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ANATOMY AND MORPHOLOGY OF THE VEGETATIVE ORGANS OF SORGHUM VULGARE 1 OF 1

ARTSCHWAGER, E.

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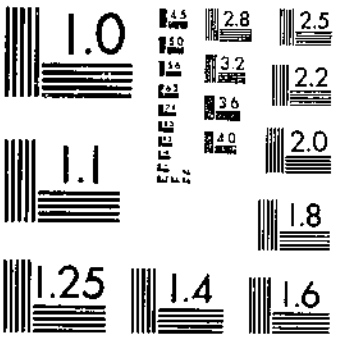

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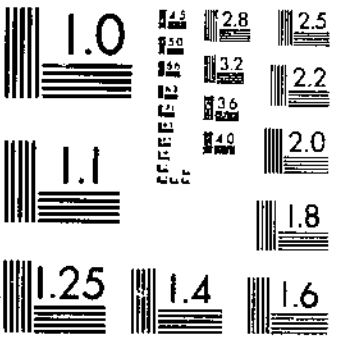

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WASHINGTON, D. C.

Anatomy and Morphology of the Vegetative Organs of Sorghum Vulgare[1]

By Ernst Artschwager, *senior plant anatomist, Division of Sugar Plant Investigations, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration*[2]

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PREVIOUS INVESTIGATIONS

Sorghum (*Sorghum vulgare* Pers.) is a plant of ancient lineage, well established as an economic crop even in the earliest civilizations. The literature dealing with its history, geographic distribution, and botanical description of varieties is extensive. It has recently been reviewed in detail by Vinall, Stephens, and Martin (*14*).[3] Their treatise gives the botanical description of many sorghum varieties and a key for separating them.

In the description of sugarcane varieties, minute morphological and even anatomical characters are used, but in sorghum taxonomy reliance has been placed chiefly on the structure of inflorescence, spikelet, and seed. To be sure, sorghum shows a relative paucity of such characters as form the basis for sugarcane classification, but some of the characters are of great distinctness and of real value in the description of varieties and in the analysis of a hybrid population.

There is no literature dealing specifically with the minute morphology and anatomy of sorghum except for a paper on the developmental anatomy and homologies in the young seedling (*11*), but its structure

[1] Submitted for publication Oct. 11, 1946.
[2] Credit is due Miss Rose Mary Schipman for the preparation of the drawings.
[3] Italic numbers in parentheses refer to Literature Cited, p. 55.

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is indirectly known through papers on the anatomy of corn (*5, 6, 12, 13*) and the morphology and anatomy of sugarcane (*1, 2, 3, 4, 7*). Important differences do exist, however, as shown in table 1, in which some of the morphological and anatomical characters of the two crops are contrasted.

TABLE 1.—*Some contrasting characters in the morphology and anatomy of sorghum and sugarcane*

Character	Sorghum (vulgare)	Sugarcane
Morphological		
Color of internodes	A shade of green	Green, purple, ivory, striped.
Wax band	Part of general bloom; rarely distinct.	Usually in the form of a distinct band.
Bud furrow	Often poorly developed	Usually prominent.
Buds	Often small and undeveloped.	Always well developed.
Hair groups on prophyllum.	Few and similar	Usually numerous and varying.
Rows of root primordia	Usually one row	Almost always several rows.
Hairs on root band	Often present	Almost always wanting.
Hairs on internode	Always wanting	Present in a few varieties.
Persistence of leaves	Stems never self-cleaning	Stems usually self-cleaning.
Hairs on lamina	Never present	Present in many wild canes.
Hairs on midrib	Prominent in many varieties.	Always wanting.
Hairs on sheath	Always wanting	Prominent in many varieties.
Hairs on sheath base	Always present, though short.	Often wanting; when present, usually long.
Cilia on sheath margin	Never present	Often present.
Typical auricles	....do....	Often very prominent.
Ligular pattern	Usually shallow crescent	Crescentiform, arcuate, or deltoid.
Ligular fringe	Sometimes taller than ligule.	Usually much shorter than ligule.
Dorsal hairs on ligule	Dense, free, or only slightly adnate.	Often sparse and partly or completely adnate.
Buttress roots	Often inserted very high (4 feet above).	Never inserted high; usually wanting.
Anatomical		
Bundles of lamina	Inner sclerenchyma sheath wanting.	Inner sclerenchyma sheath well developed.
Stomates of stem	Numerous	Scarce, often wanting.
Silica cells of stem epidermis.	Always present	Often wanting.
Starch in internode	Abundant in many varieties.	Wanting or very sparse.
Silica knobs on root endodermis.	Massive and irregular	Small and uniform.
Sclerotic layer outside root endodermis.	Wanting	Well developed.
Exodermis of root	Outer tangential wall thickened.	Inner tangential wall thickened.

In the present contribution, the morphology and anatomy of the sorghum plant is treated in some detail, since a knowledge of the structure of the mature organs is of value to the geneticist and the pathologist. An account of the ontogeny of the tissues is omitted for the most part, however, because it displays no essential deviation from that of corn and sugarcane.

MATERIALS AND METHODS

The material for study was grown at the experimental farm at State College, N. Mex. The collection included Ethiopian and Indian sorghums, sweet sorgos, and milos; altogether, 152 different varieties.

All characters were studied and illustrations prepared from fresh material. On the whole, the technique employed by the writer in the morphological studies of sugarcane varieties (*3*, *4*) was used successfully in the present investigations. As in sugarcane, some characters show to best advantage in young material, since retrogressive changes or mere injuries associated with aging or due to diseases make evaluation difficult. Most characters are studied more advantageously in older, more mature material, however. Root band pubescence is frequently limited to the basal part of the stalk, whereas typical wax bands may be found only in the upper internodes, since subsequent all-over wax deposits erase the boundary between general bloom and wax band. The stem epidermis is not so easily stripped as in sugarcane, and in certain varieties surface hand sections must be employed even though they are not very satisfactory. The usual technique of fixing and staining was used in the anatomical studies but was often abandoned in favor of hand sections of fresh material. Thin hand sections, especially of hard tissues, are equal to and often superior to microtome preparations. If properly stained, they show better tissue differentiation in photographs than could be obtained otherwise. For that reason, many of the illustrations in this bulletin were prepared by this method.

GROSS MORPHOLOGY

Sorghum, a member of the tribe Andropogoneae, family Gramineae, is a herbaceous annual. The jointed cylindrical stems, or culms, vary in height from 2 to 15 feet. They are solid, but the central part often becomes pithy and fistular. Both suckers and side branches are produced (fig. 1). The branches appear only after the main stem has headed out, and their order of appearance is basipetal, with the upper bud producing the first branch. The side branches are smaller than the main stalk and they mature much later. The number of suckers or tillers depends on climate, spacing, and varietal tendency in the development of crown buds (*14*).

The leaves are two-ranked as in other grasses, alternating on opposite sides, and appearing approximately in a plane. The number of leaves at maturity varies with the variety, from 7 to 28. Each leaf consists of sheath and blade. The blade is linear lanceolate, long and flat. It is separated from the sheath by the specialized regions of the blade joint—dewlaps and ligule. The latter is a membranaceous appendage that closely invests the culm and acts as a

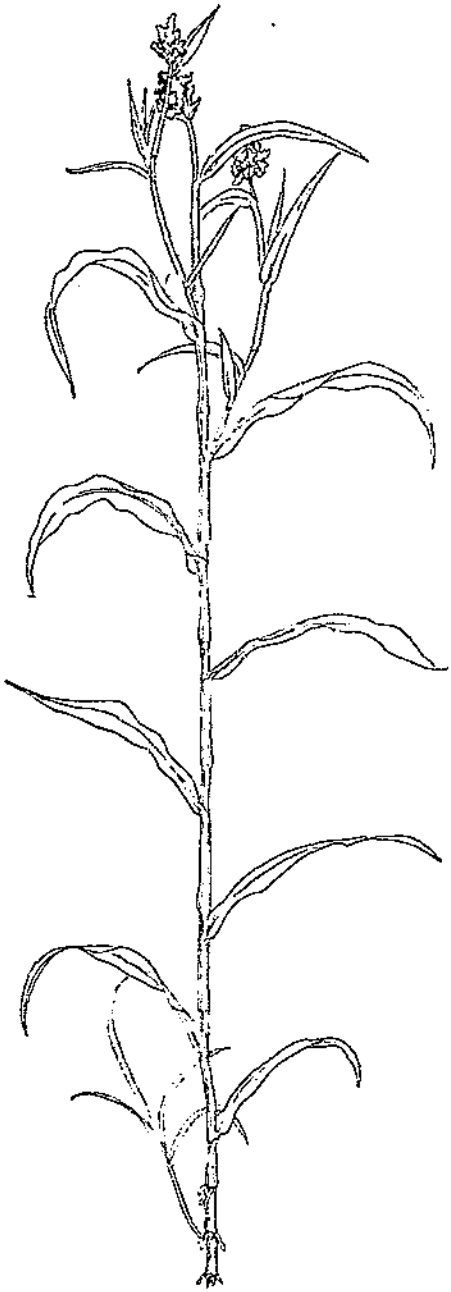

FIGURE 1.—Habit sketch of sparse-leafed sorghum with side branches and small sucker shoot. Internodes longer than subtending sheaths.

rain guard. The sheath surrounds the internode as an open tube with overlapping margins. At the base of the sheath, where the leaf joins the culm, is a distinct swelling, the leaf sheath base or sheath node.

The root system is fibrous, composed of many slender roots of about equal diameter. There is a single seminal root that grows vertically downward, giving off laterals throughout its length. It may function during the entire life of the plant but ceases to be of

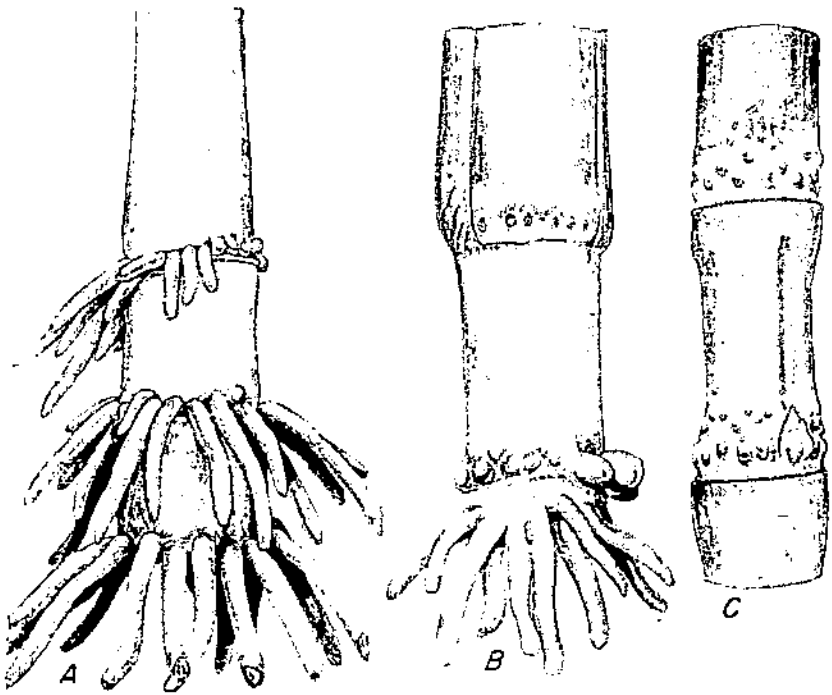

FIGURE 2.—*A*, Root crown of sorghum plant with three whorls of adventitious roots in various stages of development. *B*, Base of young stalk with adventitious roots in early stage of development. Part of sheath in upper internode cut away to expose growth ring and root band with root primordia. *C*, Basal internode with adjacent nodal regions. Root band has two to three rows of root primordia; bud furrow well developed.

importance after the permanent root system begins to function. The permanent roots are adventitious and develop in succession from the basal nodes near ground level (fig. 2, *A* and *B*). The whorls of adventitious roots in their entirety constitute the root crown. All laterals, especially those near the surface of the ground, are much branched, interlacing the soil in all directions. Their color is white or reddish brown, depending on age and stage of development. Many sorghum varieties develop buttress roots (fig. 3) as high as 4 feet above ground. The buttress roots are considerably thicker than the normal roots and usually a deep green. On entering the soil, they behave as ordinary roots and decrease in size to the diameter of the main laterals (fig. 3).

FIGURE 3.—Basal part of culm of an Ethiopian sorghum with prominent buttress roots.

The superficial root system of sorghum, according to Weaver (*15, pp. 192–195*), is extensive. The roots attain a working depth of 3 to 4 feet and a maximum depth of 6 feet. Miller (*8*) states that the roots are more fibrous than those of corn and may form twice as many laterals at any stage of their development, making the sorghum plant markedly drought-resistant.

The inflorescence, or "head," is, with few exceptions (broomcorn), a somewhat compact or open panicle. The head is usually erect (fig. 1),

but in certain groups it is inclined or pendent (fig. 4). The main axis is angular, variously furrowed, and usually hairy at the nodes. The side branches appear to be in whorls, one above the other. Each lateral may branch repeatedly. The final branches bear one or several paired spikelets, which are ellipitcal, of varying length and diameter, and usually compressed dorsiventrally. In the case of paired spikelets, one is sessile and perfect, the other pediceled and staminate. The fertile spikelet has two thick glumes of about equal length, but the outer partially envelops the inner, which is slightly narrower. The glumes enclose two flowers, the lower sterile, the upper perfect. The lower sterile floret has a narrow lemma clefted at the apex from which an awn arises. The palea may be absent; when present it is small and

FIGURE 4.—Habit sketch of sorghum variety with pendent or inverted panicle.

thin. There are two broad, hairy lodicules, three stamens, and two plumose stigmas.

The mature grain is entirely or partly enclosed by the glumes. It is oval, a little longer than broad, smooth, and tipped with the remains of the style. One surface is always more or less flattened and carries the embryo at its base, but in feterita the flattened surface and embryo are on different sides.

MORPHOLOGY OF THE STALK

Internode

The height of the stalk, or culm, is determined by the size and number of internodes composing it (table 2). The double dwarf milos have relatively few and short internodes (fig. 5, *B*), while in the tall Ethiopian forms (fig. 5, *A*) as many as 25 internodes may differentiate before the advent of flowering.

The internodes are longest and most uniform in the middle of the stalk and shortest at the base, but the terminal internode that bears the inflorescence is the longest of all (table 2). The form is cylindric, bobbin-shaped, or conoidal; the cross-sectional area, round or oval. The bobbin-shaped internodes are usually associated with swollen nodes, a feature of many thin-stemmed varieties. In the conoidal internode there is a sharp constriction below the sheath base and a gradual increase in diameter basipetally. It is a common type among thick-stemmed varieties with swollen nodes.

In the milo strains (*10*), the internodes become progressively longer from the ground up. The unimodal forms have one short internode between others that are longer above and below, while in the late varieties there is a double fall and rise in internode length ending with a final rise toward the peduncle.

The surface of the internode has a heavy coating of wax that often completely masks the green stem color. In the young internodes of many varieties and in the older nodes of a few, the wax deposit is concentrated below the sheath base, forming wax bands like those found in many sugarcane varieties.

On the side next the leaf, the internode is furrowed, the position of the furrow alternating at each node. The furrow is a narrow depression in the internode extending from the bud upward (fig. 2, *C*). In some varieties the bud furrow is altogether wanting; in others, it extends only part way up the internode. Often, bud furrows are observed only in basal internodes but may appear sporadically in others. False bud furrows are depressions in the stalk not in line with the bud. Their development is probably related to pressure differences during active growth.

The texture of the flesh is firm and juicy or dry and pithy. In varieties with firm flesh a freshly cut section is grayish or olive green. In some varieties the center becomes white and pithy and in many Ethiopian and some Indian varieties the entire cross section, except the narrow outer cortex, takes on a cottony-white appearance.

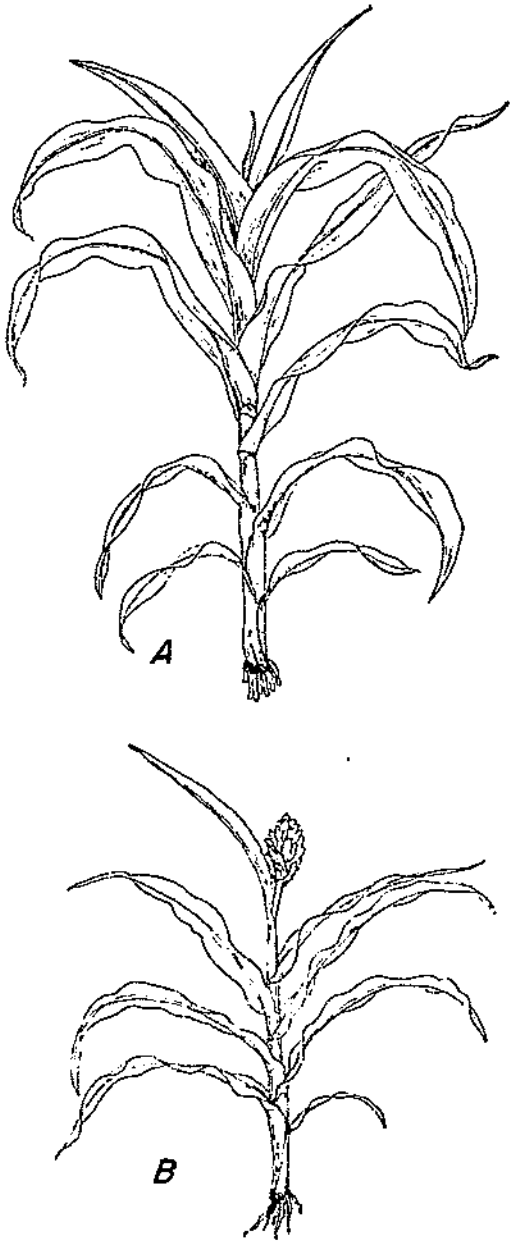

FIGURE 5.—*A*, Habit sketch of young, actively growing Ethiopian sorghum; and *B*, mature double dwarf milo.

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TABLE 2.—*Relative length in centimeters of internodes and subtending sheaths of some sorghum varieties* [1]

Number of internodes and sheaths	M. N. 672 [2]		M. N. 640 [2]		M. N. 634 [2]		M. N. 635 [2]		Milo		Sugar Drip		M. N. 472 [2]		Double Dwarf Milo	
	Internode	Sheath	Internode	Sheath	Internode	Sheath	Internode	Sheath	Internode	Sheath	Internode	Sheath	Internode	Sheath	Internode	Sheath
	Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
22	0	6														
21	0	15														
20	1	18														
19	2	19	0	3												
18	4	19	0	17												
17	9	21	1	24												
16	13	21	1	26	6	16			[3] 31	[4] 27						
15	12	21	3	26	0	24	0	5	17	18	[3] 40	[4] 36				
14	13	23	15	26	1	24	1	20	13	17	6	26	[3] 18	[4] 30		
13	15	23	22	25	2	23	1	23	18	16	9	22	11	18		
12	16	22	19	26	13	27	4	24	20	18	13	22	10	16		
11	17	23	16	27	23	28	10	26	18	20	16	23	14	16		
10	19	22	20	26	23	26	21	27	21	20	16	24	18	17		
9	21	22	15	26	22	26	21	30	20	19	12	23	20	18	[3] 28	[4] 28
8	23	23	18	28	23	28	22	30	19	19	15	22	19	19	5	17
7	23	24	12	25	23	27	24	30	20	19	17	23	22	19	3	14
6	23	26	14	27	18	30	28	29	19	20	15	23	22	19	3	13
5	24	26	14	27	18	30	30	27	18	18	13	23	23	20	2	13
4	25	26	13	24	14	30	28	27	16	18	12	23	19	20	2	14
3	24	25	7	24	11	27	21	27	10	19	12	24	17	19	2	13
2	15	24	3	17	7	26	12	24	5	18	7	19	13	17	2	13
1 (base of stalk)	4	24	4	15	4	26	6	24	4	18	3	15	8	17	1	13
Total	303	473	197	439	202	412	229	373	238	277	166	312	216	235	20	110
Average	13. 8	21. 5	10. 4	23. 1	12. 6	25. 7	15. 3	24. 9	15. 9	18. 5	11. 9	22. 3	16. 6	18. 1	2. 5	13. 7

[1] M. N.=Meridian (Miss.) number.
[2] Still actively growing.
[3] Inflorescence axis not included in averaging length of internodes.
[4] Sheath subtending inflorescence axis not included in averaging length of sheaths.

There is a slight correlation between color and texture of the flesh and starch and sugar content of the variety, as seen in table 3.

TABLE 3.—*Relationship of color and texture of flesh to starch and sucrose content of some Ethiopian selections*

Variety No.	Color and texture of cross section of internode	Starch [1]		Sucrose [2]
		Jacket	Diffuse	
				Percent
M. N. 620	Gray green; solid	+	+	10.79
M. N. 675	do	+−	+−−	4.58
M. N. 688	do	++	−	6.84
M. N. 698	do	+	+	4.82
M. N. 611	Gray green, with small white center.	+−	−−	8.34
M. N. 623	do	+−	+−−	6.17
M. N. 624	do	+	+−−	10.98
M. N. 672	do	+−	−	3.07
M. N. 673	do	+	+−	4.67
M. N. 679	⅝ of stem cross section white	+	+−−	3.00
M. N. 694	do	+−	−	4.75
M. N. 626	⅞ of stem cross section white	++	+	5.84
M. N. 619	Flesh white, spongy, and fistular	+−	+−−	7.71

[1] Designation of amount of starch: +=Cells partly filled with starch; ++=cells filled with starch; +−=starch scarce; +−−=starch very scarce; −=no starch.

[2] Figures of sucrose content taken from A. M. Schlebuber's 1944 unpublished sorgo report in files of Division of Sugar Plant Investigations.

NODE

The node is either flush with the internode or somewhat thickened. Ontogenetically, it is limited to the region just below the insertion of the leaf, but taxonomically it includes growth ring and root band.

GROWTH RING

The growth ring is a partially differentiated region that retains its cell growth potentialities. Externally it appears as a narrow band flush with the internode or protruding from it. In lodged stalks, one side of the growth ring is quite broad, since it is through the activity of the cells of this region that the stalk straightens itself from the bent position. There are no conspicuous varietal differences as regards height and contour of growth ring; it has no taxonomic value.

ROOT BAND

The root band is interpolated between sheath base and growth ring. It contains, besides the bud, one or several rows of root primordia. The height of the growth ring varies from 4 to 15 mm. Its color is lighter than that of the internode above. There is no visible coating of wax, but the basal root bands of many Ethiopian sorghums are distinctly pubescent. The hairs are usually limited to the region below the root primordia along the entire circumference of the root band or along certain sectors of it. Occasionally the hairs are confined

to the zone flanking the bud. In some forms the entire root band, including the root primordia, is covered with hair.

The root bands are usually cylindrical or *tumescent-obconoidal*. The root primordia are disposed in a single concentric ring, but in many Ethiopian sorghums the lower nodes contain two, occasionally three, rings (fig. 2, *C*).

The root primordia of the basal internodes are large and swollen and usually grow out into buttress roots, which, upon entering the soil, establish a firm support for the stem. In some varieties the buttress roots develop at a considerable height above ground (fig. 3), but they cease growing after attaining a length of several inches and never enter the soil. If the root bands are very narrow, the root primordia are disposed centrally, but in tall root bands they are close to the growth ring. Root primordia may fail to develop in the upper part of the stem; at best, they are inconspicuous.

BUD

Every node is normally gemmiferous, bearing a single bud. In some varieties the best developed buds are found in the basal internodes, becoming progressively smaller and appressed higher up the culm. Other forms (M. N. 690) have a well-developed bud on each node except the apical ones. Still others are characterized by having only one or two well-developed buds on any given stalk. In mature stalks in a dense planting the basal culm sheaths may wither and the buds of the nodes thus exposed often also dry up. This behavior is unlike that observed in sugarcane, in which the culms are normally self-cleaning and exposure does not affect the life of the buds.

The buds at ground level may develop as suckers, while the uppermost buds often elongate to form side branches. Both suckers and side branches develop heads that mature much later than the main head.

A bud primordium is initiated at the base of each internode very early in ontogeny, as demonstrated by Sharman (*12*) for the corn plant. As the internode elongates, the bud retains the basal position. It is thus always associated with the leaf above and not with the leaf in whose axil it occurs.

The buds are inserted in the tissue of the root band directly above the leaf scar or some distance above, sometimes as high as the middle of the root band. The height of insertion shows variation within culm limits, but on the whole it is a feature characteristic of the variety.

The outer covering of the buds is a prophyllum. In its entirety, the prophyllum of sorghum, like that of sugarcane (*8*, *fig. 5*), forms a hood with the front side composed of two asymmetrical overlapping halves and the back side entire. If the bud develops into a side branch, the prophyllum elongates and splits and the two sides form the first leaves of the branch.

Disregarding the numerous aberrant forms (fig. 6), two general types of buds are distinguishable—the sorghum and the sugarcane.

The sorghum type, characteristic of the sorgos and milos, somewhat resembles an arrowhead in relief. The lower part has a pronounced cushionlike extension that reaches from the base of the prophyllum to the leaf scar (fig. 7, *A*). The buds are well developed, large or medium large, and symmetrical.

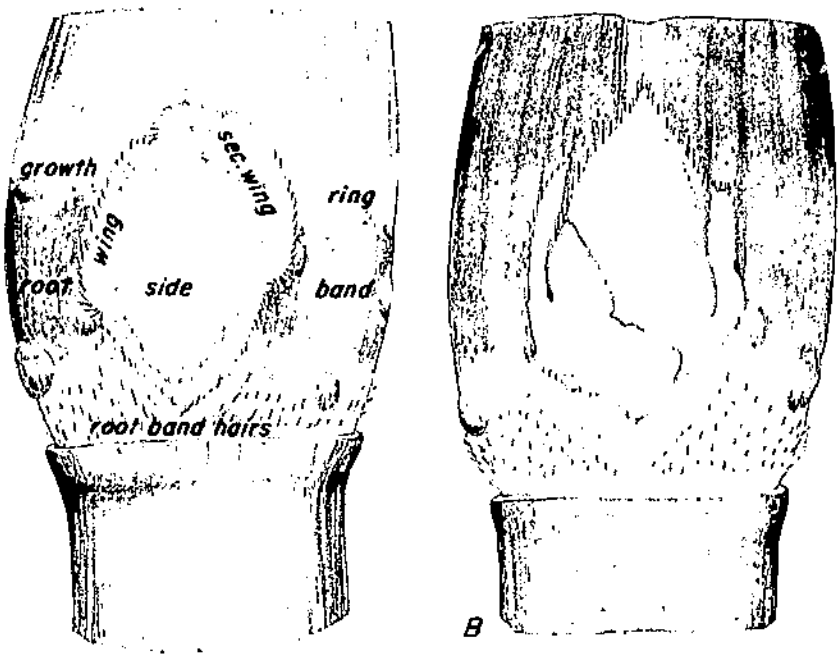

FIGURE 6.—*A*, Prophyllum of bud of indistinct "crawfish" pattern—right secondary wing very large, root band hairy; *B*, aberrant type with prominent secondary wings.

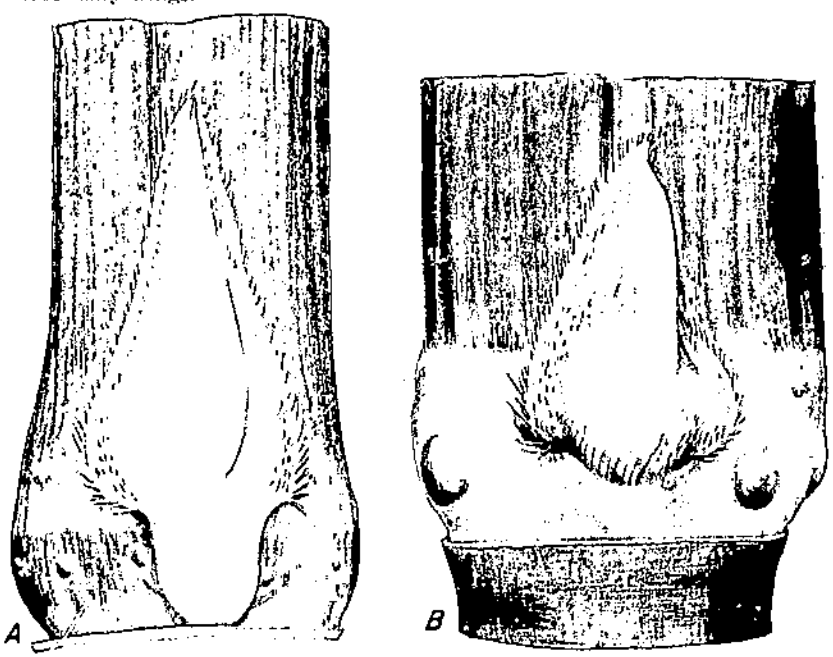

FIGURE 7.—*A*, Sorghum type of bud—obconoidal root band with one row of root primordia; *B*, sugarcane type of bud with "crossing-over" of sides in near-central position.

The anterior, or front side, of the prophyllum is elongate-deltoid; wing insertion basal, with or without prominent auricular set-off. The two overlapping halves of the anterior side are symmetrical, although frequently the overlying half is larger and may cover the entire front side. The basal appendage of the overlying margin is

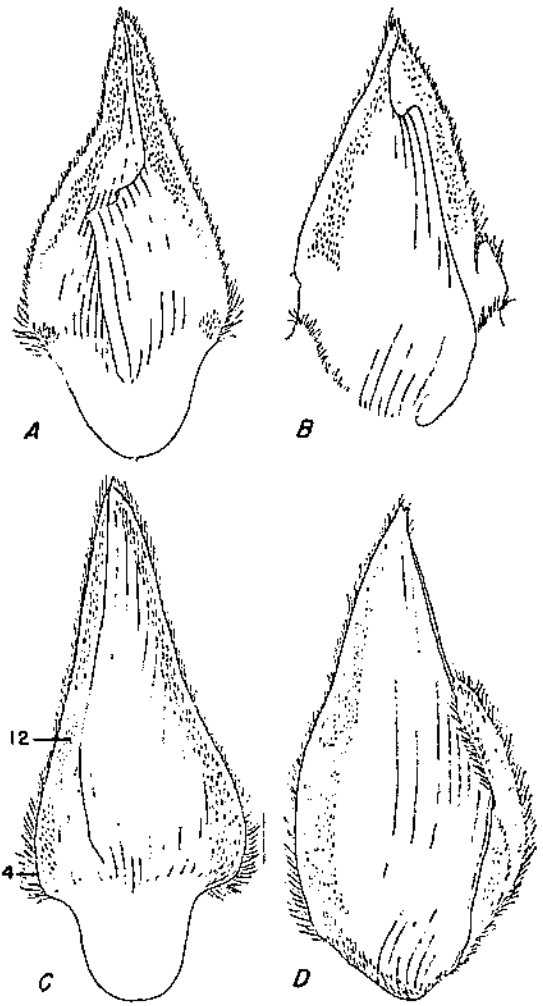

FIGURE 8.—*A*, Intermediate sorghum type of bud with crossing-over position near central. × 6. *B*, Sugarcane type of bud with large overlying side, crossing-over position apical. × 10. *C*, Typical sorghum type of bud with hair groups 12 and 4 well developed. × 6. *D*, Bud with large overlying side and one prominent secondary wing. × 6.

never conspicuous, as in sugarcane, and is often wanting. The two halves show frequent "crossing-over," i. e., the overlying half becomes the underlying half. This interlocking of the two halves may occur near the middle (fig. 8, *A*), the upper part (fig. 8, *B*), or the base of the prophyll (fig. 9, *B*, *C*).

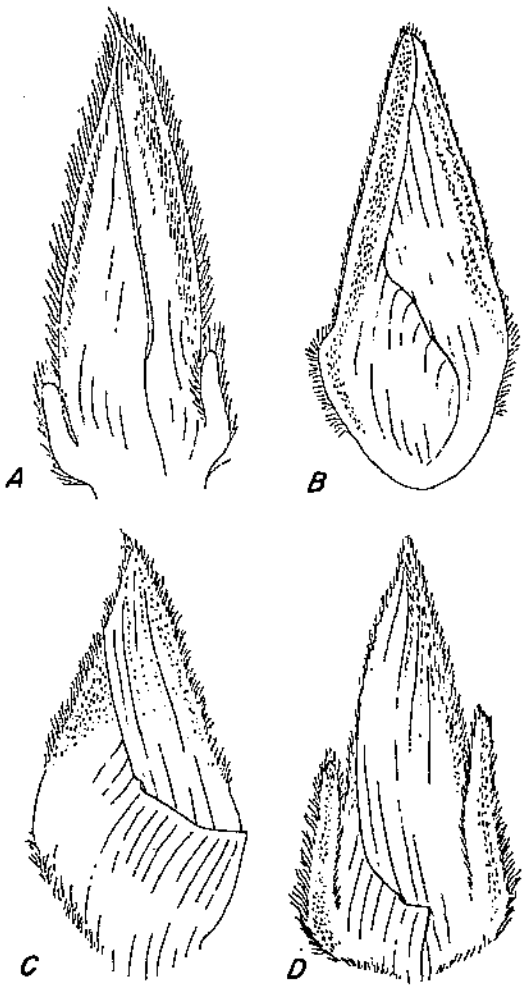

FIGURE 9.—*A*, Prophyllum with small secondary wings. × 3. *B*, Prophyllum showing central crossing-over of overlying side. × 6. *C*, Overlying side covering entire basal part of bud. × 12. *D*, Prophyllum with two prominent secondary wings. × 6.

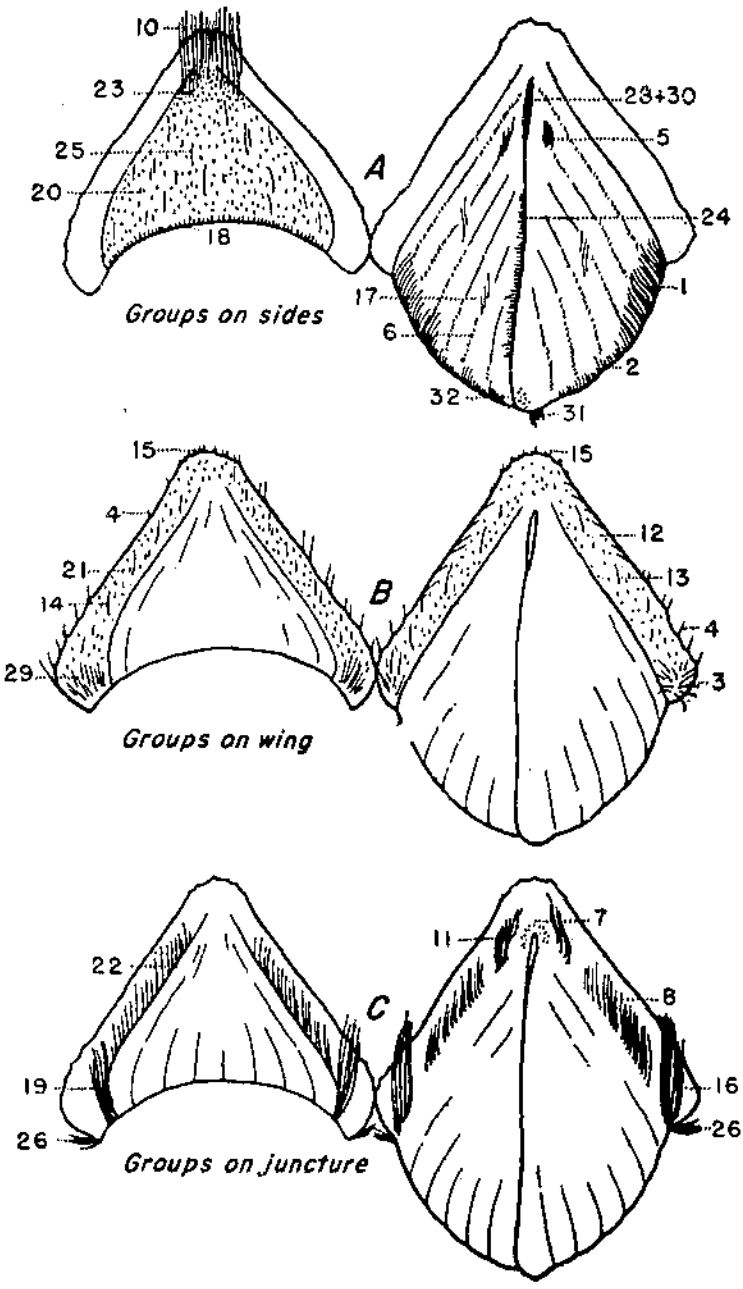

FIGURE 10.—Diagrammatic drawing of prophyllum of sugarcane replicated three times, showing location of hair groups (*A*) on sides, (*B*) on wing, and (*C*) on juncture between sides and wing. (Legend continued on facing page.)

Hair groups on anterior side (fig. 10, *A*)

(1) Lateral groups on overlapping halves of prophyllum. Hairs are white, long, and cover the base of the bud to a greater or lesser extent.
(2) Basal groups on overlapping halves of prophyllum. These strips of short hairs are often interspersed with groups of longer hairs alternating with the veins and often covering the short hairs.
(5) Groups of straight or wavy, very appressed white hairs on one or both sides of the germ pore and usually associated with long buds.
(6) Bands of short brown hairs between the veins.
(17) Groups of long, often wavy, appressed white hairs between the veins, giving the side a silky appearance.
(24) Short lashes along the upper half of the membraneous margin.
(28) Incurved and downward-pointing hairs immediately above the germ pore on the posterior side of the prophyllum.
(30) Short, inward-pointing lashes on edge of germ pore.
(31) A group of long, white, downward-pointing hairs implanted at the point of insertion of basal appendage.
(32) Short brown hairs on the surface of basal appendage.

Hair groups on posterior side (fig. 10, *A*)

(10) Group of long hairs implanted on the tip of the side between the veins and possibly extending into region of wing. Hairs may or may not protrude above the bud.
(18) Strip of long white hairs along basal edge. The hairs may be long or very short, restricted to the center or distributed over entire basal curve. The hairs may form a compact row or small groups.
(20) Short, brown hairs between the veins.
(23) Short, brown hairs on tip, often masked by hairs of group 10.
(25) Long, white hairs between the veins.

Hair groups on anterior wing (fig. 10, *B*)

(3) Long, white hairs on base of wing.
(4) Long, white oblique or appressed lashes on edge of wing, limited to basal region or occurring over entire edge.
(12) Small, brownish hairs on surface of wing.
(13) Long, appressed hairs on surface of wing.
(15) Lashes at tip of wing; may be considered a part of group 4.

Hair groups on posterior wing (fig. 10, *B*)

(14) Long, appressed, white hairs on surface of wing; rarely found in *Saccharum officinarum*.
(21) Short, brown hairs on surface of wing.
(29) Long, white hairs on base of wing. Groups 4 and 15 shared with anterior of wing.

Hair groups on anterior juncture (fig. 10, *C*)

(7) Groups of short, brown, or long, white hairs above central germ pore.
(8) Long hairs appressed in regard to the wing or projecting above the wing.
(11) Long, wavy, white, appressed or protruding hairs on juncture of wing just beneath the wing tip.
(16) Groups of long white hairs implanted on a broad base in the basal depression between sides and wing.
(26) Long lashes in corners of the wing.

Hair groups on posterior juncture (fig. 10, *C*)

(19) Groups of long, white, and appressed hairs inserted in the basal corners and sometimes protruding above wing.
(22) A narrow band of appressed, long hairs, often forming a connection between groups 19 and 10. Group 26 is shared with anterior juncture.

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The pubescence of the prophyllum is prominent or inconspicuous. There is never the wealth of individual hair groups found in sugarcane, and for that reason prophyll pubescence will never be an important character in sorghum taxonomy. The anterior side of the prophyllum has hair groups that are roughly equivalent to groups 1, 2, 4, 12, and 26 in sugarcane (fig. 10).[4] Groups 4 and 12 are usually present (fig. 8, *C*), while the others may be wanting. Frequently groups 1 and 2 are fairly massive and often constitute a continuation of the hairs of the root band. The anterior side of the prophyllum shows an all-over pubescence of wing and sides. No distinct hair groups are recognizable.

The basal bud cushion that characterizes the sorghum type of bud is most prominent in buds that are inserted high or fairly high in the tissue of the root band. This cushionlike swelling (fig. 7, *A*) is always paler than the adjacent root-band tissue. The swelling is thickest near the insertion of the prophyll, whence it gradually tapers in the direction of the leaf scar. If the bud is inserted very low, the cushion is inconspicuous but seldom actually wanting.

The sugarcane type of bud (fig. 7, *B*) is found in many Ethiopian varieties. In its typical form it is similar to that of sugarcane except for the paucity of hair groups. The prophyllum is usually deltoid, with wing insertion near-central or somewhat lower. The overlapping half of the two sides is always the larger. There is frequently a well-developed apical appendage. The interlocking of the sides already described for the sorghum type of bud is a very common feature, even in prophylls where the overlapping half is very large (fig. 9, *C*). The pubescence is sparse.

A feature that is conspicuous in the sugarcane type of bud, but not entirely absent from the sorghum type, is the formation of secondary wings that are outgrowths from the flanges of the normal wing (fig. 8, *B*, *D*, and fig. 9, *A*, *D*). As a rule, their location is basal, but they may develop along any part of the wing. Often one secondary wing is suppressed or underdeveloped (fig. 8, *D*), giving the bud an asymmetrical appearance. In plump buds with high wing insertion, the addition of secondary wings may produce the "crawfish" type (variety M. N. 699), which is especially conspicuous whenever the basal cushion (fig. 7, *A*) that connects the base of the prophyllum to the leaf scar is very prominent. Plump buds with prominent basal auricular set-offs of the wing, but lacking secondary wings, may show a distinct "clover-leaf" pattern. This type is usually restricted to basal internodes with swollen root primordia.

MORPHOLOGY OF THE LEAF

The leaf of sorghum, as in all grasses, consists of two parts—the sheath and the blade. At the juncture of sheath and blade is the blade joint with its specialized regions, the ligule, and the dewlaps.

The leaves vary in number from 7 to 25 and are arranged alternately with a divergence of 180°. Early varieties have 7 to 9 leaves above the crown, while late varieties may produce as many as 28. Varieties that average 10 or fewer leaves above the crown are classed as sparsely

[4] Fig. 10 is fig. 4 of (3) and is reproduced here to aid the reader.

leaved, those with 11 to 13 as midleafy, and those with 14 or more as leafy (*14*).

Leaf Blade

The blades of young leaves are stiff and erect; on maturing, they spread fanlike in a gentle curve.

There is little variation in the length of the blade among different varieties. The majority of sorgos have medium-long blades (100 cm.), whereas the milos have short blades (60 cm.). The width of the blade varies between 5 and 13 cm. Most blades are linear lanceolate, widest near the center or upper central zone. In certain varieties the blade is lanceolate, widest near the base and tapering gradually in the direction of the apex. Mature leaves are smooth-edged or serrate, but the margins of young leaves are always scabrous.

The color of the blade is medium or dark green, and the surface is shiny. The basal part of the upper midrib surface is often conspicuously farinose. The powdery wax deposit that characterizes this condition forms a broad zone just above the blade joint, narrowing acropetally and fading out some 20 cm. higher up.

The blade is divided by the midrib into symmetrical, or sometimes slightly asymmetrical, halves. The spacing of the principal veins is similar for most varieties, except that in the broad-leaved forms the veins are set farther apart than in plants with narrower blades; sometimes narrow and medium-wide leaves have their veins extra far apart.

The midrib of the leaves of most varieties is very prominent. It is always very wide at the base, gradually tapering toward the apex and disappearing altogether before reaching the tip of the lamina. The upper surface is channeled, the lower convex. A conspicuous character is the difference in color of the two sides of the midrib. While the lower surface is always green except for a light stripe that runs along the center, the upper surface may be variously colored, depending on the variety and the state of maturity of the organ. The upper midrib surface of all young leaves is cloudy or light olive in color. As the leaf ages, the surface turns completely white or remains cloudy except for a narrow or medium-wide central zone that is either pure white or somewhat paler than the flanges. The milos have a yellow or olive-colored midrib, caused by a yellow pigment in the subepidermal parenchyma cells.

Varieties may be classified as having white, cloudy, or yellow midribs (*14*). The classification white-ribbed is applied only to those varieties in which the entire midrib of mature or half-grown leaves is pure white (fig. 11, *A–D*). Varieties with a central white streak and with the flanges or margins cloudy (fig. 11, *E*, *F*) are classified as cloudy (*14*).

The midrib of the leaves of many varieties is scabrous, especially in the lower part, and may even feel hairy to the touch. In some forms the pubescence extends upward for only 1 or 2 cm.; in other varieties two-thirds of the midrib is hairy. The hairs are always densest and longest in the basal part of the midrib. Here, they cover the entire width of the midrib, while higher up they thin out and become localized along the flanges. In many forms the midrib pubescence is dense only in the very basal zone, with some scattered

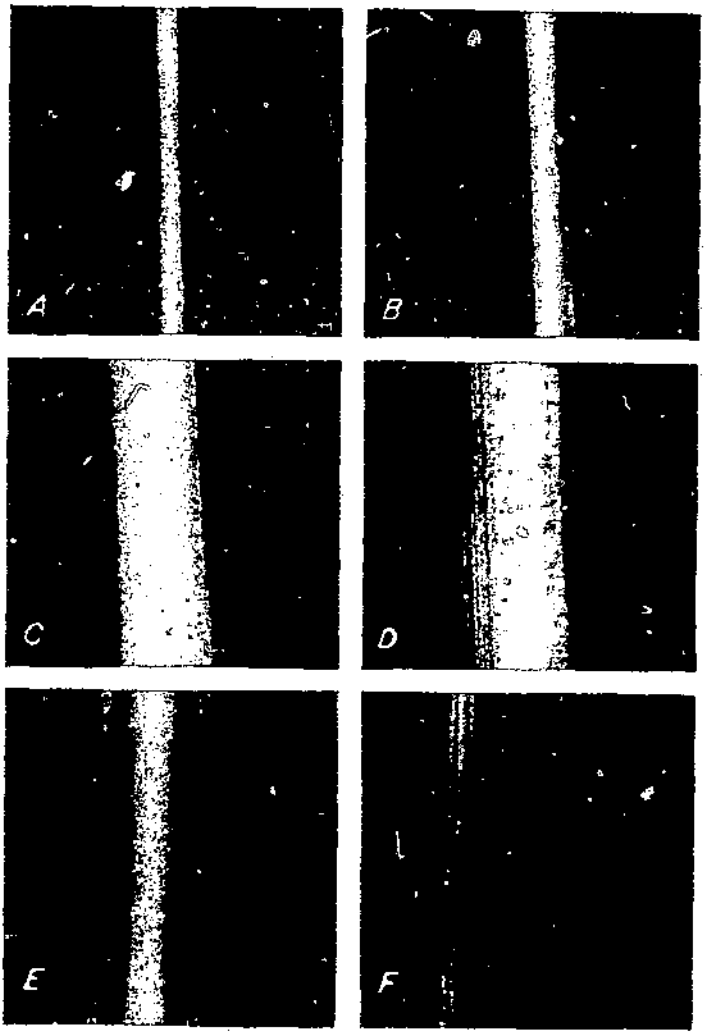

FIGURE 11.—Midribs with adjacent blade tissue: *A*–*D*, White-ribbed varieties; *E*, midrib with broad white center and cloudy flanges; *F*, midrib cloudy. All ×1½.

hair, localized medially or laterally, reaching up as high as 10 cm. Many varieties, including the milos, have a smooth midrib.

Midrib pubescence is an important character, useful for group classification and important for purposes of identification when used in connection with other characters.

LEAF SHEATH

The sheath is attached to the node and encircles the culm. It forms an open tube extending about one and a third times around the base of the internode. The outer margin of the sheath overlaps the

inner, the overlapping margins being alternately the right and the left in successive nodes. The sheath is thickest medially, gradually becoming thinner toward the margin where it is membranaceous. The outer surface is glabrous, the inner surface white and glistening.

The length of the sheath varies comparatively little, averaging about 25 cm. for most varieties. However, there are varieties (M. N. 628 and 694) with rather long sheaths, attaining a length of 33 cm., or relatively short ones (M. N. 448, 462, and 463) with a length of only 16 cm. Within culm limits the length is fairly constant (table 2), except that the basal and apical sheaths are shorter and the lower near-central ones longer than the average. There is often a certain degree of overlap because of variation in length of internode. In many of the medium-tall, sparsely leaved sorghums the sheaths are shorter than the internodes they envelop, so that the nodal region of the next higher leaf is plainly visible (fig. 12). In other forms the near-central sheaths and their respective internodes are of equal length (fig. 12, *B*), while the basal and apical sheaths show a certain degree of overlap. The greatest extent of overlap is found in the double dwarf milos, whose internodes are only a few centimeters long.

The principal veins of the leaf sheath are much closer together than those of the blade, giving the outer surface a finely ridged topography. The venation is tesselate, with transverse veinlets clearly visible.

The inner surface of the sheath is white and glossy, often purplish at the base. The outer surface is dark green or whitish, depending on the degree of waxiness. The wax deposit is usually very heavy in the upper part of the culm and more conspicuous in some varieties than in others. Occasionally wax deposits may be very scant or altogether wanting.

The surface of the sheath is always smooth. The only hair is found on the sheath base, the region where the sheath is attached to the node. The hairs that invest the sheath base are short and white. They occupy a concentric band of varying width, covering the entire sheath base and partly investing the stem tissue immediately below the insertion of the leaf. The sheath base region is also set off from the rest of the sheath by a slightly different color, generally a light olive.

Blade Joint

At the juncture of sheath and blade is a specialized region, the blade joint. The inside of the blade joint is delimited basipetally by the ligule. The flanges of the blade joint are formed by two deltoid or curved strap-shaped areas known as dewlaps or joint triangles. These areas are soft-textured and often gauffered to give the leaf mobility.

LIGULE

The ligule is formed ontogenetically from epidermal cells and is made up altogether of elongated parenchyma cells. The side next to the leaf is covered with free or slightly adnate hair. The upper free edge is ciliate, the cilia sometimes exceeding in length the height of the ligule. In its immature state the ligule is translucent; later it becomes dry, locally discolored, especially below the attachment of the cilia, and sometimes torn.

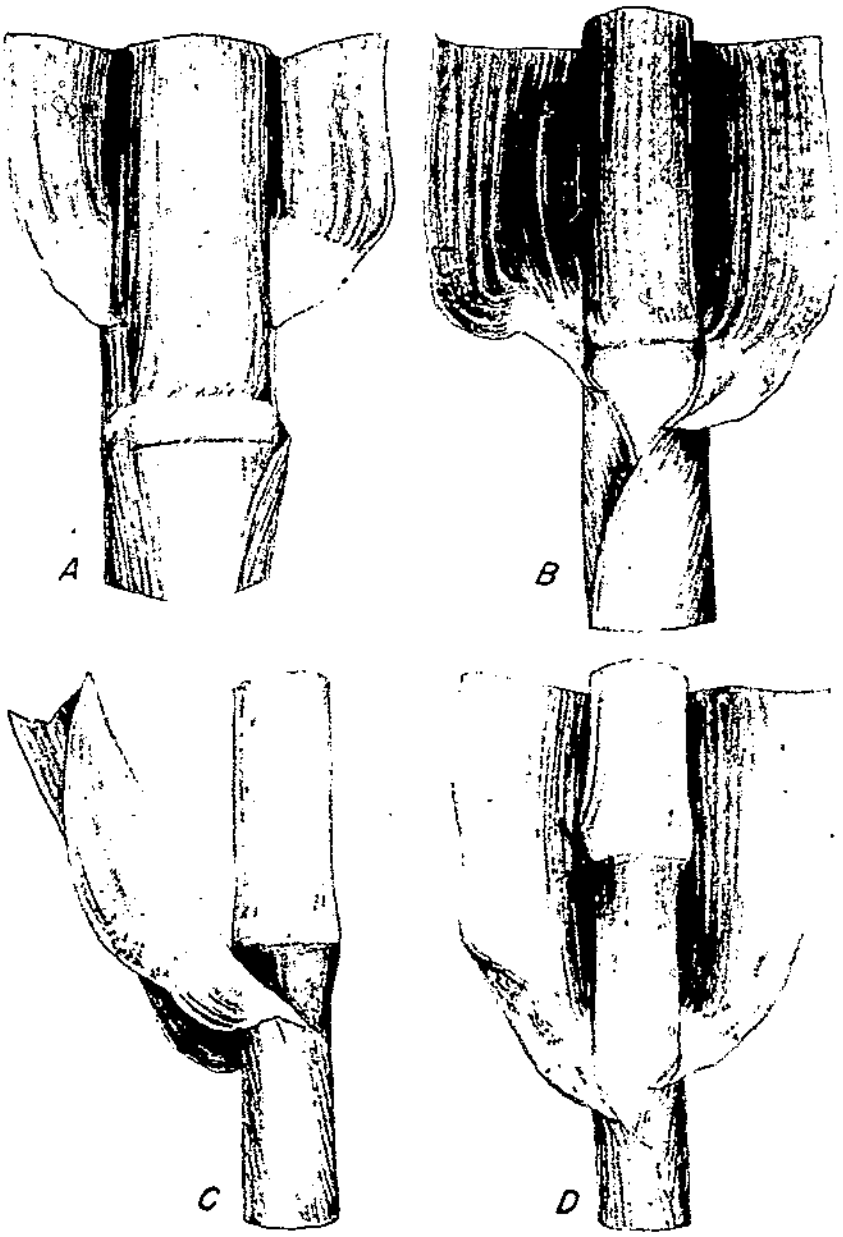

FIGURE 12.—*A*, Leaf sheath extends beyond node of next leaf, dewlaps deltoid; *B*, leaf sheath even with node; *C*, leaf sheath shorter than internode, edge of dewlap and base of lamina folded back; *D*, internode longer than sheath (compare with fig. 1).

Fundamentally, there is only one ligular pattern, the shallow crescent. Most ligules are about 2 mm. high, somewhat taller at the middle, and gradually thinning out toward the margin of the leaf. In a few forms, the ligule is considerably higher at the center than near the margin of the leaf. Such types may be designated as shallow-deltoid. On the other hand, the ligule may be depressed in the center, giving rise to a shallow-arcuate type. In one variety (M. N. 683), the base line of the ligule in the region of the midrib was found to be thrust upward like a narrow horseshoe or inverted V.

Since the outer margin of the dewlap curves sharply inward, the ligular flanges with their conspicuous dorsal pubescence are clearly visible from the outside (fig. 13, *E–G*). The flanges commonly abut squarely on the narrow-deltoid extension of the sheath margin (fig. 13, *F*). Occasionally they thin out almost to a line and extend to the very margin of the sheath (fig. 13, *E*) or may terminate earlier (fig. 13, *G*).

DEWLAP

There are two common dewlap patterns: The curved ligulate (fig. 13, *B*, *D*) and the deltoid (fig. 13, *A*). The form of either type is somewhat influenced by the slope of the ligule that marks the lower boundary. The shape of the dewlap is usually characteristic of the variety, but it may vary within culm limits. Young leaves commonly have a narrow-ligulate dewlap, whereas in older ones the deltoid type predominates. Many forms retain the juvenile type through maturity, however. The two dewlaps of a given leaf often show conspicuous variation in regard to slope and form (fig. 14). The dewlap in continuity with the overlying sheath margin is apt to be ligulate and steeply sloping, the other deltoid and less sloping, but some leaves on the same stalk may have very symmetrical dewlaps (fig. 14, *A*).

The older dewlaps of many varieties have a pronounced tendency to fold back (fig. 13, *C*), whereas in others vertical folds and gauffering give the leaf mobility.

Young dewlaps are usually concolorous with their respective leaves. Upon aging, the dewlap color fades, becomes ivory, ivory-yellow, or a shade of olive. The outer marginal zone of the dewlap is always lighter in color than the region next to the midrib, which often retains the natural green of the adjacent leaf tissue.

The degree of waxiness of the dewlap varies from a mere bloom to a heavy wax deposit that often masks the natural color of the outer dewlap surface. This surface is sometimes glabrous, but usually has some sort of pubescence. The hairs may cover the entire surface uniformly or may be restricted to certain regions (fig. 15, *A*). Most conspicuous, and visible to the naked eye, is a small hair group extending from the midrib outward. Next in importance is the broad marginal group; here the hairs are usually sparse and not recognizable without the aid of a lens. Sometimes these two hair groups are connected by a narrow band of scattered hairs along the base of the dewlap; however, this band of hairs is often wanting. The top of the midrib may show a few solitary hairs, but usually this region is glabrous.

The inner dewlap surface always has a dense hairy covering except in the marginal zone, which may have fewer hairs than the outer surface adjacent to it. From the marginal zone inward the hairs become

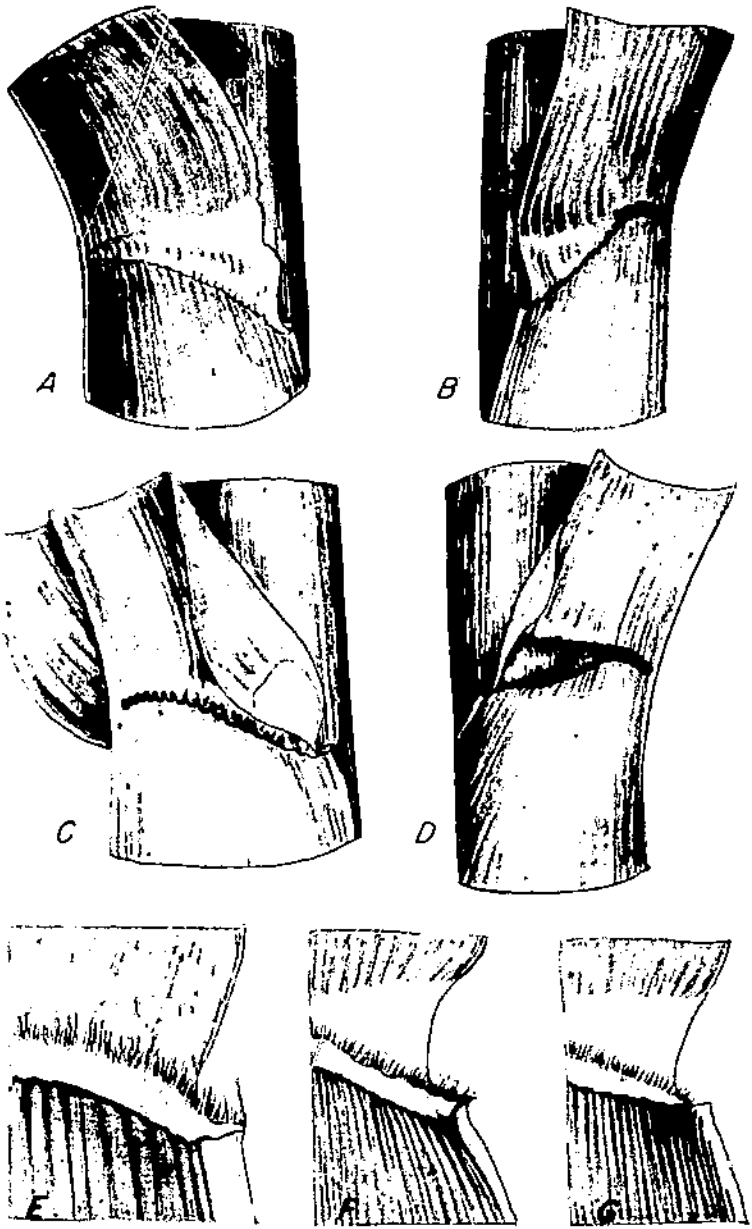

FIGURE 13.—*A*, Dewlap broad-deltoid and slightly gauffered; *B*, dewlap narrow-ligulate and steeply sloping; *C*, deltoid dewlap with margin sharply folded back, surface not gauffered; *D*, narrow-ligulate dewlap with base line nearly horizontal; *E*, flange of ligule attenuated and extending to very edge of membranaceous sheath margin; *F*, flange of ligule abuts with broad base on triangular extension of sheath margin; *G*, attenuated flange of ligule terminates before reaching sheath margin.

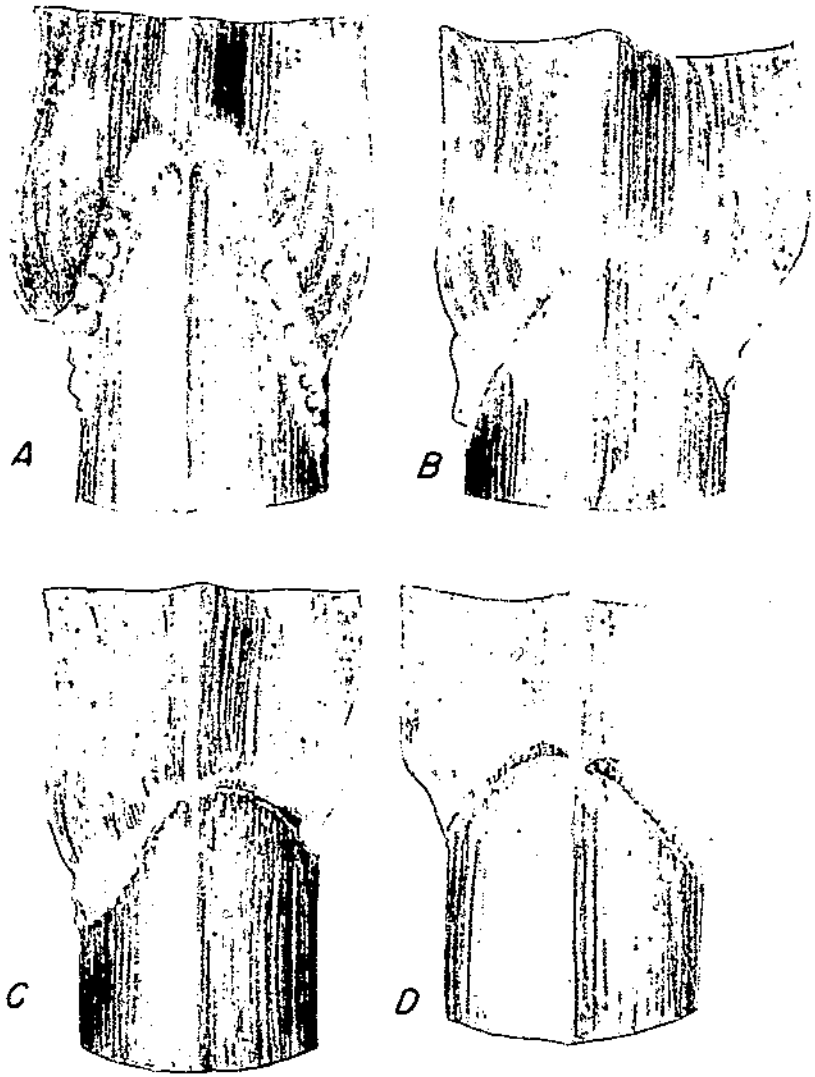

FIGURE 14.—Blade joints showing variation in dewlap pattern on the same stalk: *A*, Blade joint from near-central part of stalk showing symmetrical, sharply sloping ligulate dewlaps; *B*, asymmetrical dewlaps from leaf higher up—the left dewlap in continuity with the overlying sheath margin is ligulate and steeply sloping, the one to the right is deltoid and less sloping; *C*, dewlaps from blade joint above *B*; *D*, narrow ligulate dewlaps from youngest blade joint.

long and dense, reaching their fullest development in the midrib itself (fig. 15, *B*). In a few varieties the basal midrib hairs are not so long as the adjacent flange hairs, sometimes not extending up to the marginal fringe of the ligule. The flange hairs have a tendency to converge over the midrib, making the midrib group appear especially massive.

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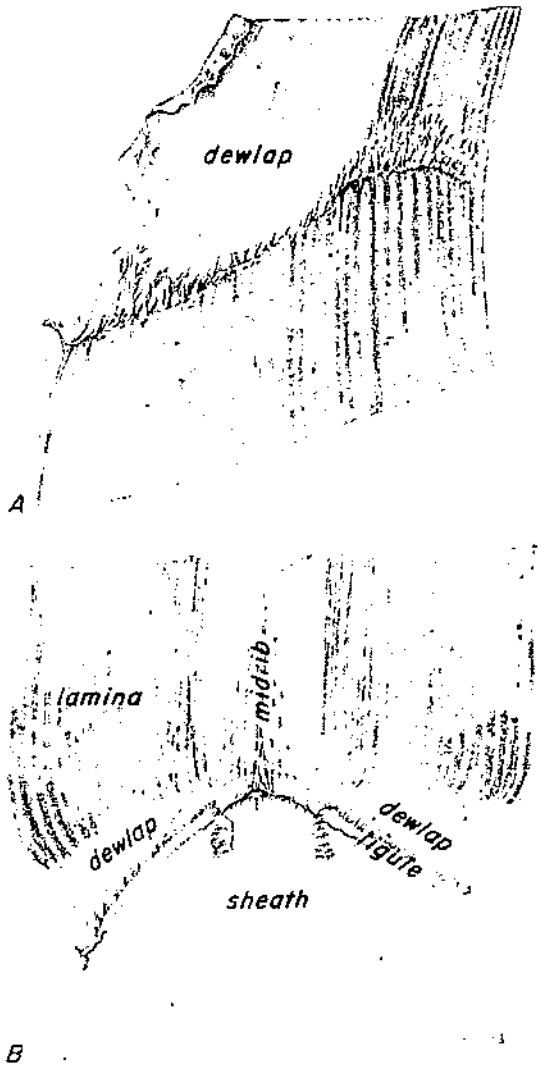


FIGURE 15.—*A*, Outer surface view of dewlap, showing pubescence. Flange of ligule abutting on membranaceous sheath margin visible at left. *B*, Detailed structure of inner surface of blade joint, showing pubescence of dewlaps and midrib. Ligule partly folded back to expose hair groups in back.

Because of its relative uniformity, the inner dewlap pubescence has little taxonomic value. The outer dewlap pubescence may be useful as a qualitative character if exceptionally well developed, with the hair groups visible to the naked eye. The midrib pubescence, however, especially if extending far up the leaf, is a character of primary importance.

ANATOMY OF THE STEM

Internode

The stem of sorghum, like that of sugarcane, is a meristele with vascular bundles scattered throughout the fundamental parenchyma. At the periphery (fig. 16, *A*) the bundles are small and so close together that they form practically a solid ring. The parenchyma cells between the inner bundles are thin-walled with small intercellular spaces at their angles. Those between the peripheral bundles are small, thick-walled, and lignified. There is a narrow lignified hypodermis, its vertical continuity occasionally broken by the interpolation of parenchyma cells that abut externally on a stomate. Since the stem epidermis of sorghum contains relatively numerous stomates, compared to sugarcane, these passage areas are also rather numerous.

In addition to plastids, the parenchyma cells of the internodes of many varieties contain starch. Starch deposits are first noted in the cells surrounding the vascular bundles, and in many varieties this "jacket" starch is the only kind formed. In other varieties, starch also accumulates in the parenchyma between the bundles. This accumulation of "diffuse" starch (fig. 16, *B*), especially in the sweet sorghums and the milos, can be very massive.

Freshly cut cross sections of young stems have a uniform gray-green color. As the stem matures, the cells near the center may become filled with air and take on a cottony-white appearance. This process of pith formation is often limited to the center of the stem, but it may extend outward until the entire cross section, except the peripheral zone, is involved. The transformation of parenchyma into pith is sometimes followed by a complete cellular break-down that leaves the central vascular bundles suspended in air with the remains of broken tissue.

Except in the peripheral region, the vascular bundles of the internode are rhomboid (fig. 17, *B*) or narrow oval in cross section (fig. 17, *A*). Xylem and phloem are disposed collaterally in relation to each other. The protoxylem consists of annular and spiral elements. Since it matures before the internode elongates, the unthickened part of the walls of these elements becomes crushed during subsequent growth. Simultaneously, the small-celled protoxylem parenchyma recedes, forming an air space, or lacuna, into which project the remains of the secondary wall of the annular or spiral vessels. Above and lateral to the protoxylem are two large metaxylem vessels (fig. 17) with pitted or reticulate-pitted secondary walls. Between the two large vessels is a connecting band of small pitted tracheids and xylem parenchyma. The tangentially flattened parenchyma cells surrounding the vessels are thick-walled and lignified and possess reticulate thickenings. The phloem forms an oval mass of tissue of regular design, composed of large sieve tubes and small companion cells. The protophloem is nearest the outside; in mature bundles it is crushed and lignified.

The vascular bundles are enclosed by a well-marked sheath, which is most strongly developed on the inside and the outside of the bundles, where it forms typical bundle caps. At the flanks, the sheath is uniseriate or biseriate, occasionally wider. The sheath cells are

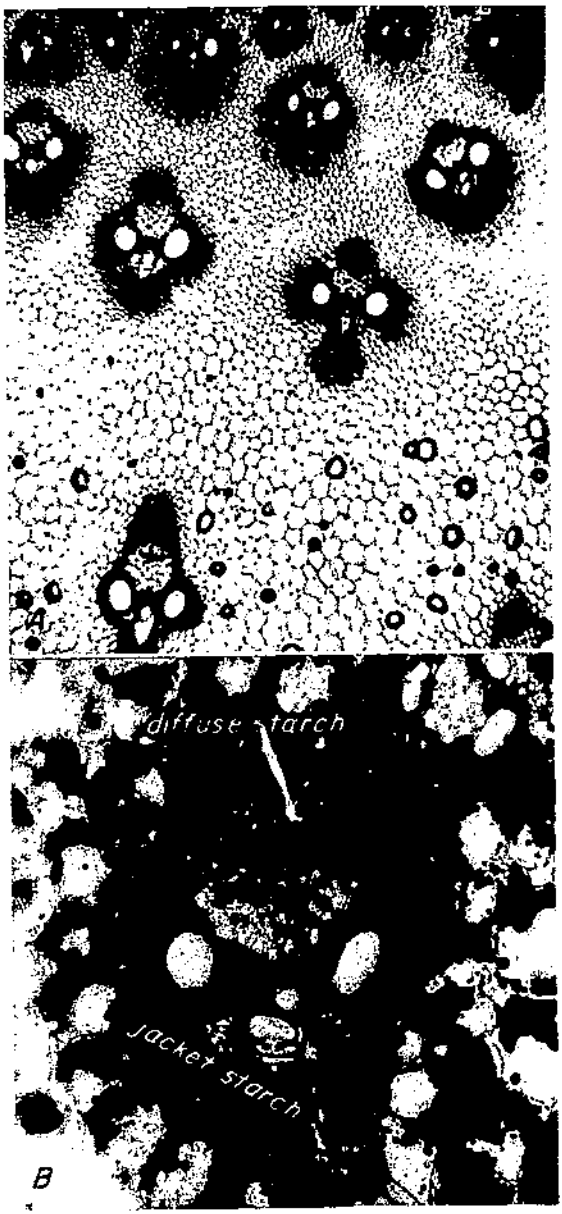


FIGURE 16.—*A*, Cross section through the peripheral region of internode (hand section of fresh material). × 40. *B*, Bundle from central region of internode surrounded by parenchyma cells densely filled with starch (hand section of fresh material). × 190.

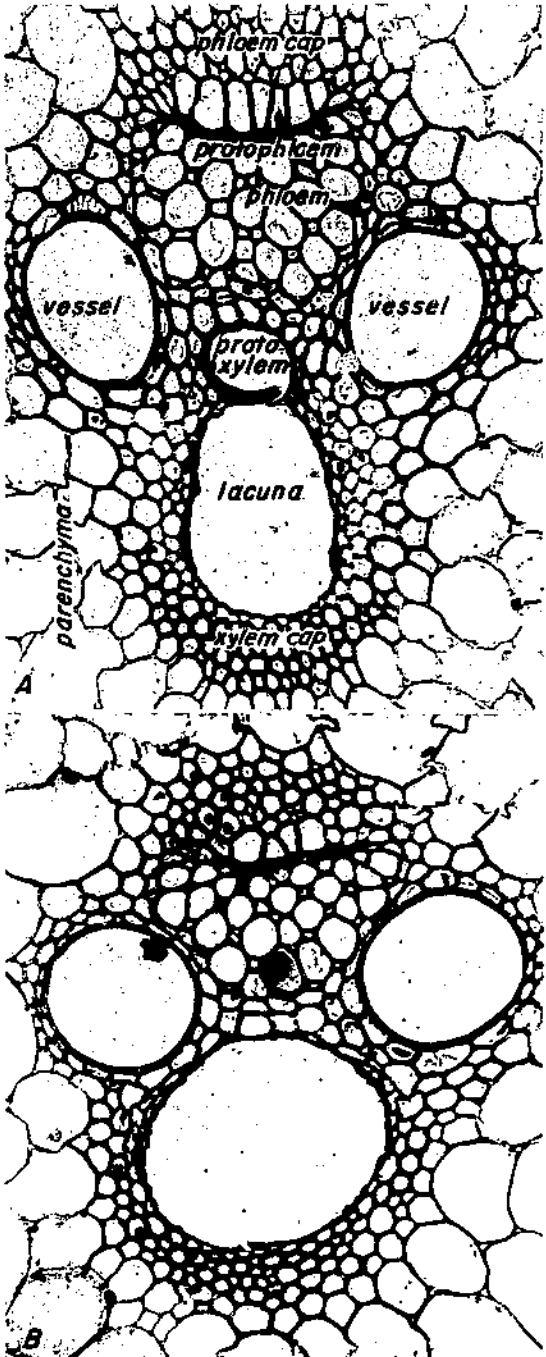


FIGURE 17.—*A*, Large oval bundle from central region of internode; and *B*, large rhomboid bundle from central region of stem. Both × 222.

compactly arranged with no intercellular spaces between them. They are long and tapering and sparingly pitted except at the flanks. Here they are short and rectangular, with circular pits. The sheath cells are in direct contact with the protophloem, but laterally they are separated from the metaphloem by parenchyma cells. The sheath cells bordering the protophloem are always conspicuously large (fig. 17, *A*) and thinner walled than the other sheath cells.

The ring of vascular tissue just inside the epidermis is composed of very small and medium-sized bundles buried in thick-walled parenchyma. The sclerenchymatous bundle cap of the phloem pole is small, and its cells are usually continuous with the hypodermal sclerenchyma. The bundle cap at the xylem pole is large, and the sheath along the flanges is also well developed. The xylem of these small bundles is reduced to one or two large metaxylem vessels. If two vessels are present, they are adjacent to each other or separated radially by small-celled, lignified xylem parenchyma or tracheids. The phloem is relatively well developed, its area being proportional to the size of the bundle.

Among the outermost bundles are a few extremely small ones composed of one metaxylem vessel and some phloem. They are surrounded by a single-layered lignified sheath. This type of bundle is characteristic of the basal internode just above the growth ring and is also met with in the lower nodal region.

The medium-sized bundles of the peripheral ring are not always in contact with the hypodermal sclerenchyma. They differ chiefly from the smaller type by having a very large sclerenchymatous cap at the xylem pole. There are always two metaxylem vessels and occasionally a protoxylem element.

The bundles of the second and third concentric ring also possess a large sclerenchymatous cap at the xylem pole, with an increase in the number of protoxylem elements. There is a progressive reduction in the thickness of the sheath in bundles farther away from the periphery. The number of protoxylem cells is larger and a small protoxylem lacuna may be formed. Beginning approximately with the fourth circle, 2 mm. centrad from the epidermis, the bundles are like those of the central internode.

The ontogeny of the stem bundles of sorghum is in agreement with that of corn (*5, 12*) and sugarcane (*1*). The precursors of the bundles are small procambial strands that first increase in size by division within the strand. To conform with the future shape of the bundle, the divisions are at first periclinal and later at the flanges. Within these groups of procambium, tissue differentiation proceeds until all the components of the bundles have been formed. The first sieve tubes appear at the outer margin—the first protoxylem elements—maturing somewhat later than the first sieve tube, at the inner margin of the procambial strand. Additional cells differentiate until all xylem and phloem is formed. As the conducting elements of the protoxylem are destroyed during elongation of the internode, a protoxylem lacuna is formed.

The bundle sheath is initiated during early procambial differentiation. It surrounds the emerging bundle as a single layer, but it

soon becomes several-layered at the xylem and phloem pole. There is no distinction between sheath and vascular tissue precursors in the early ontogeny of the bundle, as pointed out by Esau (*5*) in her detailed study of the ontogeny of the vascular bundle in corn. The sheath is a composite of cells derived from the procambium and adjacent parenchyma cells.

The procambium cells of the emerging vascular bundle and their immediate derivatives have the appearance of a typical cambium from which xylem and phloem cells are formed. This radial seriation of the cells and their brick-shaped appearance in cross section, however, is not sufficient to argue the existence of a lateral meristem in sorghum or other herbaceous monocots (*6*).

The epidermis of the internode is formed by a single layer of cells and is very similar in appearance to that of sugarcane (fig. 18). There are three kinds of cells: Long, cork, and silica. Stomates are rather numerous, disposed singly (fig. 18, *C*) or in vertical files. The long cells form four-sided prisms with undulating silicified walls. The mean diameter varies between 7μ and 16μ, depending on the variety. There is much variation in the length of the long cells within both varietal and culm limits. But varietal differences are quite apparent when forms with very short cells (M. N. 611) and those with very long cells (M. N. 459) are compared. The end wall of the long cell is always straight, never sloping, as in many sugarcane varieties.

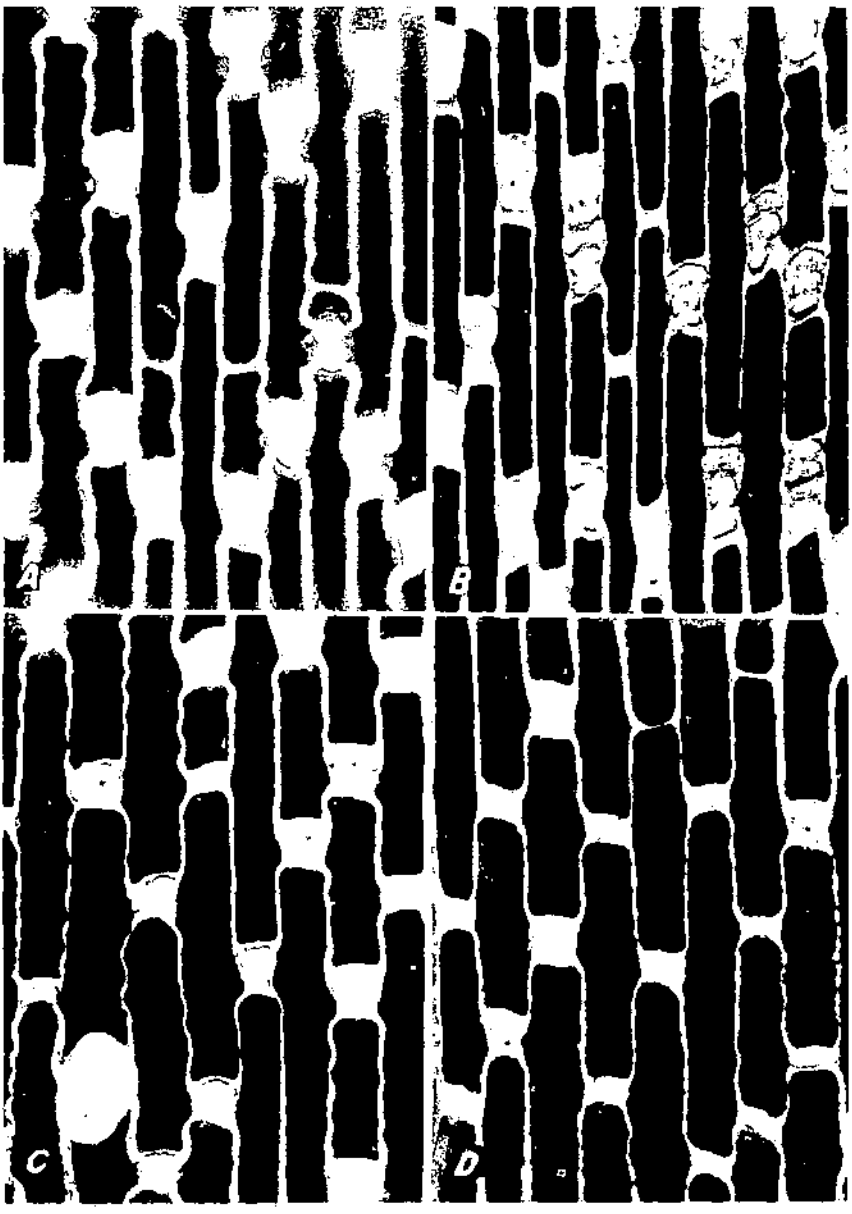
The cork cells are suberized and relatively thin-walled. They are kidney-shaped, with the greatest diameter at right angles to the vertical axis of the stem. Although usually associated with a silica cell, they may occur alone (fig. 18, *D*).

The silica cells are typically biscuit-shaped, with a constricted center and overhanging margins, and with the long diameter parallel with the long axis of the stem. Occasionally they are broad like the cork cells.

Using group structure and distribution of short-cell groups as criteria, three epidermal patterns may be recognized. Since there is often much variation within culm limits, they are of questionable importance in the designation of varieties. These patterns are—

Pattern 1.—Cork and silica cells always in single pairs alternating with long cells (fig. 18, *A*).
Pattern 2.—Short-cell groups prevalently in double pairs (fig. 18, *B*).
Pattern 3.—Many short-cell groups lack silica cells (fig. 18, *C* and *D*).

It is apparent that the epidermis of sorghum is very uniform compared to that of sugarcane, and is of little taxonomic value. Not a single variety out of 152 studied showed a complete absence of silica cells, whereas in sugarcane many varieties show that characteristic. There is also only one type of cork cell instead of the great variety of forms observed in sugarcane. Stomates are very numerous, occurring in connected or interrupted vertical files. Since their distribution is very uniform, they are of no value in classification of varieties. Also, epidermal hairs, while observed only rarely in sugarcane, are always wanting in the stem epidermis of sorghum.


A
B
C
D

Growth Ring

A cross section through the growth ring, or intercalary zone, differs from a similar section through the internode in having a peculiar type of bundle structure and a narrow bundle-free zone inside the epidermis.

The cells of the outer layers of the bundle-free cortex are very small and slightly thickened; those farther inward are large, with intercellular spaces at their angles.

Adjoining the cortex is a zone of very large bundles that are so close together that they appear like a honeycomb (fig. 19, *A*) in which the walls of the comb represent the interstitial parenchyma that separates the bundles. The central or near-central bundles (fig. 20, *B*) are more widely spaced and similar in size to normal internodal bundles.

The vascular part of the large peripheral bundles (fig. 19, *A*) is very small, consisting of a few protoxylem elements and some phloem. Surrounding this small vascular core is a massive collenchymatous jacket, which is soft at first, but hard and lignified in old stalks.

The central stem bundles resemble the ordinary type, except that all vessels are of the annular or spiral types. No protoxylem lacuna is present. The vascular tissue is surrounded by a single layer of thin-walled lignified cells (fig. 21, *A*). This cell layer forms the inner boundary of the sclerenchymatous jacket, which is very massive in the phloem region, but forms only a narrow crescent over the xylem pole (fig. 21, *B*). The jacket cells investing the narrow lignified bundle sheath thicken and lignify progressively outward (fig. 21, *B*) until the narrow sheath, as illustrated in figure 21, *A*, and the sclerenchymatous jacket over the xylem pole and along the flanges become one tissue. The cells of the large phloem cap are more like collenchyma than the sheath cells investing the bundle, as shown by their appearance and staining reaction (fig. 21, *B*).

A characteristic feature of the bundles of the growth ring is the jacket of starch-filled cells surrounding each bundle. This jacket is most prominent at the xylem end of the bundle (fig. 20, *A*) and poorly developed or wanting at the phloem pole (fig. 21). The large peripheral bundles also have a starch jacket, but it is very narrow and less conspicuous than that of the central bundles.

The peculiar structure of the central stem bundles, characterized by the large collenchymatous phloem caps and starch jackets, extends some distance beyond the growth-ring zone as externally delimited. Also, the reduction of the cortex and the outward movement of the peripheral bundles until they again establish contact with the hypodermal sclerenchyma (fig. 22, *A*) are completed only some distance above the true growth-ring region.

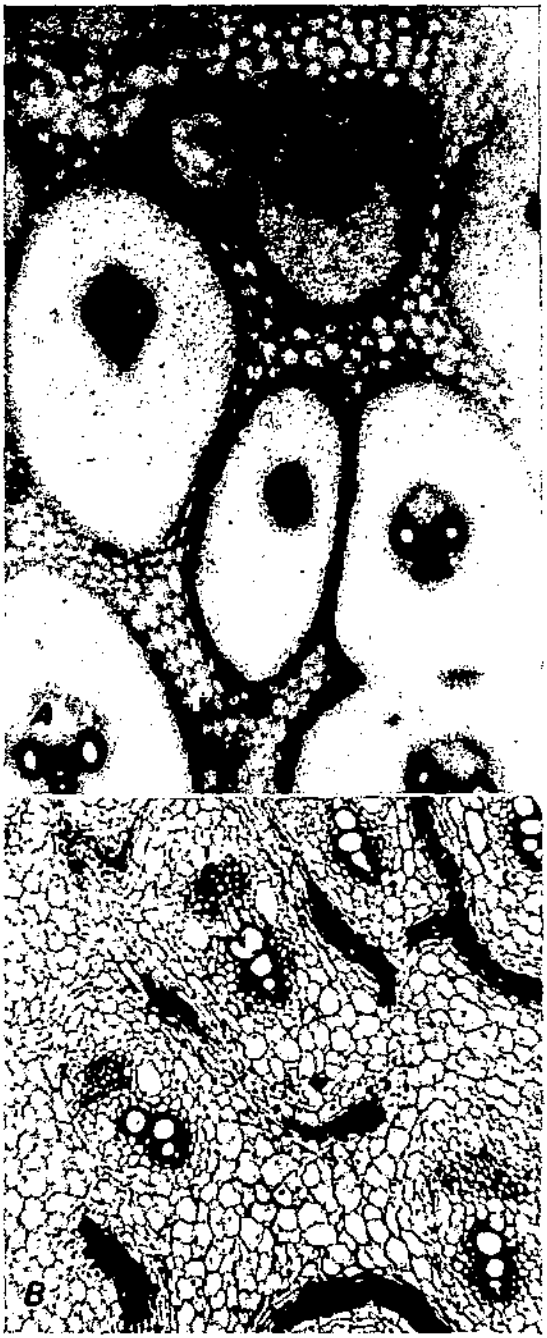


FIGURE 19.—*A*, Cross section through peripheral region of growth ring (hand section of fresh material). × 50. *B*, Cross section through young root hand showing numerous horizontal traces. × 100.

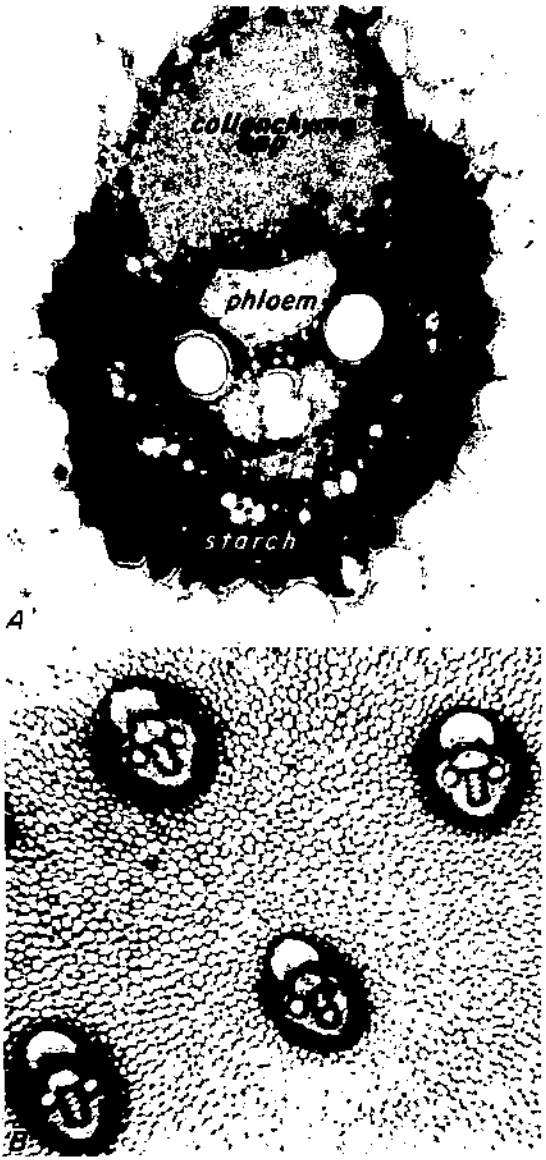


FIGURE 20.—*A*, Central bundle of growth ring with prominent starch jacket around the xylem end of bundle (hand section of fresh material). × 159. *B*, Cross section through center region of growth ring (hand section of fresh material). × 24.

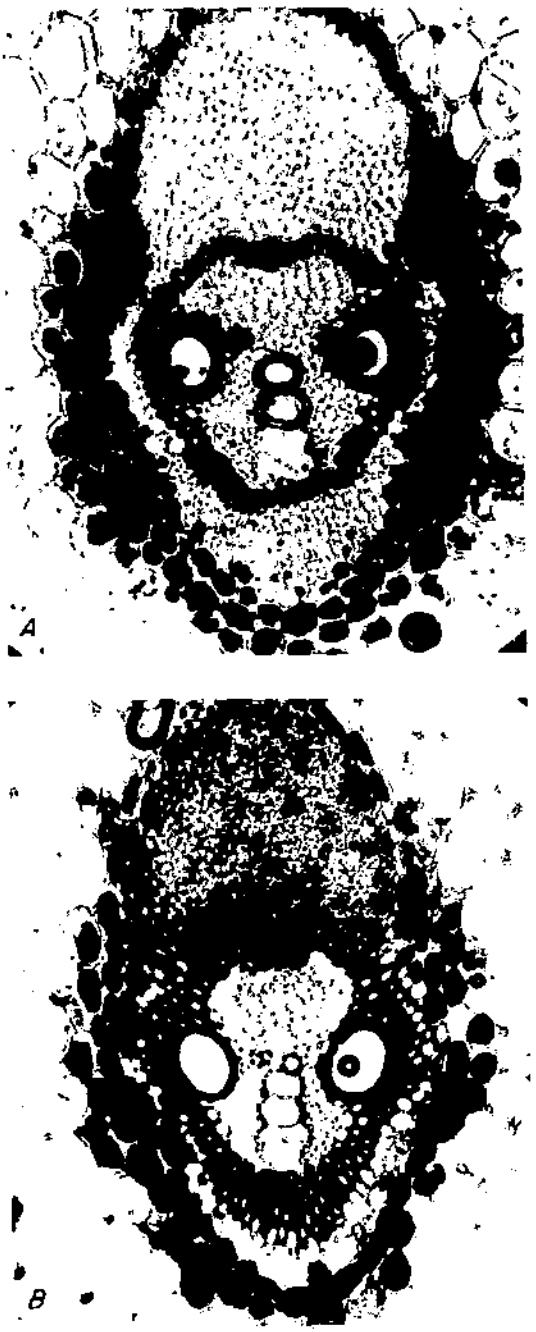


FIGURE 21.—A, Central stem bundle of growth ring, and B, central stem bundle of growth ring from old stalk. (Hand sections of fresh material.) Both ×124.

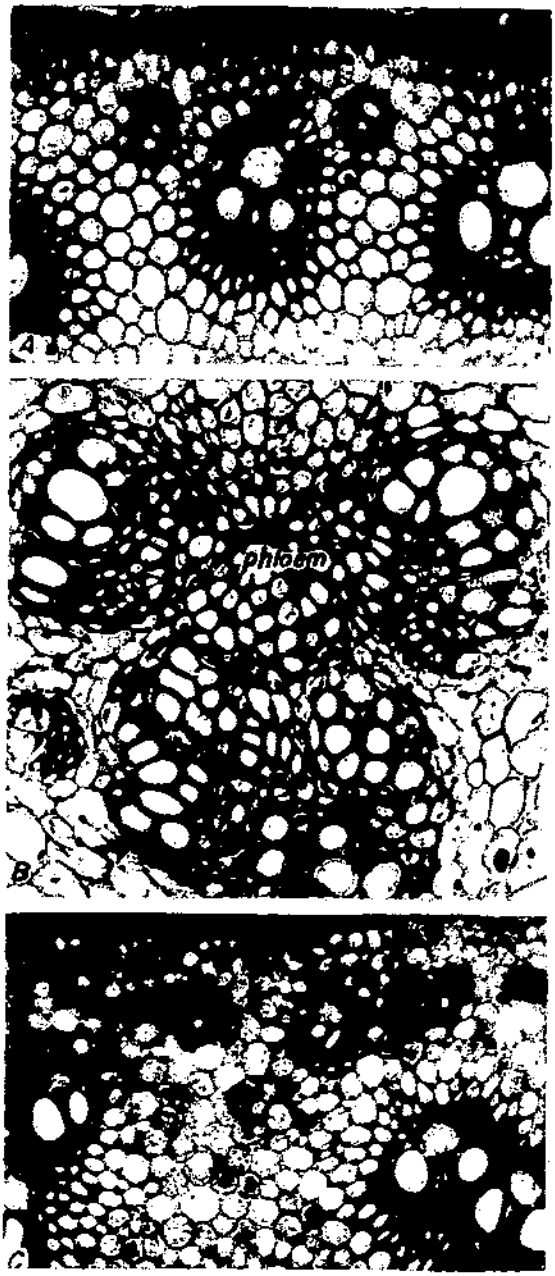


FIGURE 22.—*A*, Cross section through peripheral region of stem just above growth ring (hand section of fresh material). ×126. *B*, Compound bundle of node. ×198. *C*, Cross section of stem about 8 mm. below sheath base (hand section of fresh material). ×126.

Root Band

Certain anatomical characteristics of the growth ring region—bundle-free cortex, large collenchymatous phloem caps, and starch jackets—are also found unchanged or somewhat modified in the root band.

The outer zone of bundles shows the honeycomb appearance characteristic of the growth ring, except that the large phloem caps are strongly lignified. The outermost bundles have small phloem caps and large xylem caps. With each succeeding layer the phloem caps become larger until they greatly exceed in size the xylem caps, which eventually become reduced to one or two layers of cells. Horizontal bundles, branches of the vertical system, may be found at the very periphery of the vascular zone. Other horizontal bundles composed of short pitted elements and enclosing phloem tissue are found scattered throughout the cross section (fig. 19, *B*). They constitute the traces connecting the vascular tissue of the stem with the root primordia.

The central or near-central bundles of the upper root-band zone are like those of the growth ring. The xylem is composed of a row of elements with spiral thickenings. The two large laterally placed vessels are also of the protoxylem type. Since these two cells are not connected with a xylem bridge, the phloem and the protoxylem parenchyma form an oval mass of thin-walled tissue into which projects the row of protoxylem cells. The xylem pole of the bundle is surrounded by a broad starch jacket identical with that found in the bundles of the growth ring. In the zone below the root primordia the phloem caps are smaller (fig. 23, *A*) and strongly lignified. The starch jacket around the xylem pole has disappeared. The central bundles still lack a protoxylem lacuna, but the two metaxylem vessels have pitted secondary walls instead of spiral thickenings.

Nodal Plate

Just below the insertion of the leaf and extending about 1 cm. downward is a zone of anastomosing leaf trace bundles, the node proper.

The anatomical picture of the stem cross section, just before the bundles enter the nodal region from below, is in agreement with the anatomy of the internode in general. The bundles are more or less evenly scattered, denser near the periphery than the center, with the outermost bundles in contact with the hypodermal sclerenchyma. The central bundles are elongate-ovate with well-developed phloem and xylem caps. The metaxylem vessels are pitted and a small protoxylem lacuna is present.

Numerous small branches split off from the bundles as they enter the node. The divisions and anastomosing of these bundles produce the vascular mesh that constitutes the nodal plate.

The large central or near-central bundles of the nodal plate have changed from ovate to broad rhomboid; the phloem caps have enlarged but the xylem caps are now reduced to a single-cell layer, or have disappeared altogether. Other bundles appear irregular in shape, frequently compound (fig. 22, *B*), and anastomosing higher up into separate strands. The peripheral bundles have lost contact

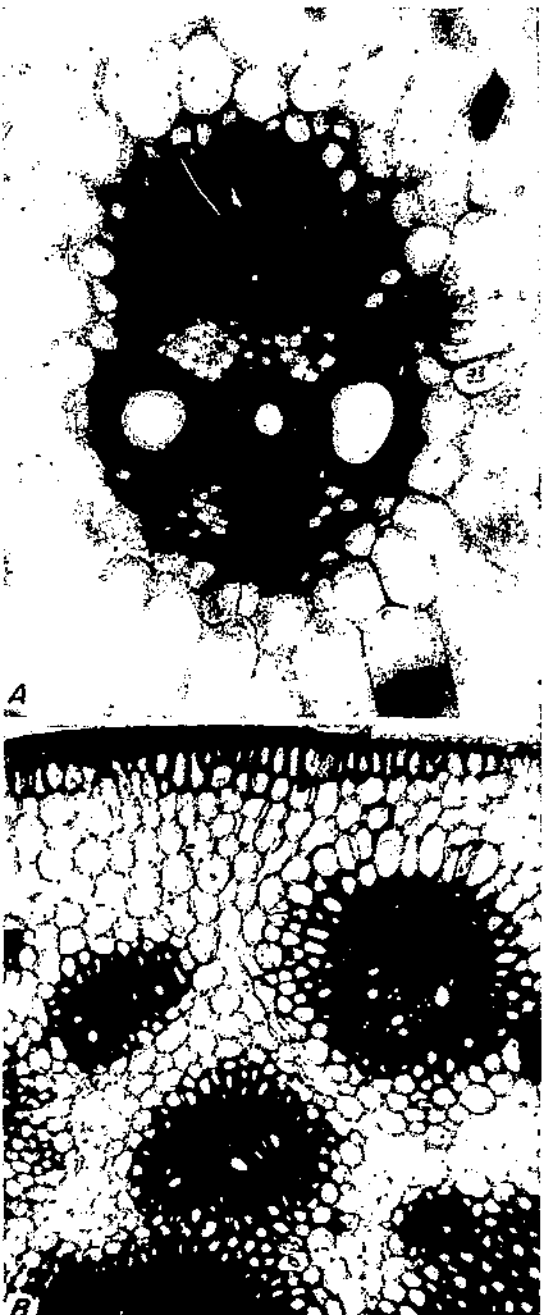


FIGURE 23.—*A*, Central bundle from basal region of root band (hand section of fresh material). ×132. *B*, Compound bundles from peripheral region of node (hand section of fresh material). × 93.

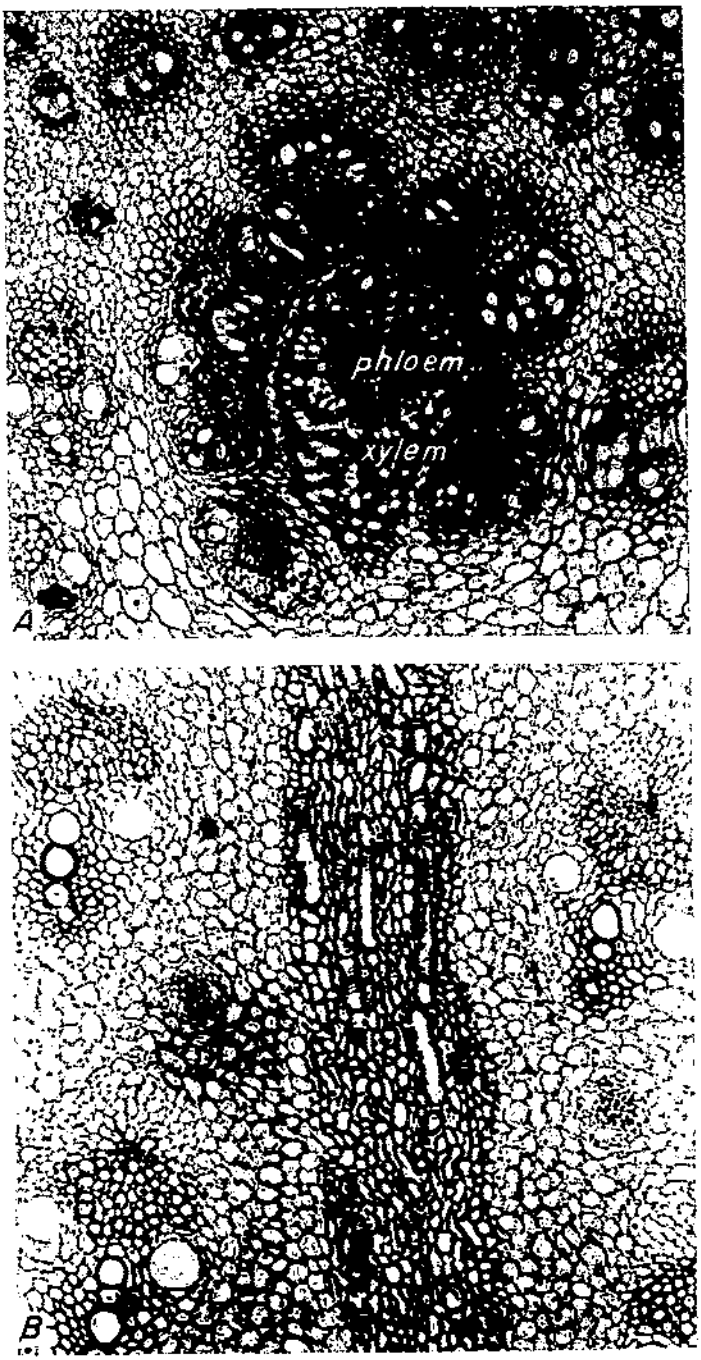


FIGURE 24.—*A*, Large lateral trace surrounded by small bundles; and *B*, part of horizontally running median trace. × 100.

with the hypodermal sclerenchyma (fig. 22, *C*) and, receding from the periphery, allow for a narrow, bundle-free, cortex. The bundles also have greatly increased in number, and frequent anastomoses indicate their intimate relationship to each other. The larger bundles, in contact with or immediately centrad to the small bundles, appear very irregular. Most of them are compound or show signs of anastomosing (fig. 23, *B*). In general, there is a great increase in bundles in the peripheral part of the stem while the center appears more parenchymatous.

Outstanding among the nodal bundles are certain large, obliquely running types that represent the median and large lateral traces (fig. 24, *A*). These large traces have amphivasal or semiamphivasal structure, with the xylem composed entirely of narrow elements with spiral secondary thickenings. The large median trace is recognized by its horizontal course (fig. 24, *B*) as well as by its structure.

Scattered among the larger bundles are numerous small traces, some running vertically, others horizontally or obliquely. They are composed of short-pitted xylem elements, enclosing some phloem in semiamphivasal, or lateral, arrangement. These small traces anastomose very frequently and change their course from the vertical to the horizontal and back again.

Just below the insertion of the leaf the peripheral bundles reenter the cortex in greatly altered form and extend thence upward into the leaf.

The course of the vascular bundles and the relationship of the leaf traces has been described in detail for corn (*5*, *12*, *13*) and sugarcane (*1*). Sorghum shows no deviation from the normal pattern. Although the median trace (fig. 24, *B*) approaches close to the center of the stem, the large lateral traces (fig. 24, *A*) bend only a few millimeters inward, a behavior that is more in agreement with Sharman's conclusion (*12*) than with Esau's (*5*), who investigated the leaf-trace relationship in corn.

ANATOMY OF THE LEAF

Sheath Base

The sheath base is composed of relatively meristematic tissue from which the sheath elongates. It is comparable to the growth ring, or intercalary zone, of the stem.

A cross section through the basal part of this region shows the vascular bundles distributed more or less evenly over the entire cross section (fig. 25, *B*). The smallest bundles are next to the outer epidermis; the largest are near-central, somewhat closer to the inner epidermis. All bundles have enormous phloem caps, but the vascular core is very small, consisting only of a few spiral elements. The larger bundles (fig. 25, *C*) are similar in structure to those of the growth ring.

In the upper part of the sheath joint, the bundles are more concentrated in the outer peripheral region of the cross section. The large bundles possess enormous phloem caps that are lignified wholly or in part (fig. 25, *C*). The vascular core is surrounded by a narrow lignified jacket as in the growth ring (fig. 21, *A*). The two metaxylem

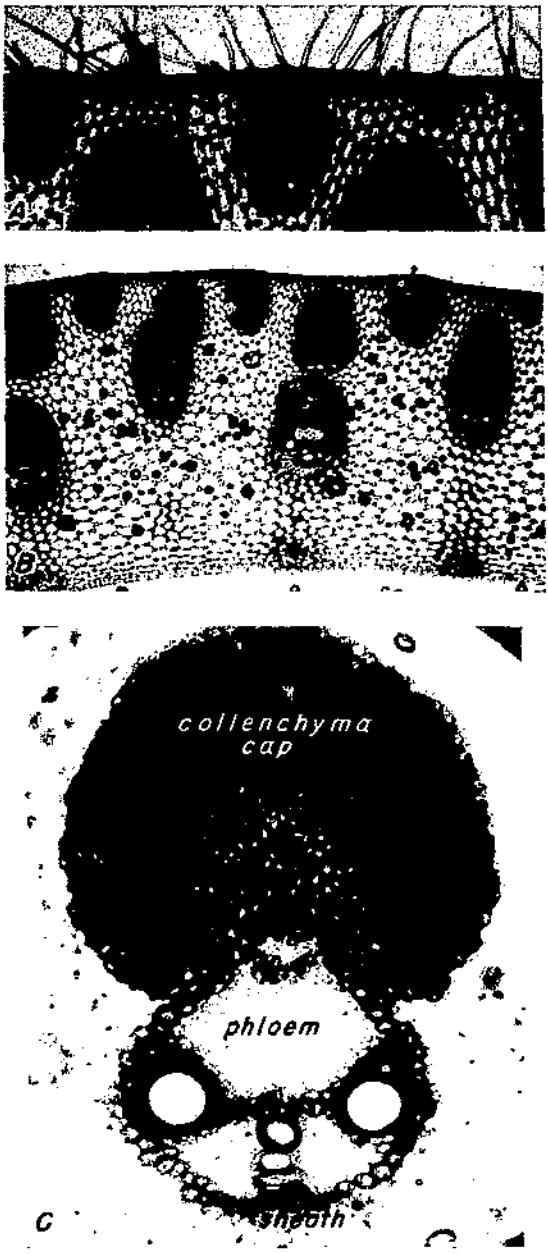


FIGURE 25.—*A*, Cross section through peripheral region of sheath base, showing hairs (hand section of fresh material). × 64. *B*, Cross section through basal region of sheath base (cross section of fresh material). × 34. *C*, Large bundle from sheath base (hand section of fresh material). × 110.

vessels are pitted and connected with one another by a narrow xylem bridge (fig. 25, *C*). A protoxylem lacuna is wanting. The phloem is especially well developed and more massive than in the bundles of the growth ring.

The dense matting of hairs (fig. 25, *A*) that delimits the sheath base externally is of subepidermal origin. The basal part of the hair is strongly lignified; the free part is of cellulose.

Leaf Sheath

The leaf sheath is traversed by vascular bundles running parallel to one another. They are joined at intervals by cross-connecting veinlets similar to those described by Moreland and Flint (*9*) for sugarcane.

A cross section of the sheath shows bundles of different ranks. In the narrow part of the sheath small and large bundles alternate, but in the broad central region an intermediate size is interpolated (fig. 26, *A*).

The smallest bundles lie close to the epidermis. Since they are formed late in ontogeny, they lack protoxylem. Their sclerenchymatous sheath is narrow at the xylem pole, massive in the phloem region, and always confluent with the hypodermal sclerenchyma.

The medium-large bundles possess protoxylem but often lack a lacuna. The bundle cap of the phloem pole is either in contact with the hypodermal sclerenchyma or separated from it by several rows of parenchyma cells (fig. 26, *A*).

The largest bundles (fig. 26, *B*) resemble in structure the central bundles of the internode except that the phloem of the sheath bundles is more massive. The sclerenchymatous bundle cap at the phloem end is in contact with the hypodermal sclerenchyma, except where the bundle occupies a near-central position. Radial sheets of chlorenchyma, about five cells wide (fig. 26, *A*) connect the xylem pole of the large bundles with small groups of thin-walled hypodermal sclerenchyma of the lower epidermis. The area between the radial sheets of chlorenchyma is filled with large empty cells. The tissue appears white and spongy in old sheaths, but there is rarely actual cell break-down as in the sheaths of sugarcane.

The transverse bundle connections are in the nature of branches that run obliquely or at right angles between the large vertical veins and effect a union between them. Structurally and ontogenetically, they are similar to the cross-connecting veinlets of the lamina, consisting of several rows of short-articulated xylem elements of the reticulate-pitted type. The bundles are formed late in ontogeny, their initials connected with the cambiumlike region of the vertical bundle system.

The outer epidermis of the sheath, in the region between the veins, consists of regular long cells alternating with groups of short cells. The epidermis overlying the veins is composed entirely of cork and silica cells. Flanking the vein area and separated from it by two rows of regular intercostal epidermal cells are single vertical files of stomates. Topographically, the vein area appears depressed (fig. 26, *A*), the intercostal area slightly raised. The inner epidermis is composed solely of long, thin-walled cells.

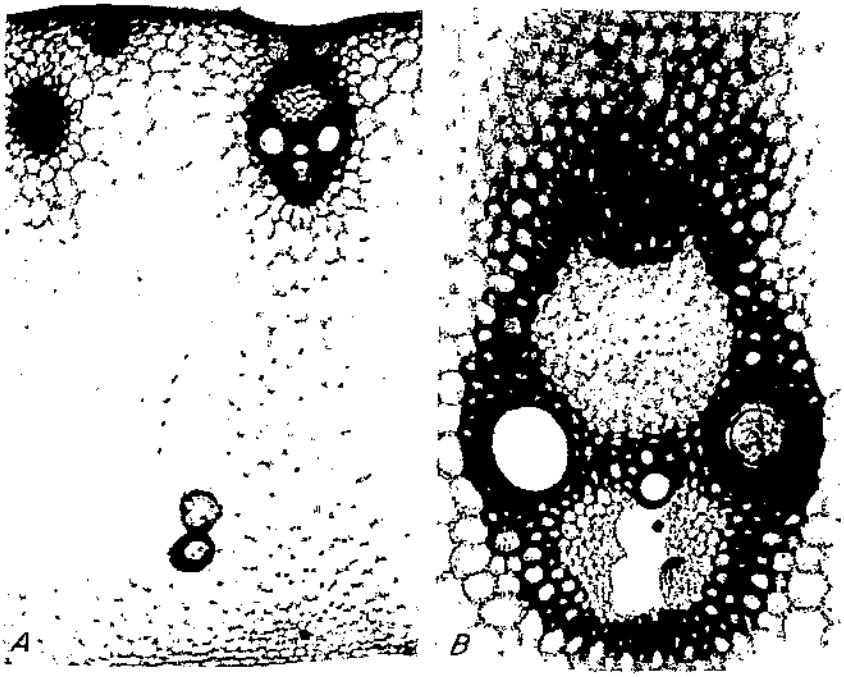


FIGURE 26.—*A*, Cross section of sheath. The large bundle is in contact with hypodermal sclerenchyma; externally this region is indicated by a shallow groove (hand section of fresh material). × 36. *B*, Large sheath bundle (hand section of fresh material). × 153.

LEAF BLADE

The leaf blade is parallel-veined like the sheath, but the cross-connecting veinlets are not so prominent as in the sheath.

There are two types of vascular bundles, small round ones in groups of 7 to 15 alternating with large oval bundles (fig. 27, *A*). The large bundles, representing the principal veins of the leaf, occupy the entire depth of the leaf cross section (fig. 27, *A*); the small round type is embedded in parenchyma in close proximity to the lower epidermis (fig. 27, *A*).

The large bundles are structurally similar to those of the leaf sheath. Each bundle is jacketed by a narrow lignified sheath, which is in continuity with the hypodermal sclerenchyma at the phloem pole, but is separated from the xylem pole by a single layer of large, thin-walled parenchyma cells. The vascular part of the bundle is like that described for the sheath.

The small bundles of the leaf blade (fig. 27, *B*) are round or slightly oval. Small and somewhat larger bundles alternate with one another. The larger type (fig. 27, *A*) occurs more central. Opposite it, but separated by five or six layers of parenchyma cells, is a small group of sclerenchyma in contact with the upper epidermis. The vascular part of the bundle consists of a few pitted xylem cells and a group of phloem cells (fig. 27, *B*). Surrounding each bundle is a jacket of large

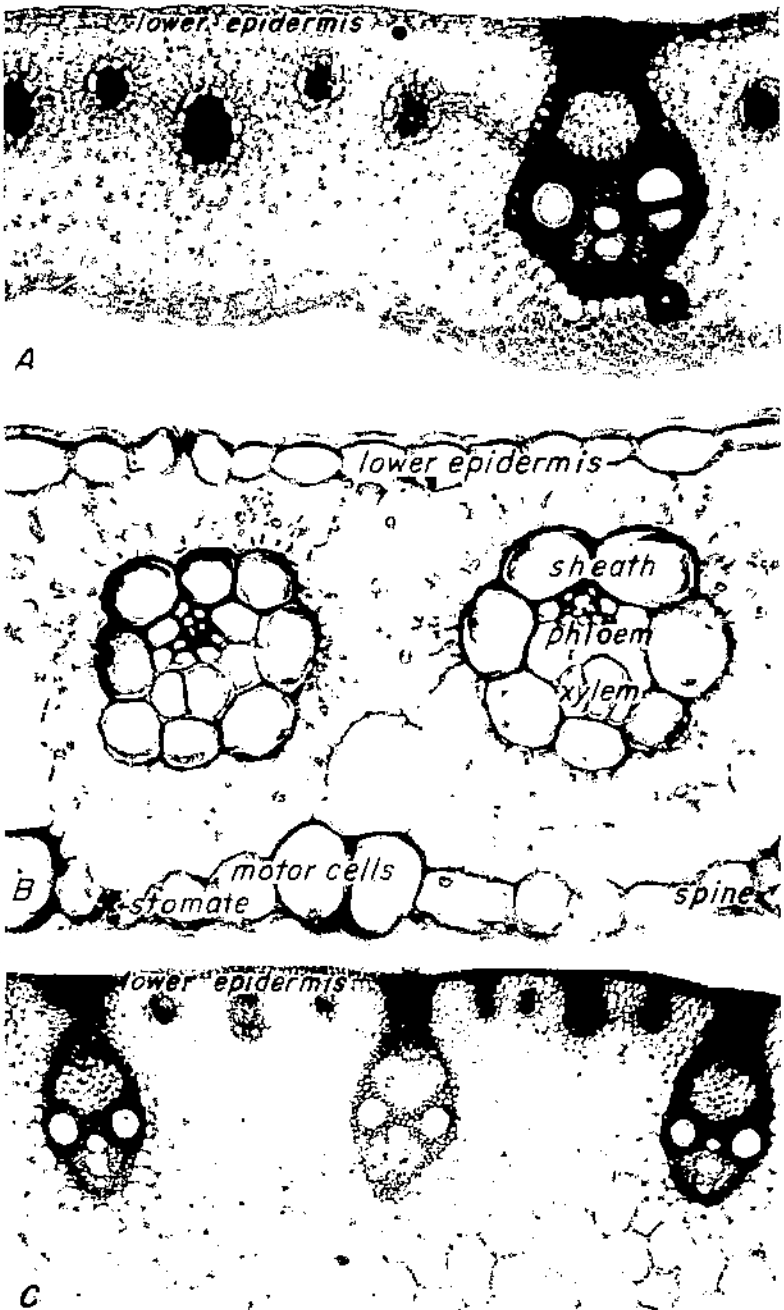


FIGURE 27.—*A*, Cross section of leaf blade (hand section of fresh material, × 60. *B*, Cross section of leaf enlarged, showing two small bundles, × 125. *C*, Partial cross section through the midrib, showing distribution of bundles (hand section of fresh material), × 60.

thick-walled chlorenchyma cells containing numerous large plastids.

All bundles are connected at frequent intervals with one another by narrow branches that run diagonally (fig. 27, *A*) or at right angles to each other. Structurally they are the same as the cross-connecting veinlets of the sheath.

The mesophyll of the leaf consists of relatively compact chlorenchyma with plastids that are smaller and more numerous than those of the chlorophyllaceous sheath surrounding the small bundles. There is no well-developed palisade layer.

The cells of the epidermis of the blade are similar to those of the stem, except that they are thinner walled and vary in the percentage distribution of the various elements. The cell patterns of the lower and the upper epidermis show a periodically recurrent design that is related to the type of cell underlying the epidermis. Except for the added presence of bulliform cells (fig. 28, *A*), there is little difference in structure between the upper and the lower leaf epidermis.

The epidermal cells that overlie the vascular bundles form several longitudinal rows, their number depending on the size of the veins. The cells are long and narrow (fig. 28, *B*) and may lie end to end in a series, but usually they abut on a cork-silica group. The center of the zone is occupied by rows of long cells alternating with rows made up of cork-silica groups only. Flanking the vein zone on either side are several rows of epidermal cells composed of long cells that lie end to end or of long cells alternating with cork-silica groups or cork cells only. Conspicuous are the vertical files of stomates occurring in single or double rows. The long cells between the rows of stomates contain small two-celled appressed hairs that take the place of the cork-silica group. Occasionally there are found short spines and two-celled hairs occurring between the long cells flanking the veins. They are of the type described for the epidermis of sugarcane (*3*). The bulliform, or motor, cells occur in single or double files (fig. 27, *B*, and fig. 28, *A*) and are not nearly so prominent as those in sugarcane.

The midrib of the blade appears crescent- or half-moon shaped in cross section. The lower surface is studded with vascular bundles (fig. 27, *C*), while the upper is underlaid with a thick band of hypodermal sclerenchyma. The mass of tissue between the bundles and the sclerenchyma is parenchymatous.

The parenchyma of the midrib of young leaves is rich in sap. Viewed from above, the tissue has a water-soaked appearance. As the leaf matures, the parenchyma becomes filled with air, giving the entire midrib a whitish appearance that contrasts strongly with the green color of the lamina. In varieties with colored midribs a pigment is found in the parenchyma underlying the upper epidermis.

The bundles of the midrib are like those of the sheath. Large and small bundles alternate (fig. 27, *C*), and all are connected with the lower epidermis by hypodermal sclerenchyma. The percentage distribution of the large bundles, however, is much greater than in the lamina, where the large bundles occur only at great intervals.

The lower epidermis of the midrib is similar to that of the lamina, except that the longitudinal files of cork-silica groups and the narrow, long cells are more numerous. This is to be expected, since all vascular bundles of the midrib abut on hypodermal sclerenchyma.

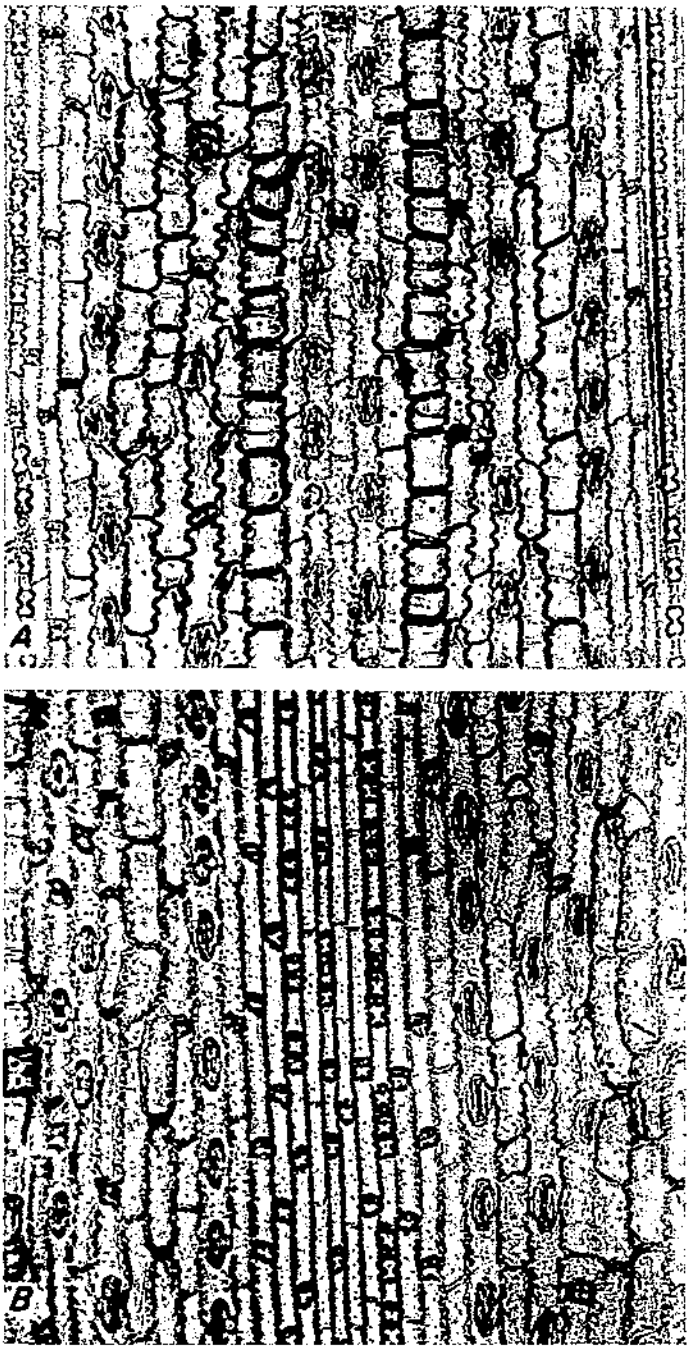


FIGURE 28.—*A*, Surface view of upper epidermis of blade; *B*, surface view of lower epidermis. Both × 170.

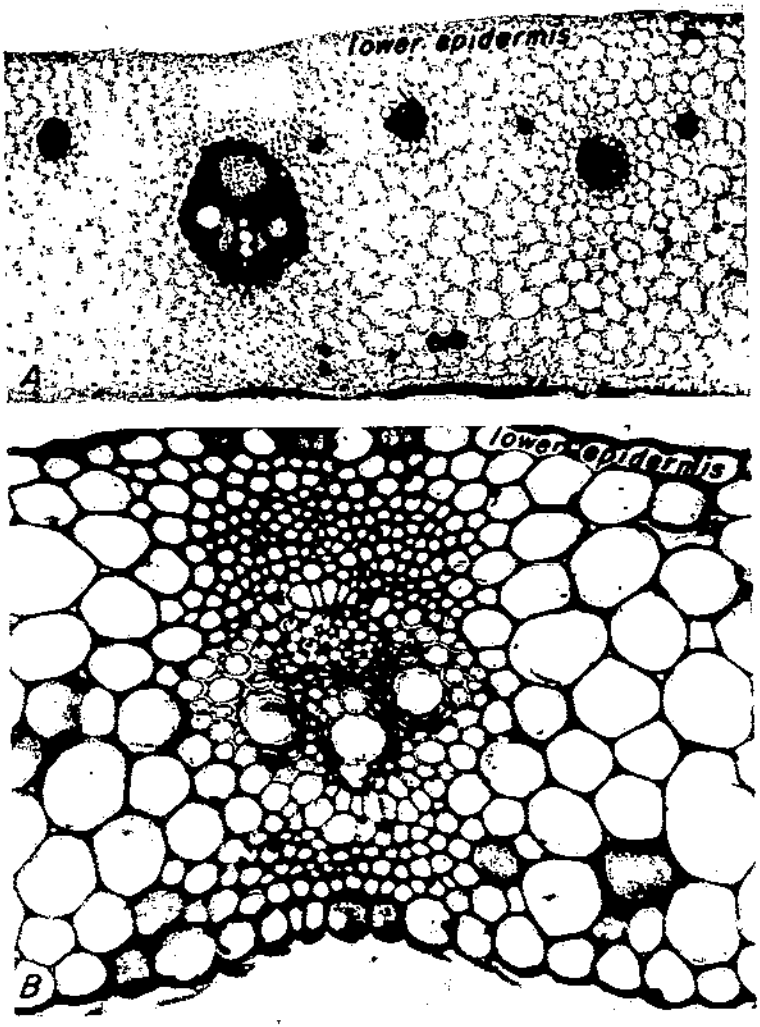


FIGURE 29.—*A*, Cross section through dewlap (hand section of fresh material). × 60. *B*, Enlarged view from marginal dewlap region, showing detailed structure of large bundle. × 240.

The upper epidermis of the midrib is made up of large long cells alternating with cork cells. There are no silica cells and no stomates. In certain varieties, many epidermal cells, especially in the central region, have grown out into large unicellular hairs. These hairs are of epidermal origin and do not become lignified.

DEWLAP

The anatomical picture of the dewlap resembles that of the lamina, but the vascular bundles bear a closer relationship to those of the sheath base.

A cross section through the dewlap (fig. 29, *A*) shows a succession of very large and very small bundles embedded in parenchyma. Several very small bundles alternate with one large bundle. The latter occupies the center of the cross section, while the small bundles have an off-central position closer to the lower than to the upper epidermis.

The large bundles are surrounded by a narrow jacket of thin-walled lignified cells (fig. 29, *B*). The phloem is capped with collenchyma that extends to the lower epidermis (fig. 29, *A*). A similar group of collenchyma is found at the xylem end of the bundle, but it is not in continuity with the sheath cells, being separated from them by one or two layers of parenchyma. The xylem is composed entirely of elements with spiral secondary thickenings. A protoxylem lacuna is wanting.

The small bundles of the dewlap contain a few narrow protoxylem elements and some phloem. They are jacketed with a broad layer of collenchyma that is especially prominent on the phloem end of the bundle.

Both epidermal surfaces are clothed with hairs like those found on the sheath joint. The cells of the epidermis are irregular and thin-walled; stomates are present.

ANATOMY OF THE ROOT

Large Laterals

A cross section through a large lateral root shows a siphonostele with a central pith and broad cortex (fig. 30, *A*). The cortex is composed of 12 layers of cells. The peripheral layer forms an exodermis that has prominent wall thickenings involving the outer tangential wall. Sorghum differs in this respect from sugarcane, whose root exodermis has U-shaped thickenings involving the inner tangential and radial walls. Externally the exodermis abuts the usual type of thin-walled root epidermis, in which many of the cells have elongated to form root hairs. The bulk of the cortex is composed of large regular cells with squarish intercellular spaces between them. The cells of the two most centrad layers, closest to the endodermis, are brick-shaped, narrow, and very regular.

The cells of the endodermis are very uniform, and there are no intercellular spaces between them. At maturity the cells have the U-shaped type of thickening in which the inner tangential wall and part of the adjacent radial walls are reinforced (fig. 30, *C*). The tangential wall thickenings are topped with silica knobs of irregular contour (fig. 31, *A*). Silica excretions similar to these but more regular in shape have been described by the author for the endodermis of sugarcane (*1*, *pl. 23*, *D*).

The vascular ring is relatively narrow (fig. 30, *A*) and is limited on the inside by a sclerenchymatous jacket that follows the undulating contour of the inwardly projecting metaxylem vessels. The number of protoxylem points is variable, depending on the size of the root and the number of metaxylem elements. There are commonly three protoxylem strands and an equal number of phloem groups to each metaxylem vessel. Both protoxylem and phloem abut the pericycle. The latter consists of a single layer of cells that become thick-walled

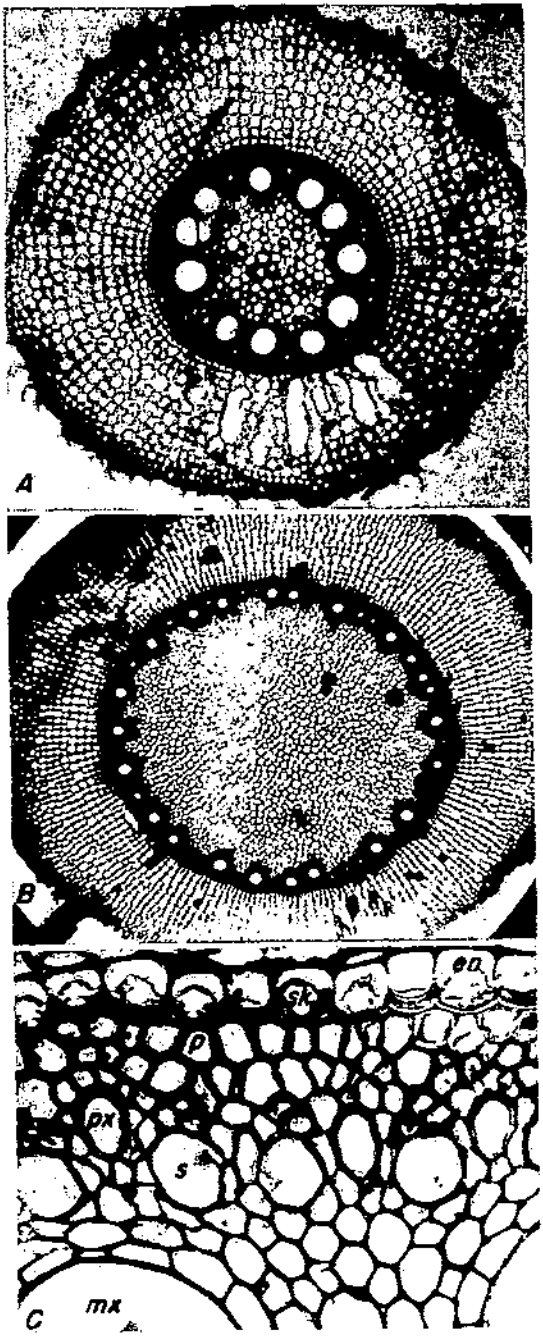


FIGURE 30.—*A*, Cross section through large lateral root (hand section of fresh material). × 33. *B*, Cross section through buttress root (hand section of fresh material). × 19. *C*, Partial enlargement of *A*, to show details in structure of endodermis and vascular tissue: *en*, Endodermis; *mx*, metaxylem vessel; *px*, protoxylem; *s*, sieve tube; *p*, pericycle; *sk*, silica knob. × 467.

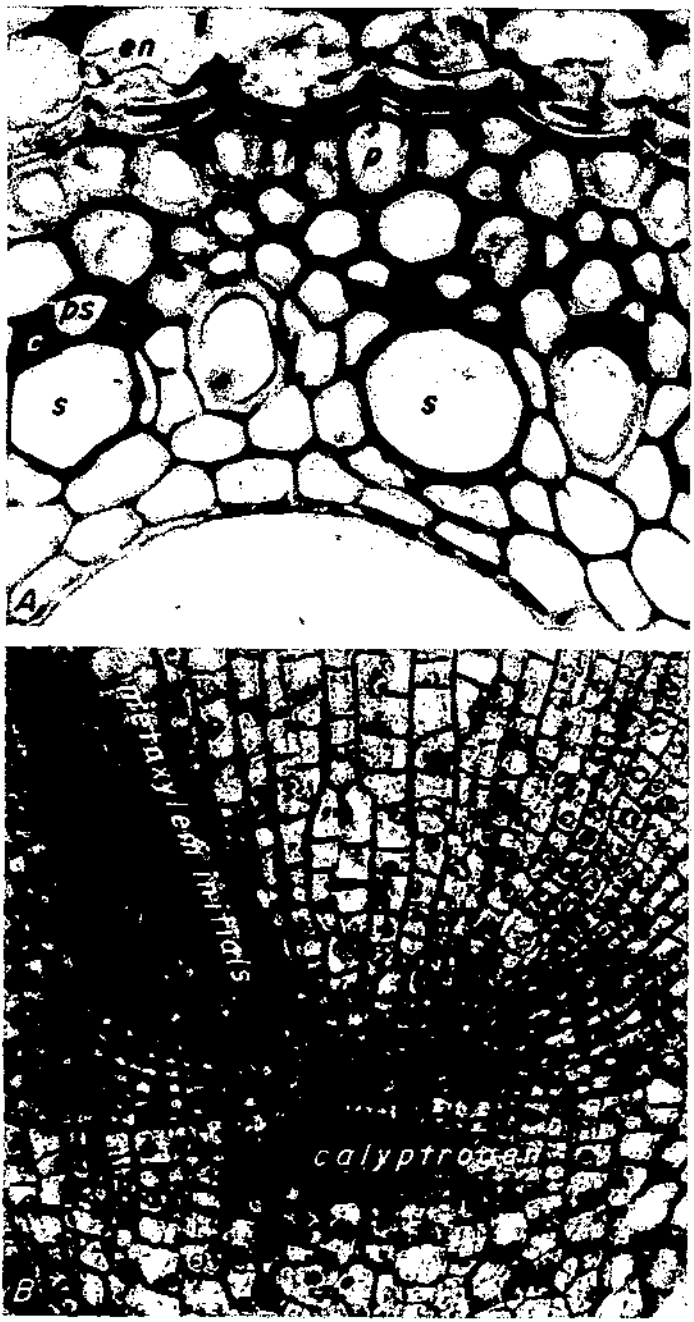


FIGURE 31.—*A*, Cross section through vascular tissue of large lateral root; *en*, Endodermis with silica knobs; *ps*, protophloem sieve tube; *s*, large metaphloem sieve tube; *c*, companion cell; *p*, pericycle. × 1,000. *B*, Longitudinal section through basal region of root tip showing apical meristem. × 425.

fairly early in ontogeny. In localized regions the pericycle is two cells thick.

The phloem groups are very uniform, consisting of five or six elements (fig. 31, *A*). There is a single protophloem sieve tube (fig. 32, *B*, and fig. 31, *A*) flanked by two companion cells of similar size (fig. 31, *A*). Centrad to this triad of cells is a very large sieve tube with a bore of 20μ to 22μ, and above it are one or two sieve tubes of smaller size.

The cells surrounding the xylem and phloem thicken and lignify with age, so that in old roots the entire vascular ring is composed of thick-walled lignified tissue in which only the phloem cells remain thin-walled and nonlignified.

The pith is composed of very regular tissue; the cells are roundish with intercellular spaces between them. The walls of the pith cells of older roots thicken, and lignification, which is at first spotty, overtakes most of the tissue.

In the development of the vascular tissue the large metaxylem elements are initiated before the protoxylem (fig. 31, *B*, and 32, *A*), but the latter mature earlier. The protophloem sieve tubes (fig. 32, *B*) mature ahead of the protoxylem, in agreement with tissue differentiation in other plants.

Buttress Roots

The structure of the underground part of the buttress roots is identical with that of the large laterals. The aerial section, however, is different. Quantitative differences consist in a greater root diameter, a larger number of metaxylem vessels, and concomitantly a greater number of protoxylem points and phloem groups (fig. 30, *B*) and a broader cortex. The groups of phloem contain a larger number of cells than the large laterals and the arrangement of the phloem cells is less symmetrical. Qualitatively, the aerial part of the buttress root differs from the underground part by having a strong epidermis in which the outer tangential wall and the radial walls are reinforced. The endodermis, while similar, lacks silica knobs. There is no distinct exodermis with tangentially thickened walls, but a modified peripheral cortex consisting of three or four layers of small thick-walled cells.

Small Laterals

The filiform laterals of the second and third order are whitish and of approximately equal diameter.

The anatomical structure is simple; each rootlet consists of a broad cortex (fig. 33, *A*) surrounding a miniature stele with the usual type of tissue arrangement. This structure differs chiefly from that of the large roots in lacking an exodermis and possessing only one or two metaxylem vessels.

The central core is exceedingly small (fig. 33, *B*), having a bore somewhat smaller than that of a single metaxylem vessel of a large lateral. The endodermal cells are of the type described for the large root, except that the silica knobs are often wanting, at best, inconspicuous. There is a unilayered pericycle consisting of alternating sectors of thick-walled and thin-walled cells. The pericyclic cells opposite the phloem groups are usually thin-walled (fig. 33, *B*). The

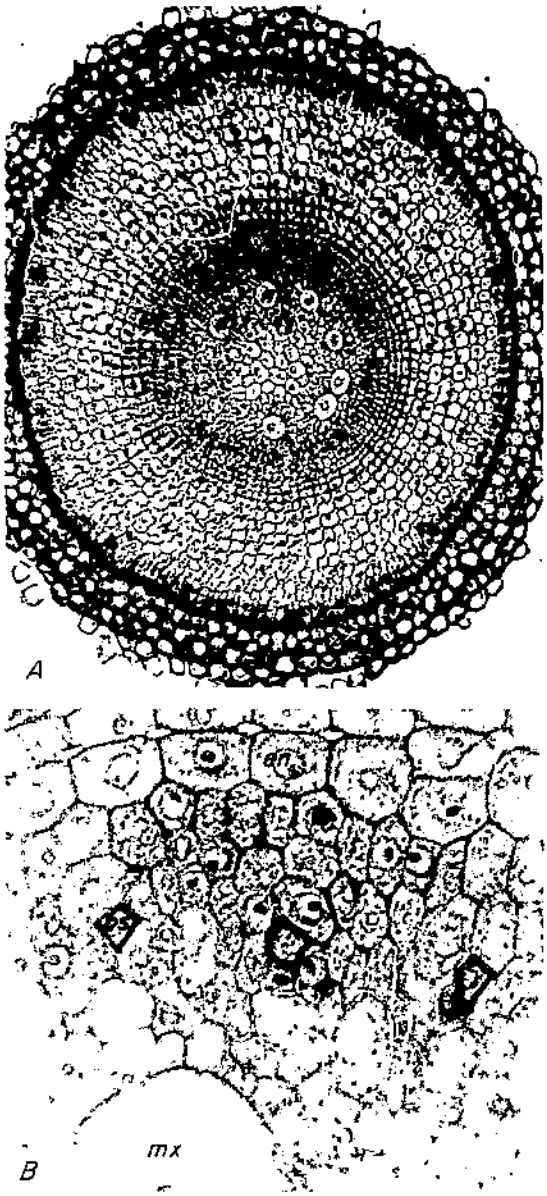


FIGURE 32.—*A*, Transverse section of root tip taken 150μ from the apical calyptrogen meristem: *r*, Root cap region; *mx*, metaxylem vessel initials. × 149. *B*, Transverse section through root tip taken 150μ from the apical calyptrogen meristem: *en*, Endodermis; *ps*, protophloem sieve tube; *mx*, metaxylem vessel. × 744.

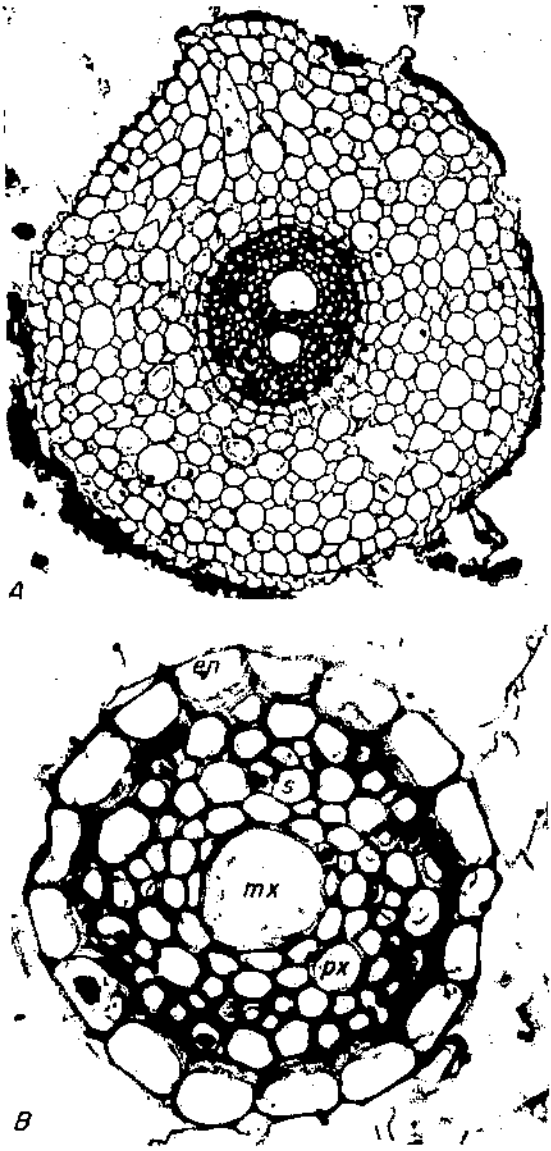


FIGURE 33.—*A*, Cross section of small lateral rootlet. × 184. *B*, Cross section of central cylinder greatly enlarged: *en*, Endodermis; *mx*, metaxylem vessel; *p*, pericycle; *px*, protoxylem; *s*, sieve tube. × 799.

smallest roots with only a single central metaxylem vessel usually have four protoxylem points and an equal number of phloem groups. In steles with two metaxylem vessels, the number is slightly larger.

The cortex of many rootlets eventually breaks down and becomes disorganized. Such rootlets have a brownish exterior. Their functional capacity as organs of conduction is probably unimpaired, however, as the vascular tissue, protected by the thick-walled endodermis, appears normal (fig. 33, *B*).

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