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## START





# Anatomy and Morphology of the Vegetative Organs of Sorghum Vulgare ${ }^{1}$ 

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## PREVIOUS INVESTIGATIONS

Sorghum Sorghum vulture Pars.) 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, ami botameal description of varieties is extensive. it hats recently been reviewed in detail by Vimull, 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 chameters are used, but in sorghum taxonomy reliance las been placed cheerly on the structure of inflorescence, spikelet, and seed. To be sure, sorghum shows a relative paucity of such characters as form the basis for sugareme 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 speeffeatly with the minute morphology and anatomy of sorghum except for ar paper on the developmental anatomy and homologies in the young seed ting (11), but its struebre

[^0]is indirectly known through papers on the anatomy of cors ( $5,6,12$, 13) and the morphology and anatomy of sugarcane (1, 2, 3, 4, 7). Important differences do exist, however, as shown in tible 1, in which some of the morphological and anatomical chiracters of the two crops are contrasted.
Table 1.-Some contrasting characters in the morpholngy and anatomy of sorghum and sugarcane

| Character | Sorghum (vulgare) | Sugarcane |
| :---: | :---: | :---: |
| Morphological |  |  |
|  | A shade of green | Green, striped. |
| Wax bend | Part of genaral bloom; rarely distinct. | Usinaliy in the form of a distinct band. |
| Butd | Often poorly developed. | Usually nrominent. |
| Buds | Often small end undeveloped. | Always well developed. |
| Hair groups on prophyilum. <br> kows of root primordia- | Few and similar | Esually numerous and varying. |
|  | Usially one | Amost always several rows. |
| Hairs on root band.-.-Hairs on internorle. |  | Almost alwnys wanting. |
|  | Alwas wantin | Present in a few variclies. |
| Persistence of leaves...- | Stems never self-eleaniug- | Sterns usually self-clean- |
| Hairs on lamina.-.-.--- | Never prese | Present in many wild canes. |
| Hairs on midrib......-. | Prominent in many varicties. | Always wanting. |
| Hairs on sheath. --...-- | Alway wanting | Prominent in many variotiss. |
| Hairs on sheath base.-.- | Always present, though short. | Oftern wanting; when present, usuall long. |
| Cilia on sheath margin. Typical ampicles. Ligular pattern | Never presen | Ofien present. <br> Often very promineut |
|  | dy shallow crescent. | Often very prominert. Crescentiform, areuate, |
|  | halow crescent. | or deltoid. |
| Ligular fringe | Sometimes taller than ligule. | Usually math shorter than ligule. |
| Dorsal hairs on ligule.-- | Dense, free, or only sligitly adnate. | Often sparse and partly or completrly adnate. |
| Buttress roots...-..---- | Often inserted very high ( 4 feet above). | Never inserted high; usually wanting. |
| Anatomical |  |  |
| Bundies of inmina | Inner sclerenchyma sheath wanting. | Tnner sclerenchyma sheath wedl developed. |
| Stoma |  | Scarce, often wantieg. |
| Silica cells of stem epiclermis. | dways pre |  |
| Starch in internode.---- | Abundant in many varieties. | Wanting or very sparse. |
| Silice knobs on root endodermis. | Massive and irregular | Small and uniform. |
| Sclerotic layer outside root endodernis. | nting | Well develope |
| Exodermis of root. | Outer tangential wall thickened. | tnner tangentia! wali thickened. |

In the present contribution, the morphology and anntomy 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 com and sugareare.

## 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 varictics.

All characters were studied and illustrations prepared from fresh material. On the whole, the technicue employed by the writer in the morphological studies of sugareme varieties $(3,4)$ was used successfully in the present investigations. As in sugareane, some characters show to best advantage in young material, since retrogressive changes or mere injuries associated with aging or due to disenses make evaluation difficult. Dost characters are studied more advantageously in older, more mathre material, however. Root band pulescence is frequently limited to the basat part of the statk, wherens typienl wax bands may be found only in the upper internodes, sinee subsequent all-over wax deposits erase the boundary between general bloom and wax band. The stem epidermis is not so casily stripped as in sugarcane, and in certain varicties surface hand sections must be employed even though they are not very satisfactory. The usual technique of fixing and staining was used in the amatomeal studies but was often abmatoner in favor of hand sertions of fresh material. Thin hand sections, especeially of hari tissues, are equal to amb often superior to microtome preparations. If properly stained, they show better tissue differentiation in photographe than could be obtained otherwise. For that reason, many of the illustrations in this bulletin sere prepared by this method.

## GROSS MORPIOLOGY

Sorghum, a member of the tribe Andropogonear, family Graminene, is a berbareous amual. The jointed cylimdrime stems, or culms, vary in height from 2 to to fret. They are solid, bat the central part of en beromes pithy and fistular. Both suckers and side branches are produced (fig. 1). The branches appear only alter the main strm has beaded out, and their order of appemanee is hasipetal. with the upper bad producing the first branch. The side hramehes are smatler than the main stalk and they mature much later. The number of surkers or tillers depends on dimate spacinge, and variwal tendener in the development of crown buds (if).

The Teuves are two-maked as in other grasses, altematine on opposite sides, and appearing approximately in a phan' The ramber of Jraves at maturity varies with the variety, from 7 to 2s. Fath leaf eonsists of sheath and blade. The blacke is linear lanecolate, long and flat. It is separated from the shemth ly the sperialized regions of the blade joint adrwaps and ligule. The fatere is a membranateons appondage that closely invests the culm and acts ans a


Figete 1.- Thabit sketh of sparec-kenfed somgham with side branthes and amall sucker shoot. Internodes fonger than sethendiog 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 semitail root that g.ows verticully downward, giving of laterals throughout its length. It may function during the entire life of the plant but ceases to be of


Figere 2.- A, Root crown of sorghan phant with three whorls of advenitious roots in varions stages of develomment. $B$, Baze of romes statk with adventitious roots in early stage of clevelophent. Part of sheatio in upper internode cut away to expoec growth ring and root band wibh rooi primordia. C, lasal internode with arljacent nodal regions. Root band has two to three rows of root primordia; bud furrow well developed.
importane after the permanent root system legins to function. The permanent roots are adventitious and develop in succession from the basal nodes near gromed level (fig. 2, $A$ and $B$ ). The whorls of adventitious roots in their entirety constitute the root crown. All laterals, especinally those near the surface of the ground, are mach branched, interlacing the soil in all diredtions. Their color is white or redidish brom, depending on agra and stage of devolopment. Many sorghum varictios derelop butterss roots (fig. 3) as high as 4 fret above ground. The buttress roots are considerably thicker than the normal roots and usually a deep green. On entering the soit, they behave as ordinary roots and decrense in size to the diameter of the main laterals (fig. 3 ).

 romes.

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 fect. Miller ( $S$ ) states that the roots are more fibrous than those of corn and may form twiec as many laterals at any stage of their dovelopment, making the sorghum plant markedy drought-resistant.

The inflorescence, or "hrath," is, with few exeeptions (broomeorn), a somewhat compact or open panicle. The hemb is ussally frect (fig. 1),
but in certair groups it is inclined or pendent (fig. 4). The main axis is angular, varicusly furrowed, and usually hairy at the nodes. The side branches appenr to be in whorls, one above the other. Each lateral may branch repeatedly. The final branches bear one or several paired spikelets, which are ellipiteal, 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 elefted at the apex from which an awn arises. The palea may be absent; when present it is small and


Furure t. - Ifabit sketeh of sorghum variety with perdent or inserted manicle.
thin. There are two brond, hairy lodicules, three stamens, and two plumose stigmas.

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

## MORPHOLOGY OF TIE STALK

## Internoine

The height of the stalk, or culm, is determined by the size and number of internotes composing it (tuble 2). The double dwarf milos have rehatively fer sad short intermodes (fig. $5, B$ ), while in the tall Whiopian forms (fig. 5, A) as many as 25 internodes may diferentiate before the advent of flowering.

The internoles are longest and wost uniform in the midde of the stalk and shortest at the base, but the deminal internode that bears the inflorescence is the lonest of all (table 5 ). The form is eylindric, bobbin-shapet, or conoidat; the cross-sectional area, round or oval. The bobbin-shaped intemodes are usualy associated with swollan nodes, a feature of many thin-stemmed varicties. In the conondal internode there is an shep constiation below the shenth base and a gradual inerease in diameter basipotally. It is a common type among firick-stemmed varieties with swollen nodes.

In the milo strains ( 10 ), the internodes become progressively longer from the ground up. The mimoth forms have one short internote betwen 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 pedmele.

The surfuce of the internode has a heavy conting of wax that often completely masks the green stem color. In the roung internodes of many varioties mad in the oder nodes of a few; the was dhposit is concontated bedow the sheath hase, forming wax bands like those found in many sugarenne sameties.

On the side next the leaf, the internode is furrowed, the position of the farrow altemating at each node. The furrow is a marrow depression in the internote extrading iom the bud upward (fig. $2,(\prime)$. In some varieties the bud furow is altogether wanting; in others, it extends only part way up the intertorde. Oftem, hat furrows are observed only in hasal internodes but may appear sporadicatly in others. Fatse bud furrows are depressions in the stalk not in line with the bud. Their developmest is probably related to pressure difterenses daring active groweth.

The texture of the flesh is fem and juicy or dry and pithy. In varicties with firn flesh a freshly cut section is gryyish or olive green. In some variedis the conter beromes white and pithy and in many Elhopian and some Ladian varieties the entire cross section, except the narrow outer cortex. takes on a cotony-white apparance.

 $h$, mature donble dwar! miles.

Table 2.-Relative length in centimeters of internodes and subtending sheaths of some sorghum varieties ${ }^{1}$


M, N. Meridian (Mlss) number. Still actively growing.

3 Infloresence axis not included in averaying length of internodes.
Sheath subtending inforescence axis not inchoded in averaging jongth of sheaths.

There is a slight correlation between color and texture of the fiesh and starch and sugar content of the varicty, 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 interuode | Starch 1 |  | Sucrose ${ }^{2}$ |
| :---: | :---: | :---: | :---: | :---: |
|  |  | Jacket | Diffuse |  |
|  |  |  |  | Percent |
| M. N. 620-- | Gray graen; solid. | $+$ | $+$ | 30.79 |
| M. N. ${ }^{\text {N. }} 6885$ | -.do. | +- | $+\cdots-$ | 4. 58 |
| M. N. 698 | do | + | $\pm$ | 6. 84 |
| M. N. 611. | Gray green, with small white | $+$ | - | 8. 34 |
| M. N. 623 | center. | + - |  | 6. 17 |
| M. N. 624 | do. | $+$ | - | 10. 98 |
| M. N. 672 | do | +- |  | 3. 07 |
| M. N. 673- |  | $+$ |  | 4. 67 |
| M. N. 679 -. | 4\% of stem cross section white-..--- | $+$ | + - - | 3. 00 |
| M. N. 694 <br> M. ㄷ. 626 | -do... <br> $2 /$ of stem cross stetion white. | $\pm+$ |  | 4. 75 5.85 5.8 |
| M. N .626 | $3 /$ of stem cross section white. Flesh white, spongy, and fisthar.- | $\pm+$ | $+\stackrel{+}{\square}$ | \%. 8.71 |

 Starch scarce; $+--=$ starih yery searce; $-=$ no sthrch
 viston of Sugur Plant Investigatlons.

## Node

The node is either flush wich the internode or somewhat thiekened. Ontogenetically, it is limited to the region just below the insertion of the leaf, but taxonomicaly it inclueles growth ring and root band.

## GROVTH RING

The growth ring is a partially differentiated region that retains its cell growth potentialities. Externaily it appears as n 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 actirity of the cells of this iegion that the stalk straightens itself from the bent position. There are no conspicuous varietal diferences as regards height and contour of growth ring; it has no taxonomic value.

## HOOT BAND

The root band is interpolated between sheath base and growth ring. It contgins, besides the bud, one or several rows of root primordin. 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 pubeseent. The hairs are usually limited to the region below the root primordin along the entire circumference of the root band or along certain sectors of it. Oceasionally the hairs are confined
to the zone flanking the bud. In some forms the entire root band, ineluding the root primordia, is covered with hair.

The root bands are usunlly cylinderal or tamescont-obconoidal. The root primordia are disposed in a single concentrie ring, but in many Ethopian sorchums the lower notes contain wo, occasionally three, rings (fig. 2, ©).

The root primordin of the basal internodes ate large and swollen and usually grow out into buttress roots, which, upon entering the soil, estabish a firm support for the stem. In some varietios the butiress roots develop at a considerable height above ground (fig. 3), but they cease prowing after ataining a fragth of several inches and nover enter the soil. If the root bands are very marow, the root primordia are disposed centrally, but in all root bands they are close to the growth ring. Root primordin may rail to develop in the upper part of the stem; at best, they are inconspicuous.

## BU

Every node is normally gemmiferous, bearing a single bud. In some varictios the best developer buads are foum in the basal internodes, becoming proderessively smaller and njpressed higher up the culm. Other forms (AL. N. G90) have a well-developed but on each node except the apimal ones. Still others nee chameterized by having only one or two well-developed buds on anv given stalk. In mature statiks in a dense planting the basal cuim shentis may wither and the buds of the nodes thus asposed often also dry up. This bohavior is unlike that ohserved in surarenne, in which the culms are nommally sclf-cleaning and exposure does not affeet the life of the buds.

The buds nt ground lovel may develop as suekers, whilo tho uppermost buds often songate to form side branches. Both suckers and side branches develop heads that mature much later than the mairn head.

A bud primordium is initinted at the base of ade internorle very carly in ontogeny, as demonstrated by Shaman (12) for the corn plant. As the internode dongetes, tho foted retains the hasal position. It is thus always associated with the lear athove and not with the leaf in whose axil it ocen's.

The buds are inserted in the tissue of the root band direetly above the leaf sene or some distance above, sometimes as high as the midelle of the root band. The height of insertion slows variation within culm limits, but on the whole it is a feature chmacteristie of be vorpely.

The outer covaring of the buds is a prophyllum. In its entirety,
 hood with the front side composed of two asymmetrical overmpping halves and the back side monere. If the bud develops into a side branch, the prophyllum dementos and splits and the two sides form the first leaves of the brenelh.

Disregreding the numerous aberrant forms (fig. 6), two general types of buds are distinguishoble-the sorghum and the sugareane.

Tho sorgham type, characteristic of the sorgos and milos, somewhat resembles an furowhend in colife. 'The lower part has a pronouncerl (enshionlike extension that menches from the base ol the prophyllam to the leaf scar (fig. $\overline{7}, A$ ). The buds are wedl developed, large or medium latge, and symmotrical.


Focme 6. - A, Prophyllum of bud of indisibuct "erawfish" patera-right secondary wing very harge, root hand hairy; $h$, aberant type with prominemt secondiry wings.


Fiocre 7.-A, fomghum type of bud-obeonoidal root band with une row of root primordin; $B$, sugarcane type of bud with "crossing-over" of sides in near-central position.

The antcrior, or front side, of the prophyllum is clongate-deltoid; wing insertion basal, with or without prominent auriculur 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 rasal appondage of the overlying margin is


Figene 8.-A, Intermediate sorghum type of bud winh crossing-over position near central. $\times 6 . \quad B$, Sugarcame $t y p e$ of bud with large overiving site, crossingover position apical. $\times 10$. $C$, rypieal sorghum type of bul with hatr groups 12 and 4 well developed. $\times 6$. $D$, Bud with large overlying side and one prominent secondary wing. $\times 6$.
never conspicuous, as in sugarcaze, 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. $\times 3$. $B$, Prophyllum showing central crossing-over of overlying side. $\times 6$. $C$, Overlying side covering entire basal part of bud. $\times 12$. $D$, Prophyllum with two prominent secondary wings. $\times 6$.


Ficure: 10.- Diagrammatic drawing of prophyllum of sugarcane repheated inree liates, showing location of hatr grouph (A) on sides, (B) on wing, and (C) on junchare between sides and wing. (leegend contimed 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 prophylium. 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.
(b) 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 unper 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.
(3I) A group of long, white, downward-poiating 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 mev or may not protruse above the biud.
(1S) Strip of long white haire 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 sriall groups.
(20) Short, brown hairs between the veins.
(23) Short, brown hairs on tip, oflen masked by hairs of group 10.
(20̄) Long, white hairs beiween the veins.

## Hoir groups on anterior uing (fig. 10, B)

(3) Long, white hairs on base of wing.
(d) Lons, white oblique or appresed lashes on edge of wing, limited to bnsal 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 pasterior wing (fig. 10, B).
(14) Long, appressed, white hairs on surface of wing; rarely found in Saccharam offinarum.
(21) Short, brown hairs on surface of wing.
(29) Long, white hairs on base of wing. Groups 4 atd 15 shared with anterior of wing.'

Hair groups on anterior juncture (fig. 10, 9
(7) Groups of shori, lrown, or lone, white hairs above central germ pore.
(8) Long hairs appressed in regard to the wing or projecting above the wing.
(1) Long, wavy, while, appressed or protruding hairs on juncture of wing just bencath the wing tip.
(10) 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 hetween groups 19 and 10. Group 26 is shared with anterior juncture.

The pubescence of the prophyllum is prominent or inconspicuous. There is never the wealth of individual hair groups found in sugarenne, 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 sugareane (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 continuntion of the hanirs of the root band. 'Ther anterior side of the prophyllum shows an all-over pubescence of wing and sides. No distinct lant groups are recognizable.

The basal bud cushion that charncterizes 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 alvays paler than the adjacent root-band tissue. The swelling is thickest near the insertion of the prophyll, whence it gradunlly tapers in the direction of the leaf sens. If the bud is inserted very low, the cushion is inronspicuous but seldom actually wanting.

The sugarcane type of bud (fig. $7, B$ ) is found in many Ethiopian varieties. In its typienl form it is similar to that of sugareane except for the paucity of bair groups. The prophyllam is usually delteid, 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 alrendy described for the sorghum type of bud is a very common fature, even in prophylls where the overlapping half is very large (fig. $9, C$ ). The pubersenee is sparse.

A fature that is conspicuous in the sugareane type of bad, but not entirely absent from the sorghtim type, is the formation of seondary 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. S, D), giving the bud an asymmetrical appearance. In plump buds with high wing insertion, the addition of secondary wings may produce the "erawfish" 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. Pfump buds with prominent basal auricular set-offs of the wing, but lacking secomenty 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 specinlized rerions, the ligule, and the dewhes.

The leaves vary in number from 7 to 25 and are armaned alternately with a divergence of $180^{\circ}$. Early varicties 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

[^1]leaved, those with 11 to 13 as midleafy, and those with 14 or more as lealy (14).

## Leaf Blade

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

There is little varintion in the lengtin 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 blate varies between 5 and 13 cm . Most bades 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-celged or serrate, but the margins of young leaves are always seabrous.

The color of the blade is meliam or dart green, and the surface is shing. The basal part of the upper midrib surface is often conspicuously farinose. The powfery 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 dividet by the midrib into symmetrical, or sometimes slighty asymmetrical, hatves. The sparing 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 marrower blades; sometimes narrow and medium-wide leaves have their veins extra far apart.
The midrib of the lenves of most varicties is very prominent. It is always rery wide at the base, gradually tapering toware the apex and disappearing altogether before reaching the tip of the lamina. The upper surface is chanched, the lower convex. A conspicuous chatacter is the difference in color of the two sides of the midib. While the lower surface is always green except for a light stripe that runs along the center, the upper surface may be variously coloref, 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 lenf ages, the surface turns completely white or gemains cloudy execpt for a marow or medium-wide central zone that is either pure white or somewhat paler than the fhates. The milos have a yellow or olive-colored midrib, caused by a yelow pigment in the sulspidemma paremchyma cells.

Varicties may be classified as havine white, cloudy, or vellow midribs (14). The chassification whiteribied is applind ony 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 (iig. 11, $E, F$ ) are elassified 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 toued. 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 bnsal 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 \%one; with some scattered


Fincur: 1l-Midribs with arljavent blade lissue: A-D, White-ribbed varietios; $a$, midrit with broad white ecmer and elotiy flanges: $f$, midrib efondy. Aif xis.
hair, localized medially or laterally, reathing up as high as 10 cm . Many varicties, inclating the milos, lowe a smooth midelib.

Midrib pubesconee is an important character, useful for group classification nas important for purposes of inentification when used in connection with other characters.

## Leaf Sileatia

The shenth is attached to the note ated encireles the eulm. It forms an open tube extending about one am a third fimes around the base of the internode. The outer murgin of the sheath overtaps the
inner, the overlapping margits being altemately the right and the left in successive nodes. The sheath is thickest medially, grandually becoming thinner toward the margin where it is membranaccous. The outer surface is glabrous, the inner surface white and glistening.

The length of the sheath varies comparatively little, averaging about $2 \overline{5} \mathrm{~cm}$. for most varieties. However, there are varieties ( $\mathrm{N}, \mathrm{N}$. $62 S$ 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 consiant (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 eertain degree of overiap because of variation in length of internode. In many of the medium-tall, sparsely leaved sorghoms the sheaths are shorter than the internodes they envelop, so that the nodal region of the next higher leal 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 orediap. 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 eloser 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 heary in the upper part of the culm and more conspicuous in some varifties than in others. Occasionally wax deposits may be very scant or altogether wanting.

The surface of the sherath is always smooth. The only hair is found on the sheath base, the region where the sheaths is atenched 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 shenth base and partly investing the stem tissue immediatoly 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.

## Beade Jonvt

At the juncture of sheath and blade is a specinized recion, 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 solt-textured and often ganfered to give the leaf mobility.

## LICUEE

The ligule is formed ontogenetieally from epidermal cells and is made up altogether of clongated parenchyma ectls. The side next to the leaf is covered with free or slightly adnate hair. The upper free edge is ciliate, the cilin sometimes exceeding in longth the height of the ligule. In its immature state the lignle is transfucent; later it becomes dry, locally discolored, especially below the attachment of the cilia, and sometimes tora.


 dewtat and bise of hamina folded baek; $D$ ), internode longer than sheth (eommare with fies 17.

Fundamentally, there is only one ligular pattern, the shallow crescent. Most ligules are about 2 mm . high, somewhat taller at the middle, and graduatly 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 shallowdeltoid. On the other band, the ligule may be depressed in the eenter, giving rise to a shallow-arcuate type. In one variety (M. N. 683), the base line of the ligule in the region of the midribs was fonad 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. 1.3, $E-G$ ). The flanges commonly abut squarely on the narrow-deltoid extension of the sheath margin (fig. 13, F). Occasionally they thin out almost to a lime and extend to the very margin of the sheath (fig. 13, E) or may terminate earlier (fog. $13, G)$.

## DEWHAP

There are two common dewlap patterns: The curved ligulate (fig. $13, B, D$ ) and the deltoid (fig. 13, A). The form of cither 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. Alany forms retain the juvenile type through maturity, however. The two dewheps of a given leat ofien 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 leates on the same stalk may have very symmetrical dewlaps (fig. 14, A).

The older dewhaps of many varieties bave a pronouned tendeney to Jold back (fig. 13, $C$ ), whereas in others vertical folds and gauffering give the leaf mobility.

Voung dewhaps are usually coneolorous with their respective leaves. Upon aging, the dewlap color fades, becomes ivory, ivory-yellow, or a slade of olive. The outer matrinal 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 degrec of waxiness of the dewlap varies from a mere bloom to a heary was deposit that often masks the natural color of the outer dowhy 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). Nost eonspienous, and visible to the maked eye, is a small hair group extending from the midrib outward. Next in importance is the broad margimal group; here the hairs are usually sparse and not reeognizable without the aid of a Jens. Sometimes these two hair groups are connected by a narrow band of seattered 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 execpt in the margimal zone, which may have fewer hairs than the onter surface adjacent to it. From the marginal zone inward the hairs become


Figesa 13-A, Dewlap brond-dettoid and slightly gabfered; $h$, rewlap marrowligulate and steeply sfoping; $C$, deltoid dewlap with margin sharply fokled back, surface not gantrered; $D$, narrow-ligulate dewlap with tase line nearly horizonta; $E$, flange of lignle attennated and extending to very edge of membranaceons sheath margin; $F$, flange of ligule abuts with broul base on triangular extension of sheath margit; (f, atteminted flange of ligule terminates before reaching sheath markin.



 dewlap in continuity with the overlyng sheath margin is ligntate abal sterply sioping, the one to the right is deitoid and less stoping; (', dewlaps from blate. joim abose 13 ; 1 , marrow ligulate dewlaps from youngest bate joint.
long ame dense, reaching their fullest development in the midnib, itself (fig. 15, $B$ ). In a few maties the hasal miserib hairs are not so longe as the adjacent flange hairs, sometimes not extending up to the margimal fringe of the ligule. The flange hairs have a fendeney to comverge over the midrib, making the midrib group appert ispeciallymassive.

[^2]
$B$
Fiocma 15-A, Mater surface view of dewlah, showing pubesemec. Finge of ligule abmating on membranaceons sheath margin visibie at left. $B$, Detailed structure of imer strface of blade joint, showing pubesecnec of dewlaps and midrib. Ligule partly folded track to expose hatir groups in baek.
Because of its relative miformity, the inner dewlap pubeseence has litlle taxonomic ralue. The outer dewlap pubescence may be useful as a qualitative character if exceptionally well developed, with the hair groups visible to the maked eye. The midrib pubescenes, howerer, ('spereinlly if extenting far up the leaf, is a character of primary importance.

## ANATOMY OF TIUE STEM

## Intemnode

The stem of sorghum, liko that of sugareane, 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 intercelluhar spares at their angles. Those between the peripheral bundles are small, thick-walled, and lignificd. There is a narow lignified hypodemis, its verticel contimity occasionally broken by the interpolation of parenchyma cells that abut externally on a stomate. Sinee the stam epidermis of sorghum contains relatively mumerons stomates, conpared to sugareane, these passage aroas are also mather 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 (his "jacket" stareh is the only kind formed. 'In other varieties, starchalso necumulates in the parenclyma between the bundles. This secumblation of "difluse" stareh (fir. 16, B), especially in the sweet :orghuas and the milos, can be very massive.

Freshly cut cross sections of young stems have a uniform grav-grew color. As the stem matures, the cells near the center mar berome filled with air and take on a cottony-white appearanee. This proess of pith formation is often limited to che center of the stem, but it may extend outward until the entire cross section, exeept the peripheril \%one, is involved. The transformation of parenclyma into pith is sometimes followed by a complete cellular break-rlown that lerves the eentral vascular bundles suspemed in air with the remains of brokern tissue.

Except in the peripheral region, the vascular lundes of the internode ate shomboil ( (ifg. 17, B) or narrow oval in cross section (fig. 17, A). Xylem and phlom are disposed collaterally in relation to cald other. The protoxylem consists of annular and spiral slements. Since it matures before the internode clongates, the untheremed part of the walls ol these elements becomes errished during sulseguent growth. Simultancously; the small-eelled protoxylem parenelyma recedes, forming an air space, or lacuna, into which project the remains of the secondary wall of the annular or spiral ressels. Above and lateral to the protoxylem are two large metnxylem ressels (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 parenclyym cells surroumbing the vessels are thick-walled and lignified and possess reticulate thickenings. The phlorm forms an oval mass of tissue of regular design, composed of large sieve tubes and smatl eompanion colls. The protophloem is nearest the outside; in mature bundes it is crushed fund bignified.

The vaseular bundles are enclosed by $a$ well-marked sheath, which is most strongly developed on the inside and the outside of the bunfles, where it forms typien bunde catps. At the flamks, the shemeth is uniseriate or biseriate, ocensionally wider. The sherath erells are


Fiava $16,-A$, (ross section through the peripheral region of imternode thand section of (resh materiat). $\times 40, B$, Bunde from central rerion of internode Furounded by parenchymat eells densely filled with stareh (hand section of fresh material). $\times 190$.


Finuta 17.-A, Large oval bundle from central region of internode; and $B$, large rhomboid bundle from central region of stem. Both $\times 222$.
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 protophlocm, 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 thimer walled than the other sheath cells.

The ring of vascular tiss:a just inside the epidermis is composed of very small and mediuizs sized bundes buried in thick-walled parenchyma. The sclerenchymatous bundle cap of the phloem pole is small, and its eells are usually continuous with the hypodermal selerenchyma. The bundle eap at the xylem pole is large, and the sheath along the flanges is also well developed. The xylem of these small bundes is redaced to one or two large metaxylem vessels. If two vessels are present, they are adjacent to each other or separated radially by smail-celled, lignified xylom parenchyma or tracheids. The phloem is relatively well developed, its area being proportional to the size of the bundle.

Among the outmost bundles are a few extramely small ones composed of one metaxylem veisel and some phloem. They are surronnded by a single-tayered lignified stieath. This type of bunde is characteristic of the basal intemode just above the growth ring and is also met with in the lower nodal region.

The medimesized bundles of the peripheral ring are not always in contact with the hypolermal sclerenebyma. They differ chiefly from the smaller type by having a very targe selerenchymatons cap at the xylem pole. There are always two motaxylem vessels and ocensionally a protoxylem element.

The bundeles of the second and third concentrie ring also possess a latere sclerenclymatous eap at the xylem pole, with an berease in the mamber of protoxtem elements. There is a progressive reduction in the thickness of the sheath in bundes farther away from the periphery. The number of protoxylem cells is larger and a small protoxylem lacuma may be formed. Beginning approximately with the fourth cirele, 2 mun. centrad from the epidermis, the bundles are like those of the entral intemote.

The ontogeny of the stem bundes of sorghum is in agreement with that of corn ( $\overline{5}, 12$ ) and sugarcome ( 1 ). The precursors of the bundles are small procombial strands that first iarrease in size by division within the strand. To conform with the future shape of the bundle, the divisions are at first perielinal and later at the flanges. Within these groups of procmmbium, tissue differentiation proceeds until all the componeats of the bundles have been formed. The first sieve tubes appear at the outer margin-the first protoxylem elementsmaturagr somewht later than the first sirve tuhe, at the inner margin of the procmmbiai strand. Additional cells differentiate until all xylem and phloem is formed. As the eonducting elements of the protoxylem are destroyed during elongation of the intemode, a protoxylem lacuna is formed.

The bundle sheath is mitinted during early procambind differentiation. It surrounds the emerging bumber as a single hayer, bat 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 sorn. The sheath is a composite of cells derived from the procambium and adjacent parenchyma cells.

The procambium cells of the emerging vascular bunde 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-shape: 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 internole 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 fou-sided prisms with undulating silicified walls. The mean diameter varies between $7 \mu$ and $16 \mu$, depending on the variety. There is much variation in the length of the long cells within both varietal and culm limits. But varietal differenees are quite apparent when forms with very short cells (II. N. 6II) and those with wery long cells (M. N. 459) are compared. The end wall of the long cell is abways straight, never sloping, ats in many sugareme varicties.

The cork cells are suberized and relatively thin-walled. They are kidney-shaped, with the gratest 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 wiblin culm timits, 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).
Paitern 2.-Short-cell groups prevalently in double pairs (fig. 18, R).
Pattern 3.-Many shart-cell groups lack silicat eolis (fig. 18, $C$ ind $D$ ).
It is apparent that the epidermis of sorghum is very uniform compared to that of sugareane, and is of litile taxonomic value. Not a single variety out of 152 studied showed a complete absence of silica cells, whereas in sugareane many varicties show that characteristic. There is also only one type of cork cell instead of the great variefy of forms observed in sugarcane. Stomates are very mumerous, occuring in connerted or interrupted vertical files. Since their distribution is very uniform, they are of no value in chassification of varieties. Also, epitermal hairs, while observed only rarely in sugarcane, are always wanting in the stem epidermis of sorghum.


## 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 laard 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 rasculur tissue is surrounded by a single laver of thin-walled lignified cells (fig. 21, A). This cell layer forms the inner boumlary of the selerenchymatous jacket, which is very massive in the phloem region, but forms only a narrow erescent over the xylem pole (fig. 21, $B$ ). The jacket cells investing the narrow lignified bundle shenth thicken and lignify progressively outward (fig. 21, $B$ ) matil the narrow sheath. as illustrated in figure 21, $A$, and the selerenchymntous jacket over the xylem pole and along the flanges become one lissue. The culls of the large phloem cap are more tike collenchyma than the sheath cells inversting the bunde, as shown by their appearance and staining reaction (fig. 21, $B$ ).

A characteristic frature 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 bundes also have a sarch jacket, but it is very narrow and less conspicuous than that of the eentral bundles.

The peculiar structure of the central stem bundes, characterized by the large collenchymatous phloem caps and starch jackets, extunds some distance beyond the growth-ring zone as externatly delimited. Also, the redenction of the cortex and the outward movement of the peripheral bundles until they again establish contact with the hypodermal sclerenchyma (fig. 22, 4) are completed only some distance above the true growth-ring region.


Frobere 19--A, ('roas section throngh peripheral region of growth ring (hand section of fresh materiah). $\times$ an. B, C'ross section throtgh young root band showing numerous horizontal traces. $\times 100$.



 Intaforitill.

 of growith ring from old stalk. (Hand seetions of fresh material.) both $\times 12 \mathrm{t}$.


Figene 22. - 1 , (rostsection through quripheral rexion of stem just above growth
 C' (ross section of stem abont 8 mm, below sheath base (hand section of fresh materiai). $\times 126$.

Root Band
Certain anatomical characteristies 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 eharacteristic of the growth ring, exept that the large phoom caps are strongly lignified. The outermost bundles have small phioem caps and harge xylem caps. With each suceeding layer the phoem 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. Oiber horizontal bundles composed of short pitted elements and enclosing phoem tissue are found sentered throughout the cross section (figr. $19, B$ ). They constitute the traces comecting the vasculay tissue of the stem with the root primordia.

The central or near-centmal bundles of the upper root-band zone are like those of the growth ring. The sylem is composed of a row of elements with spirn thickenings. The two harge laterally placed vessels are also of the protoxylem type. Since these two cells are not comected with a xylem bridge, the phlomm and the protoxylem parenchama fom 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 stareh jacket identical with that foume in the bundes of the growth ring. In the one below the root primordin the phloem caps are smaller (fig. 23, A) and strongly lignificul. The stareh jacket around the xylma pole has disappenred. The eentral bundles still lack a protoxylom lacema, but the two metaxylem vessels have pitted secondary walls instend of spiral thekenings.

## Nobai Plate

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

The anatomical pieture of the stem eross section, just berore the bundles enter the nodn! region from below, is in agreenent with the anatomy of the internode in qeneral. The bundes are more or less evenly seattered, denser near the periphery than the 'cater, with the outermost bundles in contaet with the hypodermal selerenehyma. The cental bundles are alongateovate with well-developed phocm 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 vaseular mesh that constitutes the notal plate.

The large central or neareentral bundles of the nodal plate have changed from ovate to broad rhomboid; the phloem caps have chlarged but the xylem caps are now redueed to a single-cell layer. or have disnppeared altogether. Other bundles appear irmgular in shape, frequently compound (fig. 22, $B$ ), and unastomosing higher up into separate strands. The peripheral bundes have lost contart


Ficcua 23.-- $A$, Central bundle from basal refion of root band (hand section of fresh material). $\times 132$. $B$, Componnd bundles from peripheral region of note (hand section of freshmaterial). $\times 93$.


Fheras 24.-A, Large lateral trace surrounded by small bundes; and $B$, part of horizontally rumbing median trace. $\times 100$.
with the hypodermal sclerenchyma (fig. 22, C) and, receding from the periphery, allow for a narrow, bundle-free, cortex. The bundles also have greatiy increased in number, and frequent anastomoses indiente their intimate relationship to ench other. The larger bundles, in contact with or immedintely centrad to the small bumdes, appear very irregular. Most of them are compound or show signs of anastomosing (fig. 23, $B$ ). In gencral, there is a grent increase in bundles in the peripheral part of the stem while the center appears more parenchymatous.

Outstanding among the nodal bundles are certain large, obliquedy running types that represent the median and large lateral traces fig. 24, A). These large traces have amphivasal or semiamphivasal structure, with the sylem 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.
Seattered among the larger bundles are numerous small traces, some running vertieally, others horizontally or obliquely. They are composed of short-pitted xylem elements, endosing some phloem in semiamphivasal, or lateral, terangement. These small traces amstomose very frequently and change their cours from the vertical to the horizontal and back again.

Just below the insertion of the leaf the peripheral bundies 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 Ienf traces has been described in detail for com ( $5,12,13$ ) and sugarerae (1). Sorghum shows no devintion from the normal pattem. Although the median trace (fig. 24, B) appronehes close to the center of the stem, the lared lateral traces (fig. 24, A) bend only a few millimeters inward, a behavior that is more in ngreement with Sharman's conclusion (12) than with Esau's (5), who investigated the leaf-trace relationship in corn.

## ANATOMY OF THE LEAF

## Sheati Base

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

A cross section through the basal part of this rewion shows the vascular bundles distributed more or less evenly over the eatire cross section (fig. $25, B$ ). The smallest humdles are next to the outer epidermis; the largest are near-central, somewhat eloser to the imer epidermis. All bumdes have enomous phloem eaps, but the vaseular core is yery small, eonsisting only of a few spiral elements. The larger bundles (fig. $25, C$ ) are similar in stucture to those of the erowth 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 momons phiocm enps that are lignified wholly or in part (fige. 25, (C). The rascular com is surounded by a narrow lignified jacket as in the growthring (fig. 21, A). The two metasylem


Tievre 2ab-A, ('ross section through periphemat mion of sheath base, showing hairs (hand section of fresh material). X ( $94 . \quad B$, ('ross section throngh basal region of sheath base (eross section of fresh material). $\times 3.4 . \quad$ C, Large bunde from sheath base (band section of fresh material). $\times 110$.
vessels are pitted and connected with one another by a narrow xylem bridge (fif. $25, O$ ). 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 Sheate

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 deseribed 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 phlocm pole is either in contact with the hypodermal selerenchyma or separated from it by several rows of parenclyyma cells (fig. 26, A).

The largest bundles (fig. 26, $B$ ) resemble in structure the central bundies of the internode except that the phloem of the sheath bundles is more massive. The selerenchymatous bundle cap at the phlom and is in contact with the hypodermal selerenchyma, except where the bunde occupies a near-central position. Radial sheets of chlorenchyma, about five cells wide (fig. 26, A) comect the $y$ verm pole of the large bundles with small groups of thin-walled hypodem mal sclerenchyma of the lower epidermis. The area between the radinl 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 aro in the nature of branches that run obliquely or at right angles between the large vertical veins and effect a union between them. Struturally and ontogenetically, they are similar to the cross-comecting veinlets of the lamina, consisting of several rows of short-articulated xylem elements of the reticulatepitted type. The bundles are formed late in ontogeny, their initials connected with the cambiumike 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 cpidermis 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 slighty raised. The inner epidermis is composed solely of long, thin-walled cells.






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Thas leaf blato is paralled-xamed like the sheath, but the amso commeding veinlels are not so prominemits in the theath.



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T'la large bumbles are struedually similar to those of the leaf sheath. Fiach bandle is jackeded by a marow lignified shoth, which is in con-


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thick-walled chlorenchyma cells containing numerous large plastids.
All bundles are connected at frequent intervals with one another by narrow branches that run dingonally (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. 2S, A), there is little difference in structure between the upper and the lower leat epidermis.

The epidermal cells that overlie the vascular bundles form several longitudinal rows, their number depenoling 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 vertienl 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. Ocensionally there are found short spines and twocelled hairs occurring between the long colls flanking the veins. They are of the type described for the epidermis of sugarcane (B). The bulliform, or motor, cells oceur in single or double files (fig. 27, $B$, and fig. 28, A) and are not nearly so prominent as those in sugareane.

The midrib of the blade appears crescent- or half-moon shaped in cross section. The lower surface is stadeled with vaseular bundles (fig. ${ }^{2}, C$ ), while the upper is maderlaid 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 abore, the tissue has a water-soaked appearance. As the leaf matures, the parenchyma beromes filled with air, eriving the entire midibls a whitish appearance that contrasts strongly with the green color of the lamina. In varicties 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 perentage distribution of the large bundles, however, is much greater than in the lamina, where the large bundles oceur only at great intervals.

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


Figere 28.-A, Surface view of upper epidemis of blade; $B$, sufface vicw of lower epidermis. Botia $\times 170$.


Figune 29. $\rightarrow$ A, (ross seetion through tewlap) (haml section of fresh matorial). $\times 60 . \quad B$, bolarget view fran marginal dewian region, showing detailed stracture of large mandie. \% 2 to.

The upper epidermis of the midrib is made up of harge long cells altemating with cork cells. There are no silien cells and mo stomates. In eertain rarieties, many epidemat cells, especinlly in the centand region, have grown out into bare unicellutar hairs. These hatrs are of epidermal origim and do not beeome lignified.

## 1)

The anatomical picture of the dewap resembles the of the lamima, but the vaseular bundles bear at closer relationship to those of the sheath base.

A cross section through the dewhap (fig. 29, A) shows a suceession of very large and very small bundes embedded in parenchyma. Several very small bundes alternate with one harge bunclle. The latter oceupies the center of the cross section, while the small bundles have an offecentral position closer to the lower than to the upper epidermis.

The large bundles are surrounded by a narrow jacket of thin-walled ligniffed cells (fig. 29, B). The phlow is rapped 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, bat it is not in continuity with the sheath cells, being seporated from them by one or two hayers of parenchymat. The xylem is composed entirely of elements with spiral secondary thickenings. A protoxylem lacuia is wanting.

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

Both epidermal surfaces are clothed with hais like those found on the shenth joint. The cells of the epidermis are irregular and himwailled; stomates are present.

## ANATOMY OF TIIE ROOT

## Large Laterals

A cross section through a large lateral root shows a siphonostele with a eentral pith and broal cortex (fig. 30, at). The cortex is composed of th havers of eells. The peripheral hater forms an exodermis that has prominent wall thickenings involving the outer tangential wall. Sorghum differs in this respeect lron sugareane. whese root exodermis has $U$-shaped thickenings involving the inner tangentina and ratial walls. Extermaly the exodernis 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 harge regular edls with squarish intercellular spaces between them. The cells of the two most centrad layers, closest to the endodermis, are brick-shaped, marrow, and very regular.
The cells of the endodermis are sery uniform, and there are no intereellular spaces betwen 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 recinfored (fig. 30, C). The tangential wall thickenings are topped with silien knobs of irregular contour (fir. 31, A). Silien exeretions similar to these but more regular in shape have heen described by the author for the endodermis of sugareane ( $1, p l .23, D$ ).

The rascular ring is relatively narrow (fige 30, A) and is limited on the inside by a selerend hymatous jacket that follows the umbluting contour of the inwardy propecting metaxtem vessels. The number of protoxylem points is rariable, depending on the size of the root and the number of metarylem elements. There are rommonly three protoxylem strands and an equal number of phlom groups to cach metaxylem vessel. Both protoxylem and phom nhut the perieycle. The latter consisis of a single layer of cells that become thick-walled

 material). $\times 33$. $B$, ('ross section threngh buttress root fhame section of fresh material). $x$ in. (', lartial entargement of $A$, to thow details in structure of endodermis and vascular (issur: ca, Endedermis; mx, meta-


 Endociermis with silica knohs; $p s$, protophoem sieve tube; $s$, harge metaphloem siese tube; $r$, companion well; $p$, bericyele. $x ~ i, 000$. IS, longifudinal section through basal region of root tip showing azieal merisiem. $\times 42$,
fairly early in ontogeny. In localized regions the pericyde is two cells thick.

The phloem groups are very whiform, consisting of fiye or six clements (fig. 31, A). There is a single protophlocm sieve tube ( $\mathrm{fig} .32,73$, 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 Lube with a bore ol $20 \mu$ to $22 \mu$, and above it are one or two sicve tuloes of smaller size.

The cells surrounding the xylem and phloem thicken and lignify with age, so that in old roots the entire waseular ring is composed of thick-wablet 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 intereellular spaces betwen them. The walls of the pith cells of odlar roots thirken, and lignification, which is at first spoty, overtakes most of the tissue.
Ia the development of the vascular tissue the large metaxylem dements are initiated before the protoxylem (fig. 31, $B$, and 32, $A$ ), but the later mature eatier. The protophbom sieve tubes (fig. $32, B$ ) mature aliead of the protoxylem, in agrement with tissue differentiation in other plants.

## Bettress Roots

The structure of the underground part of the butiress roots is identical with that of the large laterals. The aterina section, however, is different. Quantiative diflerenees consist in a greater root dinmcter, a larger number of metaxylem ressels, and eoncomitantly a greater number of protuylem points and phoem groups (ige. 30, $B$ ) and a broader coriex. The groups of phoem contain a harger number of cells than the large laterals and the armagement of the phoem cells is less symmetrical. Quaditatively, the nerinal part of the buttress root diflers from the underground part by having a strong epidermis in which the outer tnagential wall and the radial walls are reinfored. The endotermis, while similar, lacks silica knols. There is no distinet exolermis with fingentially thickened walls, but a modified peripheral cortex consisting of three or lour hyers of small thick-walled cells.

## Smali taterads

The fifiform laternis of the serond and thited order are whitish and of appoximately equal diameter.

The anatomical structure is simple; each motet consists of a brond cortex (fig. 33, A) surrounding a miniature stele with the usual type of tissue Rerangement. This struchare diflers chiefly from that of the harge roots in lacking an exodermis and possessing only one or two metarylem vessels.
The central core is exceedingly small (fig. 33, $B$ ), hating a bore somewhe smaller than that of a single metaxyem vessel of a latge lateral. The embotermal colls are of the type deseribed for the targe rone, exeept that the siliea knohs are often wanting, nt best, inconspicuous. There is a unifnyered perierele consisting of alterinting sectors of thick-walled nal thin-walled (edls. The perieyedie pells opposite the phloem groups are usually thin-walled (fig. 33, B). The




 vesel. × $7 \cdot \boldsymbol{I}$


Figure 33.-A. ('ross section of samall lateral rootlel, X 184. $B$, Cross section of central celinder greatly enlarged: en, Endodermis; mx, metaxylem vessel; $p$, pericycle; $p x$, protoxylem; s, sieve tube. $\times 799$.
smallest roots with only a single eentral metaxylem vessel ustally lave 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 roollets have a brownish exterior. Their functional capacity as organs of conduction is probably unimpaired, however, as the vascular tissue, protected by the thick-walled endodernis, appears normal (fig. 33, B).

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[^0]:    'Submitted for publication Oct. 11, 1946 .
    ${ }^{2}$ (Medit is due Miss Rose Mary Shipman for the preparation of the drawings.
    ${ }^{3}$ Italic numbers in parentheses refer to Literature Cited, $p$. 55 . $780057^{\circ}-48-1$

[^1]:    4 Fig. 10 is fig. 4 of ( 9 and is reproditeed here to aid the reader.

[^2]:    $7105^{3}-19-1$

