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An Anatomical Study of the Leaves of Eragrostis

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AN ANATOMICAL STUDY OF THE LEAVES OF ERAGROSTIS.

BY CARLETON R. BALL.

This study was undertaken in order to ascertain if the anatomical characters in the leaves of this genus were sufficiently well marked and constant to be of value in identifying the different species. The results of similar studies by others have been encouraging. Prominent among these is the series of excellent papers by Theodore Holm[1], who has studied six genera-*Uniola*, *Distichlis*, *Pleuropogon*, *Leersia*, *Oryza*, and *Amphicarpum*, and considers the anatomical characters of all except *Distichlis* to be a reliable basis for determining the different species. Emma Sirrine and Emma Pammel[2] have studied *Sporobolus* and *Panicum* and conclude that the species in these genera, so far as studied, may be differentiated by means of their anatomical structure.

In this paper the author has considered six species of *Eragrostis*, viz.: *E. reptans* Nees, *E. pectinacea* Gray, *E. purshii* Schrad., *E. frankii* Meyer, *E. mexicana* and *E. major* Host.

In these species three structural types of mestome bundles occur: primary or open bundles (Pl. XVII, Fig. 8.) in which the chlorophyll-bearing parenchyma sheath is found only at the sides of the bundles and is wanting above and below them; secondary or closed bundles (Pl. XVII, Fig. 13, vein 3,) in which this sheath completely surrounds the bundle, separating the leptome from the stereome below and the hadrome and thick-walled parenchyma from the stereome, mesophyll, or parenchyma above; intermediate bundles in which this sheath is interrupted either above or below the bundle.

[1] A Study of Some Anatomical Characters of No. Am. Gramineæ. Bot. Gaz., Vol. XVI, pp. 166, 217, 275; Vol. XVII, p. 358; Vol. XX, p. 382; Vol. XXI, p. 357; Vol. XXII, p. 403.

[2] Some Anatomical Studies of the Leaves of Spo obolus and Panicum, Proc. Ia. Acad. Sci., 1895, Vol. III, p. 148. (An extended bibliography of this subject may be found in this paper.)

These different types do not always occupy the same relative position in the leaves of the different species.

In the species studied, these bundles are found to occur in three distinct sizes with constant positions. This would have afforded a basis of nomenclature for the bundles but for the fact that it does not hold good for other genera, and hence is not used. However, for convenience in locating the structural types described above, their position in the leaf is indicated by the parenthesis "(carene)" which is the largest vein in the leaf and always central; "(vein 2)" the next smaller veins, occurring at nearly regular intervals between the carene and the edge of the leaf (Pl. xvi, Fig. 2); and "(vein 3)" the smallest veins, which occur in groups of three to six between the medium veins (vein 2) and also between them and the carene.

ERAGROSTIS REPTANS NEES.

(Pl. xvi, Fig. 1; Pl. xviii, Figs. 17 and 18.)

Epidermis —This, the smallest of the species studied, presents the most striking variations from the general type, especially in the epidermal characters. The walls of the epidermal cells on the superior surface are quite thin, while those of the inferior surface are thicker. The inferior epidermal cells are nearly equal in size, as are those of the superior surface, but these latter are much larger in proportion than those of any other species. Stomata occur frequently on both surfaces, on either side of the mestome bundles. Trichomes are long, slender, pointed, one-celled hairs, occurring in single rows on all bundles. The two adjacent epidermal cells, in some cases, extend obliquely upwards beside the base of the trichome.

Bulliform cells.—The bulliform cells are two or three in number, and in some cases not easily distinguishable from the epidermal cells.

Mestome bundles.—The mestome bundles are thirteen in number, and are all of the intermediate type. The chlorophyll-bearing parenchyma sheath is composed of four or five large cells and is open below. Leptome, hadrome and thick-walled parenchyma are well developed in all the bundles. In the bundles of the carene and vein 2 the mestome sheath is interrupted above by the stereome, but in the other bundles (vein 3) it is continuous.

The carene bundle differs from the other bundles only in being slightly larger, and in having the leptome entirely surrounded by thick-walled parenchyma.

The mesophyll is normal, and the stereome rather small in quantity.

ERAGROSTIS PECTINACEA GRAY.

(Pl. xvi, Fig. 5; Pl. xvii, Figs. 9 and 11.)

Epidermis.—The cuticle of both surfaces is well developed. Walls of superior epidermal cells thicker than those of inferior cells. Epidermal cells of both surfaces more nearly equal in size than in any other species except *E. reptans.* Stomata occur on both surfaces as in the preceding species. Trichomes short, thick, mostly blunt, of irregular size and occurence above the bundles.

Bulliform cells.—From three to five in number, the central one much the largest and flask-shaped, the long neck lying between the adjacent cells.

Mestome bundles.—These are about fifty-seven in number. Forty-six are of the secondary type (vein 3) and eleven of the intermediate type (carene and vein 2). The chlorophyll-bearing parenchyma sheath of the secondary bundles is the most striking character in this species. It is distinctly triangular in outline, with the apex directed toward the superior surface. The lateral cells are elongated transversely to the section, and the inferior or basal cells are small and nearly round. Hadrome, leptome and thick-walled parenchyma are well developed.

The intermediate bundles (carene and vein 2) are open below, with the leptome surrounded by stereome. The chlorophyll-bearing parenchyma sheath in these bundles does not have the triangular outline. Hadrome and thick-walled parenchyma are strongly developed.

The mestome sheath in both types is interrupted above the bundles by stereome. The carene can be distinguished from the other intermediate bundles only by its position.

Stereome.—Stereome occurs below all bundles as a compact group of large cells, twenty to thirty in number, and above the bundles in small groups of three to six large cells. In some of these cells the cavity is in the form of an elongated oval. Stereome also surrounds the leptome in the intermediate bundles and extends upwards partially around the hadrome.

The mesophyll presents no distinctive characters and colorless parenchyma is absent.

ERAGROSTIS PURSHII SCHRAD.

(Pl. xvi, Fig. 2; Pl. xviii, Figs. 15 and 16.)

Epidermis.—The epidermal cells of both surfaces have thinner walls than in *E. pectinacea*. The cells vary considerably in size, those directly above or below a bundle being much smaller than those adjacent to the mesophyll. Stomata occur frequently on both surfaces, and the air spaces are large. Trichomes are longer than in any species except *E. reptans*, and are thick, usually pointed. Above the intermediate bundles they occur in two or more rows.

Bulliform cells.—These, four to seven in number, are large and quite evenly graded in size from the large central cell to the smaller outer cells.

Mestome bundles number twenty-one, of which sixteen are secondary and five are intermediate in type. In the secondary bundles (vein 3) the chlorophyll-bearing parenchyma sheath is nearly round in outline and composed of seven or eight subcircular cells. Hadrome, leptome and thick-walled parenchyma are not so well developed as in the preceding species.

The intermediate bundles (carene and vein 2), five in number, are open below. Hadrome, leptome and thick-walled parenchyma are well developed, the latter especially so. The chlorophyll-bearing parenchyma sheath is composed of from ten to fifteen cells.

The mestome sheath is continuous above and sometimes below the secondary bundles, but is interrupted by stereome above the intermediate type. The carene is but little enlarged and not easily distinguished from vein 2 except by its position.

Stereome is present in quantity both above and below the intermediate bundles and occurs in small groups of three or four cells in the secondary bundles. The mesophyll passes beneath some of the secondary bundles as a single layer of cells.

ERAGROSTIS FRANKII MEYER.

(Pl. xvi, Fig. 6; Pl. xvii, Figs. 10, 12 and 12a.)

Epidermis.—Walls of the epidermal cells slightly thinner than in *E. purshii*. The epidermal cells of the inferior surface vary greatly in size, those beneath the bundles being much smaller than those beneath the mesophyll. Stomata are less frequent in this than in the other species. Trichomes are short, rounded or pointed, and occur on all bundles.

Bulliform cells.—These are five or six in number, are more evenly graded in size than in any other species.

Mestome bundles.—The mestome bundles are thirty-five in number, representing all three types. Of the primary type (vein 2) there are four bundles, in which the leptome, hadrome and thick-walled parenchyma are well developed. These veins (vein 2) are enlarged on the superior face but not on the inferior face. The chlorophyll-bearing parenchyma sheath consists of four or five cells on each side of the bundle, being interrupted below by stereome and above by a few cells of thick-walled parenchyma.

There are thirty secondary bundles (vein 3) containing normal leptome, hadrome and thick-walled parenchyma. The chlorophyll-bearing parenchyma sheath is subpyramidal in outline and composed of five to seven large, subcircular cells with two smaller cells below. The intermediate type is found only in the carene and is open below. Leptome, hadrome and thick-walled parenchyma are strongly developed, the latter passing down to the side of the leptome, which is surrounded by stereome.

The mestome sheath is continuous above the secondary bundles, but above the primary bundles it is interrupted by stereome and above the intermediate bundles by colorless parenchyma.

Carene.—The carene, already discussed as the intermediate bundle, is much enlarged on the inferior side and somewhat so on the superior side. It contains much mesophyll and stereome and some colorless parenchyma.

Stereome occurs in small quantities both above and below the primary and secondary bundles and in much larger quantity in the carene. Directly beneath the center of the carene the stereome is normal in appearance (at x pl. xvii, Fig. 12a) but on either flank it is curiously modified (z pl. xvii, Fig. 12a.) The cell wall is much thinner and does not have the strong greenish yellow color of the normal cell wall. The inner portion of the cell is dark colored and in the very center is a small black dot or cavity. This modified stereome is also found in the same part of the carene of *E. mexicana* and *E. major*. Stereome also surrounds the leptome in primary and intermediate bundles.

Mesophyll is abundant in the enlarged carene and normal elsewhere in the leaf. Four or five cells of colorless parenchyma are found in the carene between the stereome and the chlorophyll-bearing parenchyma sheath.

ERAGROSTIS MEXICANA.

(Pl. xvi, Fig. 3; Pl. xvii, Figs. 7 and 8.)

Epidermis.—The walls of epidermal cells intermediate in thickness between those of *E. purshii* and *E. pectinacea.* Epidermal cells, small below the bundles and large below the mesophyll. Stomata frequent on both surfaces. Trichomes short, thick, one-celled, occurring on all bundles.

Bulliform cells, five to six in number, the central one large and broad.

Mestome bundles.—There are forty-one mestome bundles, of the primary and secondary types. The primary bundles (carene and vein 2) are nine in number, with well-developed hadrome, thick-walled parenchyma and leptome, the latter surrounded by stereome. In the carene the chlorophyll-bearing parenchyma sheath is interrupted above the bundle by colorless parenchyma, but in the other primary bundles (vein 2) by thick-walled parenchyma.

The thirty-two secondary bundles are surrounded by a chlorophyll-bearing parenchyma sheath composed of eight or nine large cells, the two inferior cells having less chlorophyll than the rest. Leptome, hadrome and thick-walled parenchyma are not strongly developed.

The mestome sheath is continuous above the secondary bundles (vein 3) but is interrupted in the primary bundles (vein 2) by stereome or, in the carene, by colorless parenchyma.

The carene is very large, the bundle being in the inferior part of it and subtended by a large quantity of stereome, while the upper part of it is filled by fifteen or twenty large cells of colorless parenchyma, flanked by mesophyll.

Stereome is present in the usual quantity about the secondary bundles (vein 3) and in greater quantity above and below the primary bundles. Mesophyll is found abundantly in the carene, and as usual between the secondary bundles. Colorless parenchyma occurs only above the carene bundle.

ERAGROSTIS MAJOR HOST.

(Pl. xvi, Fig. 4; Pl. xvii, Figs. 13, 14, 19 and 20.)

Epidermis.—The walls of inferior epidermal cells are thick; those of the superior surface, as in *E. mexicana.* Stomata occur regularly on both surfaces. The trichomes are like those of the preceding species.

On the margins of the leaves, and on the median nerve of the sterile and flowering glumes occur numerous small button-shaped projections—the scent glands. (Pl. xvii, Figs. 19 and 20.)

Prof. Wm. Trelease[3] says of these glands: "Morphologically the glands are epidermal structures consisting of a single layer of cells, the outermost of which are but little different from those of the adjacent epidermis, but gradually elongating vertically.

Those at the center of the gland are considerably elongated at right angles to the surface, as is usual in epidermal secreting cells, but occasionally septate. While the peripheral cells have thick-pitted walls, and resemble the other cells of the epidermis in having transparent, watery contents, those at the center are much thinner-walled, and filled with coarsely granular yellow protoplasm. As compared with the unmodified epidermal cells, these elongated glandular cells are also thin-walled at top, where, in common with the other elements of the epidermis, they are invested with a rather heavy cuticle. In some cases this membrane is seen to be free from the crater of the gland in the form of a blister, while in others it had been ruptured, so that only fragments are present."

Bulliform cells.—These are small in proportion, especially above the carene, and vary from four to six in number.

Mestome bundles.—Thirty-one in number, of the secondary and intermediate types. Of the secondary type (vein 3) there are twenty-four, surrounded by a chlorophyll-bearing parenchyma sheath of eight or nine large cells, and containing leptome, hadrome, and thick-walled parenchyma. The intermediate bundles (carene and vein 2) are seven in number, open below, and contain strongly developed hadrome and thick-walled parenchyma, with leptome in greater quantity than usual, and entirely surrounded by stereome.

The mestome sheath is continuous above the secondary bundles, but interrupted by stereome above the intermediate bundles of vein 2 and by colorless parenchyma above the carene bundle.

The carene is much enlarged and contains a few cells of colorless parenchyma and considerable mesophyll. The latter is normal in quantity in the rest of the leaf.

[3] The Glands of Eragrostis major, Host, Proc. Soc. Prom. Agr. Sci., 1889, p. 70.

There is more stereome above and below the secondary bundles, than in *E. mexicana*, and strong groups are found about the intermediate bundles.

CONCLUSIONS.

The results of this study are embodied in the analytical key which follows. The characters given will clearly separate the different species, though, with the exception of the peculiar glands of *E. major*, the differences between *E. mexicana* and *E. major* are not well marked. For instance, the number of cells of colorless parenchyma is constant in neither species, nor is there an absolute line of demarcation between these cells and the mesophyll. Again, while the carene bundle of *E. mexicana* is classed as an intermediate bundle, it will be noticed that the three large cells which form the superior part of the chlorophyll-bearing parenchyma sheath resemble very closely, in their shape, cell-wall, and the almost entire absence of chlorophyll, the adjacent cells of colorless parenchyma.

In conclusion, the author wishes to acknowledge his obligation to Prof. L. H. Pammel, under whose efficient direction the work has been done, for his invaluable assistance and advice; also to Miss Charlotte M. King, artist for the botanical department, for kind suggestions and assistance. Thanks are also due to Mr. F. R. Clements, of Lincoln, Neb., and Mr. W. D. Barnes, of Blue Grass, Iowa, who kindly furnished specimens for study.

ANALYTICAL KEY.

All mestome bundles provided with a chlorophyll-bearing parenchyma sheath; mestome sheath composed of a single row of cells radially arranged; stereome above and below all bundles.

A. Superior epidermal cells of nearly equal size and all larger than the largest of the inferior epidermal cells; trichomes one-celled, long, slender, pointed. *E. reptans.*

B. Superior epidermal cells unequal in size and not larger than the inferior cells; trichomes short and thick.

I. Chlorophyll-bearing parenchyma sheath in bundles of secondary type (vein 3) distinctly pyramidal in outline, apex directed toward superior surface: lateral cells of sheath elongated transversely to the section. *E. pectinacea.*

II. Chlorophyll-bearing parenchyma sheath in bundles of secondary type (vein 3) round or oval in outline.

a. Carene not enlarged (or but little), especially on inferior side, not easily distinguishable from vein 2; trichomes equal in length to

one-fourth or one-third the width of section; no colorless parenchyma. *E. purshii.*

b. Carene enlarged preceptibly, especially on inferior side, easily distinguishable; trichomes equal in length to one-tenth or one-sixth of the section; colorless parenchyma present.

1. Leaf small; upper surface presents a fluted appearance in section; carene and vein 2 strongly developed, the latter on superior side especially; chlorophyll-bearing parenchyma sheath in secondary bundles (vein 3) subpyramidal in outline; cells of same subcircular and the inferior cells much smaller than the rest. *E. frankii.*

2. Leaf large, fluted but little on superior surface; carene enlarged on inferior side only; vein 2 not enlarged; chlorophyll-bearing parenchyma sheath circular in outline; cells subcircular, equal in size.

† Colorless parenchyma, fifteen to twenty cells, interrupting the mestome and chlorophyll-bearing parenchyma sheaths above the bundles in the carene. *E mexicana.*

†† Colorless parenchyma, three to five cells, interrupting the mestome sheath above the bundle in the carene; small button-shaped scent glands, numerous on the margins of all leaves and on the median nerve of both sterile and flowering glumes. *E. major.*

EXPLANATION OF PLATES.

All the figures were drawn from nature by the author and prepared for the engraver by Miss Charlotte M. King, artist for the botanical department.

The abreviations used are: C., cuticle; E. C., epidermal cells; Tr., trichome; Sto., stoma; B., bulliform cells; Ste., stereome; Mes., mesophyll; M. S., mestome sheath; C. P., colorless parenchyma; C. B. P., chlorophyll-bearing parenchyma; H., hadrome; L., leptome; Sup., superior; inf., inferior; Car., carene; Vein 2, vein next smaller than carene; Vein 3, smallest veins.

PLATE XVI. All drawings on this plate were made with camera, and drawn to the same scale. Fig. 1. *E. reptans*, carene to margin: Fig. 2, *E. purshii*, carene to second vein 2; Fig. 3, *E. mexicana*, carene to first vein 2; Fig. 4, *E. major*, carene to first vein 2; Fig. 5, *E. pectinacea*, carene to first vein 2; Fig. 6, *E. frankii*, carene to first vein 2. Mesophyll and epidermis colored black.

PLATE XVII. All drawings on this plate, except Fig. 12a, made with a one-sixth inch objective. Fig 12a, drawn with a one-tenth inch oil immersion objective. All reduced one-half. Fig. 7, *E. mexicana*, carene and vein 3, primary and secondary types, respectively; Fig. 8, *E. mexicana*, vein 2, primary type; Fig. 9, *E. pectinacea*, carene, intermediate type, and vein 3, secondary type; Fig. 10, *E. pectinacea* vein 2, intermediate type; Fig. 11, *E. frankii*, vein 2, primary type; Fig 12. *E. frankii*, carene, intermediate type, and vein 3, secondary type; Fig. 12a, *E. frankii*, inferior part of carene; X, normal stereome; Z, modified stereome.

PLATE XVIII. All drawings on this plate made with a one-sixth inch objective; all reduced one-half. Fig. 13, *E. major*, vein 3, secondary type, vein 2, intermediate type; Fig 14, *E. major*, carene, intermediate type; Fig. 15, *E. purshii*, vein 2, intermediate type; Fig. 16, *E. purshii*, carene, intermediate type and vein 3, secondary type; Fig. 17, *E. reptans*, veins 2 and 3, intermediate type; Fig. 18, *E. reptans*, carene and vein 3, intermediate type; Fig. 19. *E. major*, scent gland, superficial view; Fig. 20, two scent glands on leaf margin, *E. major.*

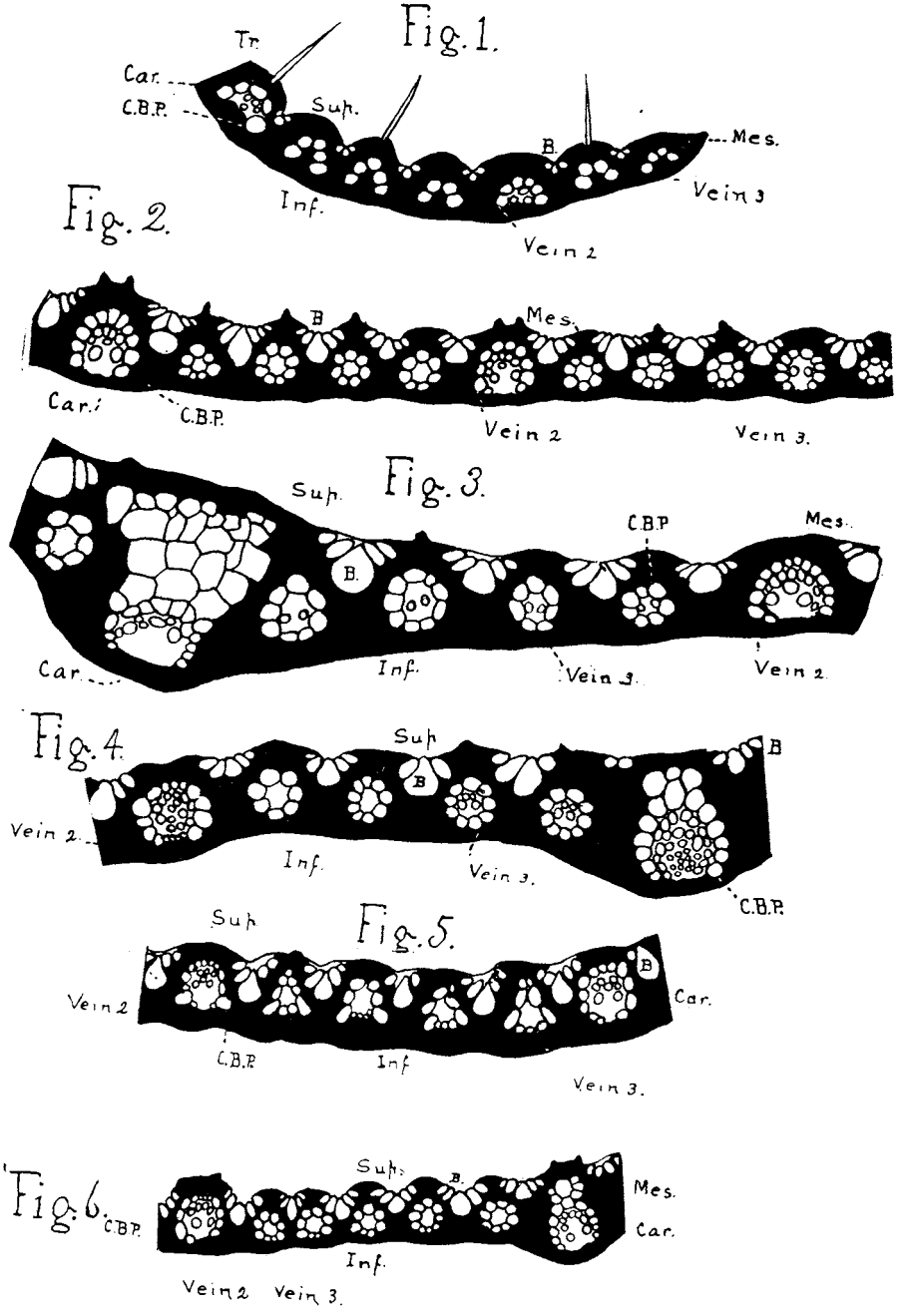
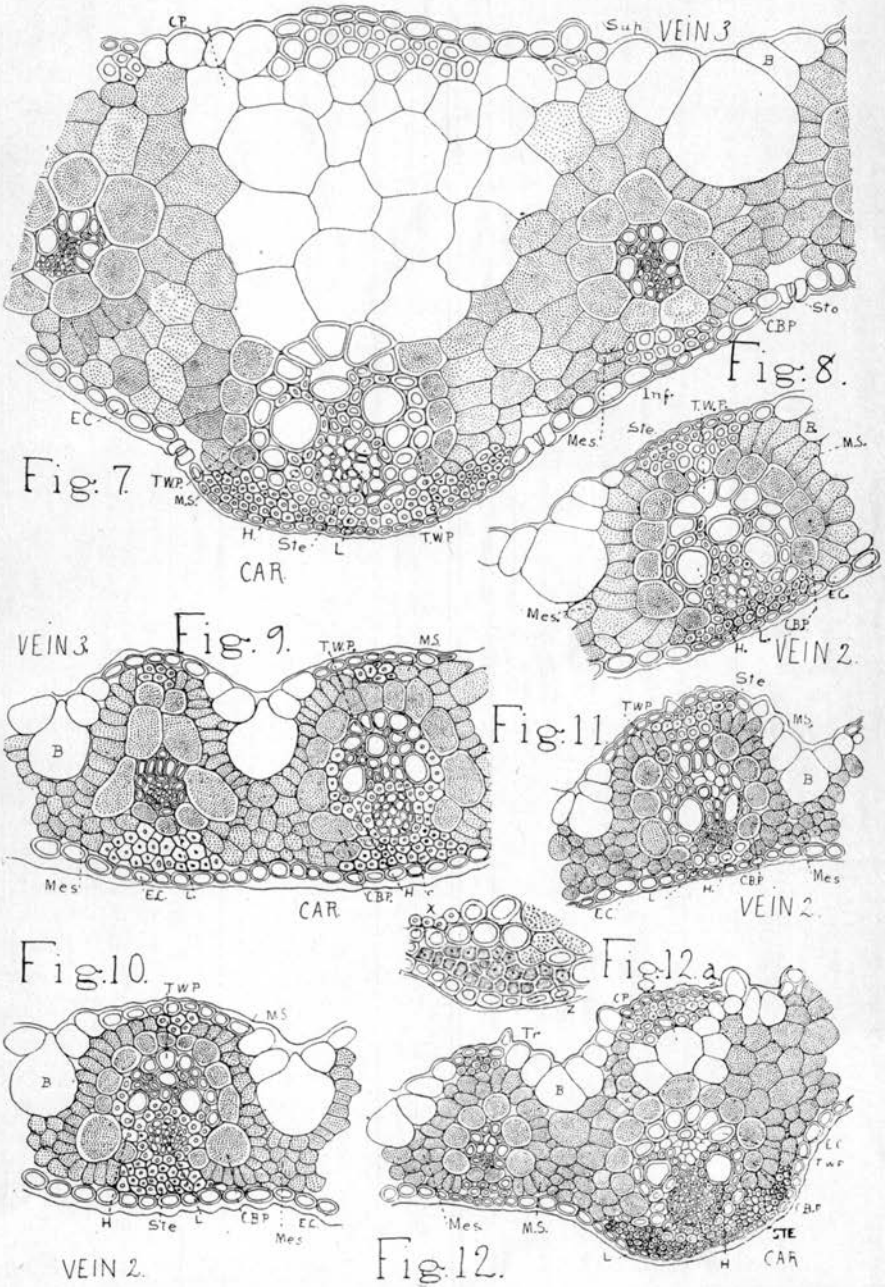


Fig. 1.
Tr.
Car.
C.B.P.
Suh.
B.
Mes.
Vein 3
Inf.
Vein 2
Fig. 2.
B.
Mes.
Car.
C.B.P.
Vein 2
Vein 3.
Fig. 3.
Suh.
C.B.P
Mes.
B.
Car.
Inf.
Vein 3.
Vein 2
Fig. 4.
Suh
B
Vein 2.
Inf.
Vein 3.
C.B.P.
Fig. 5.
Suh
B
Vein 2
Car.
C.B.P
Inf
Vein 3.
Fig. 6.
Suh.
B.
C.B.P.
Mes.
Car.
Inf.
Vein 2
Vein 3.


CP
Sub VEIN 3
B
Sto
CBP
Fig. 8.
EC
Fig. 7.
TWP
M.S.
H
Ste
L
TWP
CAR
Inf.
T.W.P.
Ste
Mes
B
M.S.
Mes
EC
CBP
H
L
VEIN 2.
VEIN 3
Fig. 9.
T.W.P.
M.S.
B
Mes
EC
L
CBP
H
CAR
Fig. 11
Ste
TWP
M.S.
B
CBP
Mes
EC
L
H
VEIN 2.
Fig. 10.
TWP
M.S.
B
H
Ste
L
CBP
EC
Mes
VEIN 2.
Fig. 12a
CP
Tr
B
Mes
M.S.
L
H
STE
CAR
Fig. 12.

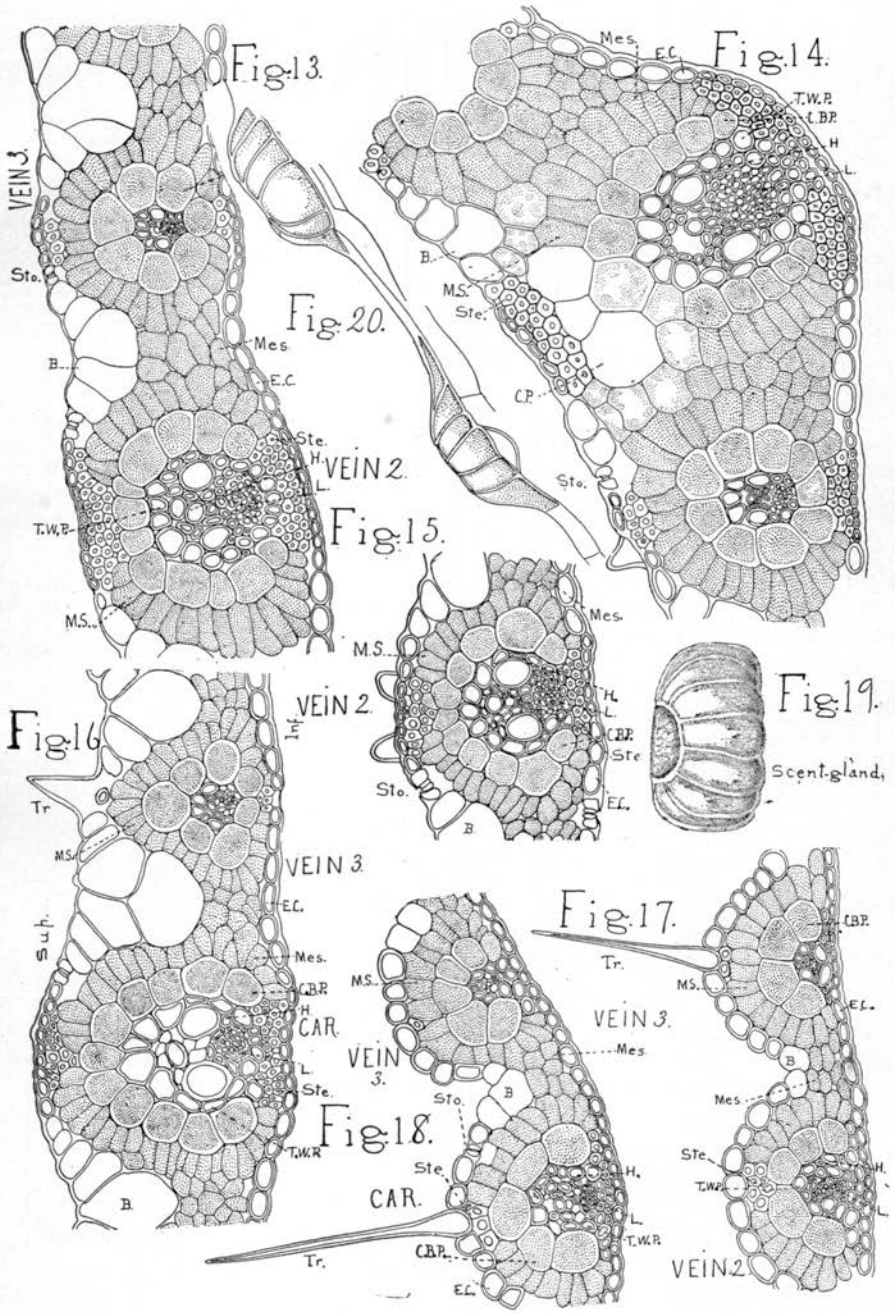


Fig. 13.
VEIN 3.
Sto.
B.
Mes.
E.C.
Ste.
H.
L.
VEIN 2.
T.W.P.
M.S.
Fig. 20.
Fig. 14.
Mes.
E.C.
T.W.P.
C.B.P.
H.
L.
B.
M.S.
Ste.
C.P.
Sto.
Fig. 15.
Mes.
M.S.
H.
L.
C.B.P.
Ste.
Sto.
E.C.
B.
Fig. 19.
Scent-gland.
Fig. 16
VEIN 2.
Tr.
M.S.
VEIN 3.
Sub.
E.C.
Mes.
C.B.P.
H.
CAR.
L.
Ste.
T.W.P.
B.
Fig. 17.
Tr.
C.B.P.
M.S.
E.C.
VEIN 3.
Mes.
B.
Mes.
Ste.
T.W.P.
H.
L.
VEIN 2.
Fig. 18.
VEIN 3.
M.S.
Sto.
B.
Ste.
H.
CAR.
L.
T.W.P.
Tr.
C.B.P.
E.C.