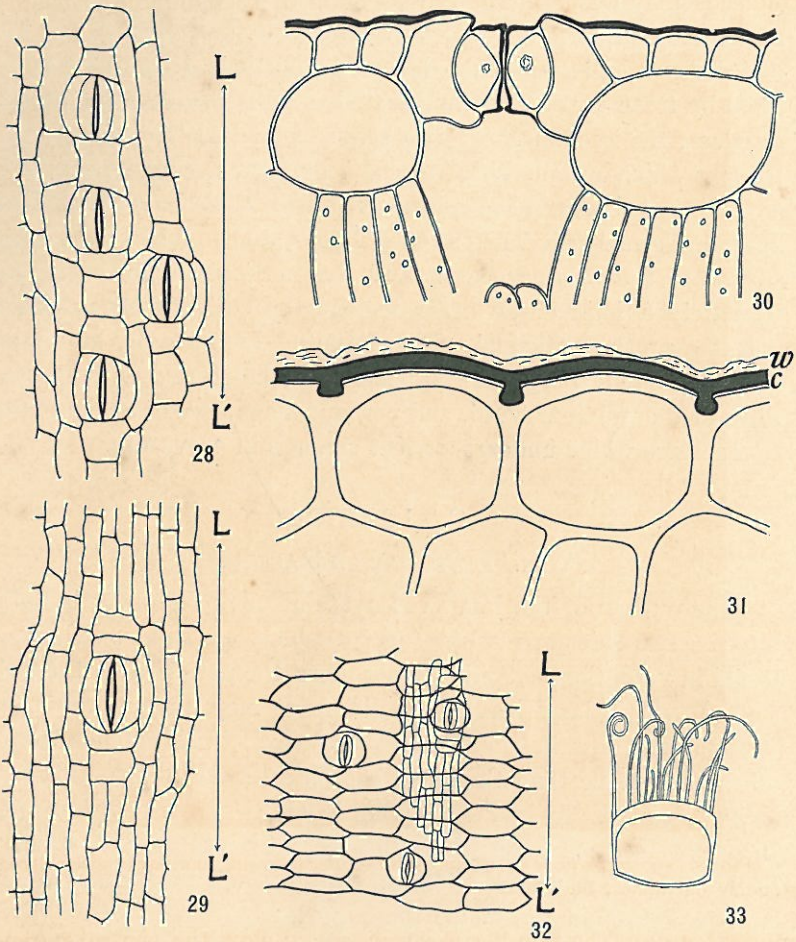
cells. Next below this is a chlorophyllous layer of close set, rounded (not palisade) cells. This borders below a region of thin-walled, rounded parenchyma cells, containing little chlorophyll, which occupies the central portion of the organ. In this tissue are situated the vascular bundles, which here are surrounded by a very thick mechanical sheath, probably an adaptation to prevent injury to the

vascular elements by the bending of the pulvinus. The small metaxylem elements (commissural connectives) are much more numerous in this region than elsewhere in the leaf, and several of the large tracheids may occur in the cross-section of each bundle. Anasto-

FIG. 27.—Same plant as fig. 26, just after sunrise following morning; "false pinnae" standing out almost horizontally.

moses between the bundles are frequent. Below the central parenchyma are 2–3 layers of large, upright prismatic cells, in which run a few fibrous strands. Abutting on the lower epidermis is another water tissue of 2–3 layers of clear cells, slightly thick-walled, elongated in a direction parallel to the midrib. The exact mechanism of the movements of the organ and the functions of the various tissues have not been determined.

A peculiarity of the cuticle over the upper epidermis deserves mention. Like that over the rest of the upper surface of the lamina, this cuticle is rather thick. Distinct knobs project from its inner



FIGS. 28–33.—Fig. 28, lower epidermis of lamina in surface view (line *LL'* drawn parallel to veins); ×315. Fig. 29, upper epidermis; ×315. Fig. 30, transverse section through stoma and accessory cells of upper epidermis, cuticle indicated by heavy black line; ×570. Fig. 31, upper epidermis from pulvinar band of mature leaf; *C*, cuticle; *W*, waxy layer; from a section stained with Grübler's cyanin and aqueous safranin; ×1100. Fig. 32, upper hypodermal layer, as seen from inner surface, showing also some of cells of upper epidermis; ×135. Fig. 33, rods of wax forming the bloom, from lower epidermis of leaf just expanded; ×about 800.

surface where it overlies the anticlinal walls of the epidermal cells, and penetrate the latter, the cellulose wall, which is here rather thick, being hollowed out to receive them (fig. 31). Often the knob is distinctly constricted at the neck, and the epidermal wall narrows around the constriction. The cuticle is thus anchored to the epidermis by a ball-and-socket device. In portions of the cuticle isolated by treatment with concentrated sulphuric acid to destroy the cellulose, the knobs appear as a series of distinct, equidistant projections which outline the epidermal cells. Often there appears to be a narrow gap between the epidermis and the cuticle over the middle of an epidermal cell. The cuticular knobs are confined to the upper surface of the pulvinar bands and the portion of the midrib immediately adjoining. In other regions the cuticle comes down in points over the anticlinal walls of the epidermal cells, but is not knobbed. The arrangement appears to be associated with the motility of the pulvinar band, and perhaps aids in securing the cuticle to a surface which undergoes great changes in curvature.

C. LAMINA

17. External characters

The outline of the lamina is ovate-oblong. The apex is blunt, but the two sides are unlike (fig. 12). The left half, which is external in vernation, extends farther down the petiole than the right (fig. 9), and in large leaves this difference may amount to 12 cm. Wittmack states that in *M. ensete* the covered half extends farther down the petiole than the one which is external in vernation, and is likewise markedly broader (external half 41 cm., internal 50 cm.). In many species of the Marantaceae, Musaceae, and Araceae, it seems to be a general rule that the half of the lamina which is covered in vernation is broader than the exterior half, often (as in *Calathea* spp., *Musa cavendishii*, etc.) pronouncedly so. The general rule holds in the case of the Gros Michel, but the difference between the halves is not so great. In the few leaves of greenhouse plants available, the right side was 2–10 per cent broader than the left.[8]

[8] The writer is indebted to P. R. White for measurements of leaves growing at the New York Botanic Gardens. He neglected to observe this point during his sojourn in Jamaica.

The thickness of the blade increases gradually from margin to midrib. The difference is quite considerable, and a large leaf may be 3.5 times as thick next to the midrib as at the margin. Both the

TABLE II

INTERNAL TOPOGRAPHY OF A LAMINA 340 CM. LONG

Position		Measurements			
Distance above base (cm.)	Distance from pulvinar band (cm.)	Thickness of lamina (μ)	Depth, upper epidermis + water tissue (μ)	Depth of palisade tissue (μ)	Depth of lacunae (μ)
10	0	718	68–91	76–95	.....
	0.6	568	76	91	317
	1.2	518	65	95	267
	2.5	484	61	99	251
	5.0	434	61	95	217
	10.0	351	57	87	134
	16.0(M)*	267	57	76	57
120	0.0	935	76	122	601
	1.9	752	57–76	118	484
	3.8	685	53	118	418
	7.5	618	49	114	351
	15.0	501	53	110	267
	30.0	367	38–53	95	156
	44.0(M)	267	42	84	57
220	0.0	768	65	122	484
	1.6	618	49	122	367
	3.3	585	53	114	317
	6.5	534	49	110	284
	13.0	451	46	106	234
	26.0	334	27–46	95	134
	39.0(M)	251	38–57	84	57
330	0.0	534	57	106	251
	0.6	468	57	95	217
	1.2	434	57	95	200
	2.3	401	53	95	184
	4.5	384	30–53	95	167
	9.0	317	30–53	91	134
	14.0(M)	301	53	80	80

* M = margin.

absolute and proportional increase in thickness are greater in the middle region of the leaf than at the base or apex. The rate of increase in thickness is not uniform from margin to midrib, but becomes greater as the midrib is approached (table II). As is apparent from the table, the increase in thickness is accounted for largely

by the increase in depth of the lacunar region, the palisade and dermal regions changing relatively little.

From the strong midrib the pinnately arranged veins follow an S-shaped course to the margin. All of the veins of the same region of the leaf are very nearly parallel. The branching of the bundles and the outward curvature of the S occur principally in the pulvinar band, and the forward curvature does not assume prominence until the vein has approached to within 5 mm. of the margin, so that across the breadth of the blade the veins follow a course which is practically straight, except at the extreme base and apex of the lamina. At their distal extremities the veins bend forward and unite in the marginal bundle, which practically surrounds the lamina. The apparent parallelism of the veins is not exact. At the base of the lamina they are directed backward as they leave the pulvinar band, forming an angle of 100°–120° with the midrib. At the apex their course is forward, the angle becoming 55°–77°, while the middle veins are nearly perpendicular to the midrib. As the result of this, all of the veins diverge slightly, and any strip across the blade, such as that torn by the wind, is wider at the margin than at the midrib.

Two orders of veins are apparent upon the most superficial examination. The strong or principal veins lie at the apex of an upward curvature of the lamina, and accordingly are situated above its general surface. This fold gives the lamina a ribbed appearance (fig. 12), which is in nowise caused by the vein itself, for this is not appreciably thicker than the immediately adjoining portions of the blade. The weak or subordinate veins lie flat in the plane of the blade. The anatomical differences accompanying these superficial distinctions are discussed later. Both the strong and weak veins exhibit great differences in development, and there are gradations between the two. Alternating with the strongest veins there is usually a somewhat weaker vein of the same character, easily distinguished from the subordinate veins lying between them. WITTMACK distinguishes six orders of veins in *M. ensete*, and presents a diagram showing their derivation from a single bundle. Since the number of subordinate veins between each pair of principal veins is not constant, it is probable that in the Gros Michel there is no very definite scheme of ordination.

Practically all of the veins which extend into the blade from the midrib continue until they reach the marginal bundle, or stop within 1.5 cm. of the margin. However, new subordinate veins may arise blindly between any pre-existing pair of them in any region of the blade, and they have been observed to begin less than 1 cm. from the margin. The intercalated veins do not arise by the branching of the original veins; their connection with the vascular bundles of the midrib is by means of the commissural bundles linking them with adjacent veins. The length of the intercalated veins may be less than 1 cm., in which case the vein ends blindly as it began, but the majority run out into the marginal bundle. As a result of this intercalation of veins, there are more subordinate veins between each pair of principal ones at a few centimeters in from the margin than near the midrib. The increase in the number of veins by intercalation is greatest at the base of the lamina, where the average increment in the two leaves for which counts were made was 36 per cent. At the middle of the leaf the increment was 20 per cent and at the apex 9 per cent. Because of the intercalation of veins, all regions of the lamina are equally well supplied with vascular bundles. The average distance between subordinate veins is practically the same at the margin as at the midrib, the variation in average separation amounting at most to 0.03 mm. The interval between veins is very nearly the same in all regions of the lamina, the averages lying between 0.19 and 0.26 mm. The average distance between the strongest principal veins is about 1.3 cm., but great variation is found here. Usually between 35 and 60 subordinate veins, as well as the weaker principal vein, occur between each pair of the strongest veins, the count being made at the midrib. The number may rise to 100, however, in large leaves. Taking 0.24 mm. as the average interval between veins, a lamina 394 cm. long would have about 17,000 veins on each side near the midrib, and correspondingly more near the margin.

One other feature in the external topography of the lamina seems worthy of notice. On many leaves one can distinguish longitudinal streaks running along the lamina parallel to the midrib, often giving a faint suggestion of ribs (faintly visible in figs. 12 and 13). The ribbed appearance is due to nothing more than kinks in the blade slight furrows being impressed upon the upper surface, with

corresponding low narrow ridges upon the lower, although occasionally the direction of the curvature is reversed. The furrows are conspicuous chiefly in consequence of their great length, stretching from end to end of the lamina. These furrows are associated with no structural differentiation of the blade, but result from unequally distributed pressure upon the young leaf still rolled within the pseudostem, causing folds which are not entirely lost by the lamina in expanding. The number and distribution of the furrows on the two sides of the lamina lend weight to this view. Generally there are 14–20 on the right half at its widest part, and 4–5 on the left, although it is difficult to give figures, because some furrows are so indistinct that one is at a loss to decide whether they should be considered as such or not, and there is great variation between individual leaves. The spacing also differs on the two halves. On the right half the furrows are very close together near the margin, and the interval between successive furrows increases as the midrib is approached. On the left half the 4–5 furrows are almost equidistant. These two circumstances agree with the number and diameter of the coils in vernation (see Section 7). The most distinct furrows are near the right margin of the leaf, corresponding to the narrower coils in this region.

In vernation the coiled lamina usually does not show two perfect helices in cross-section, but, especially in the later stages, the inner helix is generally flattened in the plane of the expanded lamina (fig. 8). In some cases the coils may be flattened like cloth rolled around a board, and even folded back upon themselves in the form of a V. This departure from the ideal form in vernation is responsible for the permanent disfigurement of the tissues of the right half of the lamina. The furrows on the left half probably result from pressure exerted on the blade where it crosses the keel of the midrib in vernation, this being rather sharp at certain stages.

18. Dermal system of lamina; number of stomata

Both the upper and lower epidermis are composed of straight-walled cells, almost rectangular in surface view, elongated in a direction parallel to the veins (figs. 28, 29). The upper epidermis is covered by a rather thick (1–2 μ) cuticle, while that over the lower

is considerably thinner (0.5 μ or less). The lower surface of the lamina is covered by a thick "bloom" which gives it a glaucous color. In leaves just expanded it may be seen that the "bloom" is formed by innumerable close-set rods of wax, which are very slender and often curl up at the free ends (fig. 33). The rods soon crumple and slump together, and in old leaves they are represented only by irregular waxy masses. The "bloom" on the young leaves is so thick that it can be rubbed off on the fingers in large quantities as a white powder.

The stomata are all oriented with their long axes parallel to the veins and to the length of the epidermal cells. On the lower surface, where they are most numerous, they lie over the lacunae in narrow bands stretching across the blade from midrib to margin, while the adjacent strips of epidermis over the veins are almost devoid of them. The stomata of the upper epidermis are somewhat larger than those of the lower, the guard cells of the former measuring about 32 μ in length, those of the latter 28 μ, and other dimensions are in proportion (cf. figs. 28 and 29). The ventral ridges are not very pronounced, and the front and back cavities of the pore are small or indistinct. The cutinization of the guard cells is indicated in fig. 30. The passage between the guard cells is lined with a cuticle which extends over the inner periclinal walls, and over the outer walls is continuous with the general cuticle of the epidermis. The guard cells are bordered by accessory cells (figs. 28, 29, 30), and the short broad cells at either end of the stomatal group have a characteristic shape. The thick outer walls of the accessory cells are constricted to a more or less pronounced hinge where they join the guard cells. The statement of SCHUMANN (20) that the rods of wax which make the "bloom" on the lower epidermis bend over the stomata to form *einem oben offenen Dom* seems to the writer to convey an exaggerated idea of the definiteness of the structure in question and the part played by it in reducing transpiration. Individual rods arising from neighboring cells do bend over into the free space above the guard cells, but, in the Gros Michel at least, are arranged to form no definite structure.

The average of 35 separate determinations of the number of stomata per sq. mm. of the lower surface of the lamina is 168.5.

The variability in different leaves, and different regions of the same lamina, is so great that the figure just given has little significance. Individual counts (of an area of about 0.7 $\overline{mm.}^2$) varied from a maximum rate of 261 per $\overline{mm.}^2$ to a minimum of 96 per $\overline{mm.}^2$ Certain definite tendencies of distribution were manifest in all of the

TABLE III

DENSITY OF STOMATA ON LAMINA

Region	Number of stomata per sq. mm.					
	Lower surface*			Upper surface†		
	Midrib	Middle	Margin	Midrib	Middle	Margin
Base	134	169	143	36	31	26
	Mean for base = 149			Mean for base = 31		
One-fourth up	223	229	128	69	55	34
	Mean = 193			Mean = 53		
Half-way up	184	214	114	87	62	39
	Mean = 181			Mean = 63		
Three-quarters up	232	242	224	78	66	44
	Mean = 233			Mean = 63		
Apex	259	261	182	50	54	56
	Mean = 234			Mean = 41		
Mean	206	223	158	64	54	40

* Lamina 391 cm. long, 104 cm. in greatest width. Stomata in an area of epidermis 0.686 $\overline{mm.}^2$ counted in each case.

† Lamina 353 cm. long, 97 cm. in greatest width. Stomata in an area of 1.372 $\overline{mm.}^2$ counted in each case.

leaves of which a series of counts was made. Thus the basal quarter of the lamina has fewer stomata per unit area than those portions distal to it (table IV).

TABLE IV

Average no. of stomata at base of lamina . . . . . 124.1 per $\overline{mm.}^2$ (maximum 169, minimum 96)

Average no. of stomata in central half of lamina . . . . . 174.8 per $\overline{mm.}^2$ (maximum 240, minimum 97)

Average no. of stomata at apex of lamina . . . . . 170.6 per $\overline{mm.}^2$ (maximum 261, minimum 117)

Ratio, central half 1.41 : apex 1.37 : base 1.00

In every leaf the average density in the central and apical portions was greater than the maximum density found at the base of the same leaf. Likewise there are more stomata in the region of each blade near the midrib than in that near the margin, except at the base of the lamina, where the order seems reversed (table V).

TABLE V

Average no. of stomata near
midrib . . . . . 185.2 per $\overline{mm}.^2$ (maximum 259, minimum 145)
Average no. of stomata near
margin . . . . . 148.9 per $\overline{mm}.^2$ (maximum 224, minimum 97)
(Counts at base of lamina not included in average)
Ratio, midrib 1.24:margin 1.00

The maxima and minima overlap because some leaves have everywhere more stomata than others. When the counts at the margin and the midrib of a given level of the same lamina are compared, the midrib exceeds the margin in every case except at the base. There are some indications that the density of stomata midway between midrib and margin is greater than in either the interior or marginal region of the blade (table III). The individual counts of a representative leaf are recorded in this table.

On the upper surface the average based upon 28 counts is 40.1 stomata per sq. mm. The maximum density found was 89 per $\overline{mm}.^2$, the minimum 3 per $\overline{mm}.^2$ Here again the basal portion fell behind the more apical regions in number of stomata. The ratios of frequency were central half 1.83:apex 1.75:base 1.00. The stomata are again more numerous in the central than in the marginal region of the lamina, and the difference is even more pronounced than in the lower surface, the ratio being midrib 1.51:margin 1.00. Finally, it may be recorded that large leaves near the crown of the plant seem to have more stomata per unit of area (both surfaces) than smaller leaves from lower down.

A larger number of determinations might have been made, but since the tendencies of distribution just recorded repeated themselves on every leaf with much constancy, these conclusions are stated with a fair degree of confidence, although the figures given are of value only as examples of what differences are to be expected. There would be little point in presenting those obtained in greater detail. Per-

haps their principal worth is to serve as a caution to those who might attempt to employ large leaves, such as that of the banana, in experiments in which the rate of transpiration or assimilation is to be correlated with the number and condition of the stomata. WITTMACK's figures on the number of stomata of the leaf of *Musa ensete*, 260 per $\overline{mm.}^2$ on the lower surface, 7 per $\overline{mm.}^2$ on the upper surface, are given here for comparison with those of the Gros Michel.

Beneath both the upper and lower epidermis there occurs a water tissue of thin-walled cells with clear contents (figs. 30, 35, 36, etc.). The cells in this tissue lie with their long axes parallel to the midrib and transverse to the veins; they are crossed with the epidermal cells (fig. 32). The thickness of the water tissue varies according to the region of the lamina. The upper water tissue is usually two layers thick just within the marginal bundle, somewhat farther in it is often single-layered, but usually double, near the midrib it becomes triple, and still closer it is often quadruple. The transition from the double to the triple condition is illustrated in fig. 36. The tissue is usually thicker where it overlies a vein than in immediately adjacent regions. The lower water tissue is often double near the margin, and double or triple near the midrib; over most of the lamina it is single or sparingly double.

Where one of the stronger of the longitudinal ribs just described crosses one of the principal veins, a node or swelling, paler in color than the rest of the lamina, may often be seen upon the upper surface of the leaf. Since a node at these places is not of constant occurrence, and they are absent from many ribbed leaves, the swelling is obviously not the cause of the rib, but rather a result of its presence. It is caused by a hypertrophy of the cells of the water tissue at the points in question, which elongate enormously in a direction normal to the surface of the lamina. Where the water tissue is two-layered only the cells of the inner layer elongate, and where it is three-layered only the inner two, the outermost layer remaining normal and being pushed passively upward. Not only the cells above the principal vein, but those on either side, often passing over several subordinate veins, exhibit the hypertrophy (fig. 34). Cells of this character may reach 317 μ in depth, about thirteen times the normal dimension, and a three-layered water tissue, of which the two inner

layers have hypertrophied, may become 568 μ thick. The hypertrophy at the intersection of vein and rib occurs only in the case of furrows upon the upper surface; where the upper surface is ridged, the swelling is manifest along that portion of the vein between the ridges. Hypertrophy of the water tissue over a principal vein may occur close to the midrib at points where it is not associated with a longitudinal furrow.

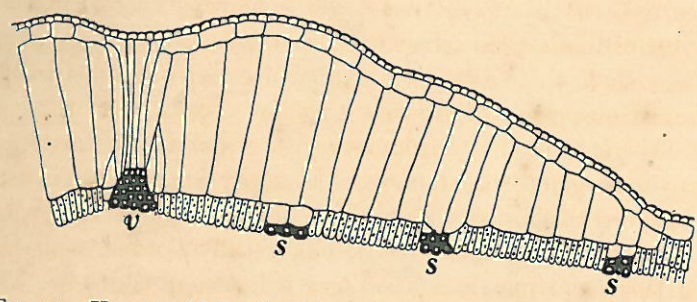
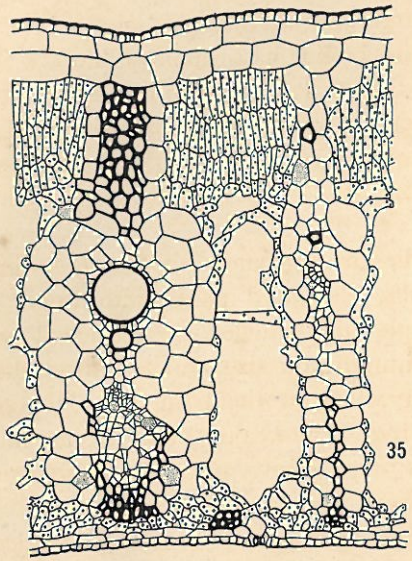


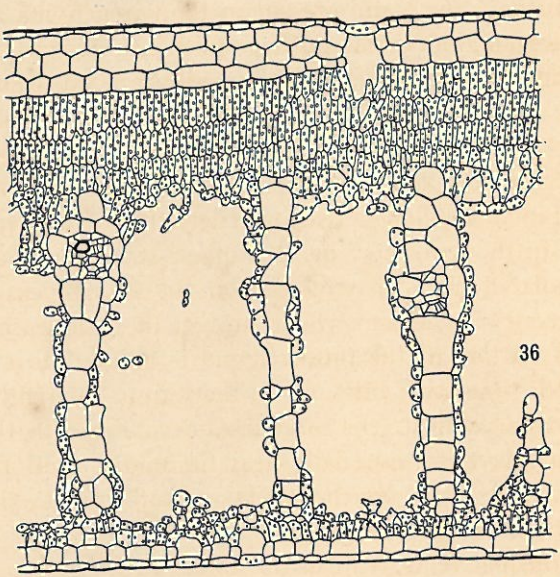
FIG. 34.—Hypertrophied cells of hypodermal layer at intersection of principal vein (*V*) with longitudinal furrow; *S*, subordinate vein; ×60.

18. INTERNAL TISSUES OF LAMINA

The interior of the lamina is divided by the veins into a series of canals which stretch from midrib to margin (fig. 35). Each canal is cut up by transverse septa into chambers or lacunae (fig. 36). The average length of the lacunae (the dimension parallel to the veins) increases markedly from margin to midrib. The average distance between transverse septa at the base of the lamina was 95 μ at the margin, 182 μ midway between margin and midrib, and 230 μ near the midrib. In the middle of the lamina the corresponding figures were 68–122–204 μ; near the apex 75–119–127 μ. On the contrary, the average width of the lacunae is greatest near the margin, where the veins are thinnest, and diminishes toward the midrib; it ranges between 170 μ and 73 μ. (For the depth see table II.)

Between the veins and above the lacunae lies the palisade tissue (figs. 35, 36), composed of three layers of distinct palisade cells, with frequent suggestions of a fourth. The palisade tissue is not interrupted by the transverse septa, and forms a continuous narrow band from midrib to margin. It is somewhat deeper near the





FIGS. 35, 36.—Fig. 35, section of lamina transverse to veins, at about midway between margin and midrib; both veins of "subordinate" type; ×135. Fig. 36, section parallel to veins, septa to right and left being supplied with vascular bundles, while central septum is devoid of them; ×135.

midrib than at the margin, but its thickness does not increase nearly so rapidly as that of the lamina as a whole (table II). The lacunae are lined with spongy parenchyma, which occurs beneath the palisade and above the ventral water tissue, and borders the veins and transverse septa. Frequent elongated chlorophyllous cells, somewhat resembling the algiform cells of moss capsules, stretch across the lacunae.

The vascular bundles are surrounded by one to several layers of clear parenchyma cells, elongated parallel to them. The larger bundles contain a single large tracheid strengthened by twelve or less spiral bands, according to the size, and several smaller tracheids (commissural connectives) below them (fig. 35). The spiral bands of the xylem are suberized. The weakest bundles contain only a few very narrow tracheids; more rarely, near the margin, no xylem at all. The phloem is always present and more fully developed. The latter contains the same schizogenous mucilage cavities described for the sheath, and sieve tubes with the same dark-staining contents occur. Mucilage ducts are present in the parenchyma surrounding the bundles, and individual mucilage-filled cells occur in the phloem.

Accompanying all but the weakest veins are two strands of prosenchyma, one above and the other beneath the vascular bundle. The fibers in the lower strand are lignified, but those of the upper are suberized. The lower strand is accordingly more durable, and in portions of a leaf along a tear it persists after the upper strand has decayed. In the weakest veins, the upper strand is reduced to one or two isolated fibers in cross-section. In strong veins the lower strand extends out as arms which protect the phloem, but in weak veins this portion of the prosenchyma is reduced to a horizontal plate of cells one layer thick (as in the vein to the right in fig. 35). Strands of mechanical cells sometimes occur beneath the lacunae, apart from the veins, especially near the midrib, and at times are associated with a wall which projects upward into the lacuna, but does not reach the palisade tissue.

The principal veins, lying at the apices of the transverse folds of the lamina, are distinguished from the subordinate ones by a much greater development of the two mechanical strands accompanying them, and by the series of protoxylem elements which are dis-

rupted and occluded by neighboring parenchyma cells. The subordinate veins do not contain protoxylem. The stronger of the subordinate veins contain as much metaxylem and phloem as the principal veins in the same part of the leaf.

Except where a commissural bundle is present, the transverse septa are a single layer of cells in thickness, with a broken layer of spongy mesophyll on either side. The central cells have clear contents, and in surface view are very irregular in shape. The irregular projections and re-entrant angles interlock and a close tissue is formed. The mesophyll cells are elongated parallel to the wall, much branched, and very complex in outline. One, two, or three together of the central cells (in septa where there are no commissures) may become thick-walled mechanical cells. These cells are often very broad and long, stretching most of the way across the septum, and have the same irregular outline as the other cells of the central layer. The walls are penetrated by prominent pits. These mechanical elements are not numerous, but are most frequent near the margin of the lamina.

The commissural bundles which connect the veins run through the transverse septa. They consist of a single tracheid (in cross-section) and a small amount of phloem, but no mechanical elements, and resemble the commissures in the sheath and midrib (fig. 36). Their course is usually not horizontal, because the bundles of the veins which they join are not always at the same level. By no means every septum contains a vascular bundle, and as many as fourteen septa devoid of a bundle may intervene between two having them, although often only a single one intervenes. If the veins supplying a certain portion of the lamina are severed near the midrib, so that its supply of water must travel longitudinally through the commissural tracheids, and the petiole is then placed in solution of eosin, the commissural bundles are stained and stand out clearly when held up to the light. They appear as thin, tortuous red lines with frequent anastomoses, the general direction of which is parallel to the midrib. They are not distributed at random among the septa, but arranged as though with some regard to their continuity as water courses transverse to the veins. The commissures are often continuous across one or more veins; however, usually the septa equipped with com-

missures are not in line on the two sides of the vein, but one is displaced slightly in or out with reference to the other, so that the sap must move along the vein for less than the length of one lacuna to pass from one commissure to the other. Thus they do not form an independent system like the veins, and their continuity as a water course is dependent upon the latter. The apparent anastomoses occur where two commissures join a vein almost opposite a single one on the other side. The efficiency of the commissural bundles as water courses was demonstrated in many experiments, a few of which are recorded here.

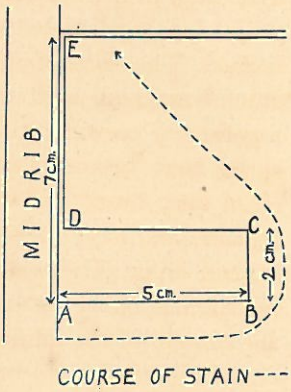


FIG. 37.—Diagram to illustrate Experiment 2.

1. A strip of the lamina extending 35 cm. in the direction parallel to the midrib, and about 15 cm. in the direction of the veins, was cut from a large leaf while the dew was still upon it. The severed ends of the veins were smeared with vaseline. The lower end was cut into fringes to increase the absorbing surface, and the strip (*A*) was hung with this end dipping into a 0.75 per cent solution of eosin. Another strip (*B*) from the same leaf was cut with the length perpendicular to the midrib and parallel to the veins, and hung in the same manner beside the first. The preparations were cut under water. The solution could ascend the strip *B* through the veins, but in *A* it could move upward only through the commissural bundles. The strips were left thus for four hours on a sunny morning (August 27, 1926). At the end of that time the solution had stained *A* 20 cm. above the lower end, while in *B* it had risen 34 cm., to within 1 cm. of the top, and probably would have gone farther had the strip been longer.

2. A lamina was cut as shown in fig. 37. To reach the portion marked *E* it was necessary for the solution to travel 5 cm. outward along the vein from *A* to *B*, then 2 cm. upward through the commissural bundles from *B* to *C*, then inward through the veins and upward through the commissures from *C* to *E;* altogether at least 7 cm. upward through the commissures. The severed petiole was

placed in a 0.75 per cent solution of eosin at 9:00 A.M., and the experiment terminated at 10:00 A.M., August 25. The stain had reached *D*, and the upper margin of the segment 1.5 cm. out from *E*. *A* was about 150 cm. above the cut end of the petiole.

3. The lamina was torn across from margin to midrib, and then severed from the midrib for a distance of 34 cm. upward, so that a loose flap hung downward, attached to the midrib only by the commissural bundles. The cut petiole was placed in a 0.75 per cent solution of eosin. After 2 hours 26 minutes the stain had reached 25 cm. below the last intact vein at the top of the flap, having moved this distance through the commissural tracheids, in addition to 220 cm. upward through petiole and midrib.

20. Margin

The young blade as it emerges from the pseudostem is margined by a delicate wing, white or tinged with red, but containing no chlorophyll, about 2.5 mm. broad. About 170 μ thick where it joins the marginal bundle, the wing narrows to a fine edge, and the outermost portion is scarious and transparent. It is composed entirely of thin-walled parenchyma, with an upper epidermis of small unthickened cells, and on the lower surface are individual cells containing mucilage, similar to those occurring in the epidermis of the precursory appendage. The marginal wing withers almost as soon as the leaf is exposed to the air, and dies off as far as the marginal vascular bundle.

Within the wing there occur a few small tracheids, followed by a very large tracheid about 125 μ in diameter, which occupies most of the cross-section of the lamina at this point, and a few somewhat smaller ones inside it. These elements must be regarded as forming a marginal bundle which is a separate entity, and not merely the longitudinal continuation of the veins, since the latter contain as they approach the margin no tracheids of this size. An almost continuous band, 1–1.5 mm. broad, of much smaller tracheids stretches inward from the large tracheids, and represents the marginal continuation of the veins. Very little phloem is present. The first mechanical tissue strengthening the margin occurs as narrow bands, 1–2 cells deep, of not very thick-walled fibers lying above and below

the bundles interior to the large marginal tracheids. Within this, strands of mechanical cells are present at intervals, and represent the distal extremities of the fibrous strands of the veins.

21. Splitting of lamina

The newly expanded leaf is entire. Older leaves are torn by the wind into narrow strips, parallel to the veins, which are usually distinct from one another as far as the pulvinar bands, and the tear may even proceed longitudinally along the midrib for a short distance (fig. 38). The leaf then appears to be pinnately compound, and the strips into which it is torn may well be called "false pinnae," since their physiological significance is the same as that of pinnae (compare the banana leaf in fig. 38 with the coconut leaves in the upper left corner of that figure).

The line of the tear made by the wind follows no course predetermined by the structure of the lamina, other than that it must run parallel to the veins; there are no anatomical differences which cause it to lie between one pair of veins rather than another. On the other hand, the resistances offered to the initiation or continuation of the tear are almost negligible. The marginal wing is short lived and is supplied with no mechanical elements; the marginal bundle contains a few weak mechanical strands which eventually bend parallel to the veins, and so present but a slight obstacle to the tear; the transverse septa include only isolated, inefficient thick-walled cells, and the commissural bundles are equipped with no mechanical elements to retard or stop its progress. Lippitsch (12) has made an interesting study of the development in several genera of the Scitamineae of those mechanical features which may retard the transverse tearing of the lamina. Many of these are better protected than *Musa sapientum*, and are still incapable of maintaining their integrity in the face of the wind. He believed the splitting to be autogenous, in that "primary tears" at right angles to the margin and penetrating the outer portion of the marginal bundle are initiated by the tension set up by the drying and contraction of the wing. These tears are continued inward as "secondary tears" by the action of external agents, of which the wind is the principal. Considering the ease with which the lamina may be split inward at any point, it

does not seem necessary to postulate any mechanism for the initiation of the tear to account for the laceration of the enormous lamina under the force of the breeze. According to PETERSEN (16) the cleft often begins in the body of the lamina and thence proceeds inward and outward. One certainly sees many incompleted splits

FIG. 38.—Old leaf, much frayed by wind, no longer able to support itself; such effete leaves wither in this position and drape the pseudostem.

of this character, but apparently they also are to be attributed to the shearing force of the wind. KARSTEN (quoted by GOEBEL 7) found that the margin of the lamina of *Heliconia dasyantha* dies before the central protion has ceased to enlarge. The dead margin persisting, tensions arise which result in the splitting of the lamina under the force of impact of rain drops, etc. GOEBEL (7) traces a suggestive

series in the compounding of monocotyledonous leaves. In the banana the false pinnae arise from the action of external forces on the mature leaf. In *Cyclanthus bipartitus* the time of the splitting of the two-lobed leaf is pushed forward, and occurs during its unfolding, resulting from tensions already present. In the palms the compounding of the leaf occurs still earlier, in the bud, where certain strips of tissue die or become slimy, isolating from each other the strips which make the pinnae.

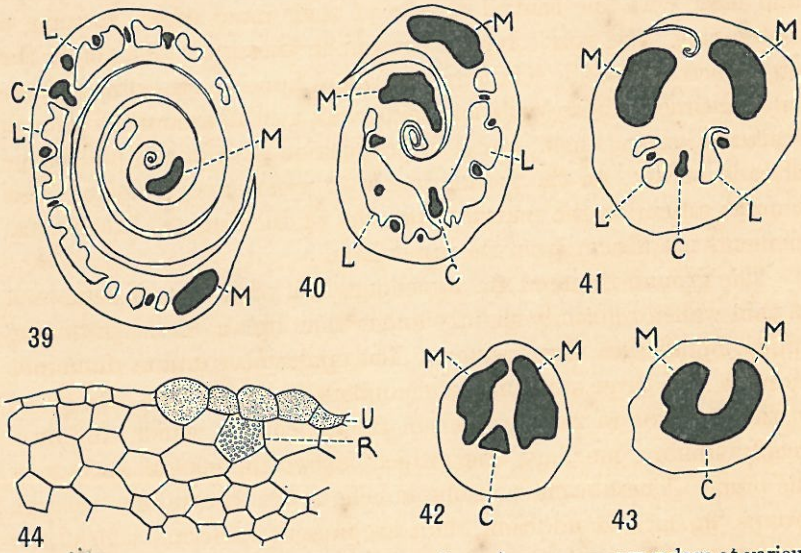
In the Gros Michel the behavior of the tissues adjacent to the tear is similar to that reported for *Musa ensete* by LIPPITSCH. The tissues die off as far as the second or third vein from the line of separation, and the pinna is bordered by a narrow (0.2–0.4 mm.) band of brown dead cells. The parenchyma surrounding this vein, especially on the side toward the wound, the water tissue, and the epidermal cells become thick-walled and suberized, the outer anticlinal walls often becoming considerably thickened. Often, however, the palisade cells between the first and second veins become suberized, at times in 5–6 vertical rows, as well as the water tissue and epidermis in continuity with them. At any rate, a complete wall of suberized tissue, often very irregular, closes off the wound. Fungal infections, however, sometimes spread inward from the tear as large yellowing areas. The wound left by the dying off of the margin is also closed off by suberized cells, so that the false pinna is protected on three sides by suberized membranes. Wound cork is never formed. LIPPITSCH points out that the tissue lost as a result of splitting represents a smaller outlay of material than would be necessary adequately to strengthen the leaf. He believes that this habit therefore conforms to the principle of conservation of material; and the lack of mechanical protection, inviting as it does the splitting, may be regarded as adaptive.

D. PRECURSORY APPENDAGE

22. STRUCTURE AND POSSIBLE FUNCTION

The cylinder formed by the convolute leaf narrows at its apex into the precursory appendage (figs. 9, 11), which in large leaves may reach 15 cm. in length. The coiled halves of the lamina continue upward as part of the appendage, which in its basal portion is

a helix in cross-section (figs. 39, 40). They gradually become narrower, and finally merge into the terete structure which is characteristic of the upper portion of the appendage (fig. 42). The veins at the apex of the lamina bend inward and upward very sharply, changing their course through as much as 135°, and joining the marginal bundle, with which they continue upward into the appendage. Because the appendage is so intimately connected with the blades



FIGS. 39–44.—Figs. 39–43, transverse sections of precursory appendage at various levels; ×12. Fig. 39, at base of appendage; fig. 40, 1 cm. above base; fig. 41, about 2.5 cm. above base; fig. 42, about 6 cm. above base; fig. 43, 7–8 cm. above base; *C*, central vascular bundle; *M*, marginal bundle; *L*, lacuna. Fig. 44, peripheral region of appendage in transverse section; *U*, mucilage cells; *R*, raphid bundle; ×135.

it must be torn off, along with the end of the right half, before the lamina can uncoil.

The appendage is a direct continuation of the midrib, and the bundles and lacunae of the latter extend upward into the base of the former (fig. 39 *C*, *L*). The lacunae contract and finally drop out, and the smaller bundles fuse and disappear. At about one-third the length of the appendage above the base only three bundles remain, the central one representing the continuation of the bundles of the midrib (fig. 42 *C*), and the other two the marginal bundles of the lamina (fig. 42 *M*). Already at the base of the appendage the mar-

ginal bundles were the most prominent, and as they continue upward their cross-sectional area relative to that of the entire appendage increases, until they occupy a large proportion of the cross-section of the organ. Finally the three bundles fuse and become indistinguishable. This was observed to happen in two ways. The marginal bundles may remain distinct from each other and fuse with the central bundle at their inner edges, forming an open ring (fig. 43), or they may first fuse with each other by their outer edges, and later with the central bundle at their inner edges, forming a closed ring. The single bundle present in the upper quarter of the organ becomes solid. The large marginal bundles are composed almost entirely of fairly wide tracheids, with a small amount of phloem scattered among them, and a larger portion of it at the inner edge of each bundle. In the predominance of xylem over phloem, these bundles resemble the marginal bundles of the lamina. Mechanical elements are absent from the appendage.

The ground tissue of the appendage is a parenchyma composed of thin-walled cells only slightly longer than broad. Cells containing raphid bundles are very frequent. The epidermis contains numerous stomata with large substomatal chambers, and large cells, elongated in the direction of the long axis of the appendage, which contain a deeply staining mucilage, and project above the general surface of the organ. These occur as isolated cells or are continuous in large groups (fig. 44). In addition, there are present epidermal cells of the usual type. The appendage never contains chlorophyll, and is white so long as it is still tightly inclosed in the pseudostem. When it emerges from the top of the latter it has already begun to turn brown, as a result of the withering and discoloration of the epidermal cells. Long before the lamina has completely emerged the appendage is black and shriveled, although it usually remains attached until it is torn off by the expansion of the lamina. The end curls up in drying, but the organ never assumes the corkscrew form described for other species.

Whatever may be the physiological function of the appendage, its mechanical significance seems clear.[9] It serves to maintain the

[9] For an interesting view on the morphological nature of the appendage, which space does not allow me to discuss here, see A. Arber, On the leaf tips of certain monocotyledons. Linn. Soc. Jour. Bot. 45: 467–476, and the literature there cited.

young leaf in its coiled condition, and to prevent its fouling against the sheath which surrounds it during its long progress upward through the pseudostem. If the lamina ended abruptly, the folding back of its ends through friction against the sheath and the consequent entanglement of the leaf would be possible. By its tapering form the appendage is well adapted to push its way through the close-packed organs of the pseudostem, and to make a passage for the lamina which follows. This passage may be further aided by the lubricous surface created by the mucilaginous epidermal cells. The conclusion of GOEBEL (6) that the appendage is an *Abschlusskörper* seems a sound one.

The physiological function, if any, of the appendage in the Musaceae is not so clear. RACIBORSKI (17), whose studies were devoted principally to lianas, found that the stomata, vessels, intercellular spaces, and chlorophyll apparatus of the appendage mature earlier than in the body of the leaf, and that it transpires and assimilates before the latter. He observed that the earlier maturation of tissue is also true in the banana, although here photosynthesis is out of the question. Lianas, with their retarded leaf development, present conditions peculiar to themselves, and quite foreign to the banana. GENTER (5) suggested that the appendage is of service in closing off the central cavity of the pseudostem and preventing the access of rainwater and foreign matter to the young leaf. He also observed that if the appendage is freed from the surrounding sheaths and placed in a moist atmosphere, it guttates through the stomata. However, there is no experimental evidence that the organ has any non-mechanical physiological value to the plant.

In conclusion, it may be well to point again to the large number of scars which the leaf of the banana receives during the usual course of its development, both from the dying off of temporary organs and the imperfect adjustment between its parts. The withering of the margin and the precursory appendage, the tearing off of the end of the right side, all leave extensive scars which surround the lamina. These changes would occur in the most sheltered greenhouse as well as in the field, and perhaps it is not stretching the point too far to include the withered margins of the false pinnae in the same category, since the leaf is not adjusted to its habitat until

comes first suberized, then lignified, as the sheath is pushed toward the exterior of the pseudostem.

7. The protoxylem elements of sheath, midrib, and principal veins are disrupted and their lumina occluded by parenchyma cells.

8. The lower surface of midrib and petiole is strengthened by two hypodermal strata of lignified cells.

9. A peculiar mode of anchoring the cuticle over the pulvinar bands is described.

10. Longitudinal furrows in the lamina are caused by pressure in the bud.

11. There is considerable variation in the density of stomata in different portions of the same surface of the lamina.

12. There is a marked increase in the number of veins near the margin over that near the midrib.

13. The efficiency of the commissural bundles in water transport was clearly demonstrated by experiment.

14. The wounds caused by the splitting of the lamina, and the dying off of the margin, are closed by the suberization of pre-existing cells.

15. The marginal bundles of the lamina become the most important vascular supply of the precursory appendage.

ARLINGTON, MARYLAND

[*Accepted for publication May 31, 1927*]

LITERATURE CITED

1. BACCARINI, P., Intorno ad un singulare accumulo d'acqua nel sistema lacunare delle guaine foliari di una *Musa Ensete*. Bull. Soc. Bot. Ital. Firenze 276–279. 1904.
2. BUCHHOLZ, MARIA, Über die Wasserleitungsbahnen in den interkalaren Wachstumszonen monokotyler Sprosse. Flora **14**:119–186. 1921.
3. COOK, O. F., Dimorphic branches in tropical crop plants. U.S. Dept. Agric. Bur. Pl. Ind., Bull. 198. 1–64. 1911.
4. FAWCETT, W., The banana, its cultivation, distribution and commercial uses, 2d ed. pp. xi+299. London: Duckworth and Co. 1921.
5. GENTER, G., Über die Vorläuferspitzen der Monokotylen. Flora **95**:327–383. 1905.

6. GOEBEL, K., Über die Bedeutung der Vorläuferspitze bei einigen Monokotylen. Flora **88**:470–472. 1901.
7. ———, Organographie der Pflanzen. 2d ed. Jena: Gustav Fischer. 1923.
8. GREVE, GERHARD, Beitrage zur physiologischen Anatomie von *Musa ensete*. Dissertation, Kiel. pp. 59. 1909.
9. HABERLANDT, G., Physiological plant anatomy, transl. by MONTAGU DRUMMOND. London: Macmillan and Co. 1914.
10. JOHOW, F., Über die Beziehungen einiger Eigenschaften der Laubblätter zu den Standortsverhältnissen. Jahrb. Wiss. Bot. Pringsheim **15**:282–310. 1884.
11. KÜSTER, ERNST, Über Kieselablagerungen in Pflanzenkörper. Ber. Deutsch. Bot. Gesell. **15**:136–138. 1897.
12. LIPPITSCH, C., Über das Einreissen der Musaceen Blätter und einiger verwandten Pflanzen. Oester. Bot. Zeitschr. **39**:206–210; 259–263. 1889.
13. MAXWELL, W., The rate of growth of banana leaves. Bot. Centralb. **67**:1–5. 1896.
14. MORREN, CHARLES, Bullet. Accad. Bruxelles **6**:178–190. 1839.
15. PAXTON, J., Mag. Bot. **3**:55. 1837.
16. PETERSEN, O. G., Bidrag till Scitameernes Anatomi. Danske Vid. Selsk. Skrift. 6. Raekke Nat. Afd. **7**:337–418. 1893 (with résumé in French).
17. RACIBORSKI, M., Über die Vorläuferspitze. Flora **87**:1–25. 1900.
18. REYNOLDS, P. K., The story of the banana. pp. 53. Boston: United Fruit Co. 1921.
19. ———, The banana, its history, cultivation, and place among staple foods. pp. xvii+181. Boston: Houghton Mifflin Co. 1927.
20. SCHUMANN, K., Musaceae, in Das Pflanzenreich IV. 45. Leipzig. 1900.
21. TRELEASE, SAM, Night and day rates of elongation of banana leaves. Phil. Jour. Sci. **23**:85–96. 1923.
22. WITTMACK, LOUIS, *Musa ensete*, Ein Beitrag zur Kenntniss der Bananen. Linnaea **35**:209–290. 1867.