

# DEVELOPMENT AND DIFFERENTIATION OF TISSUES IN THE STEM TIPS OF GRASSES.

E. L. STOVER,  
Eastern Illinois State Teachers College,  
Charleston, Illinois.

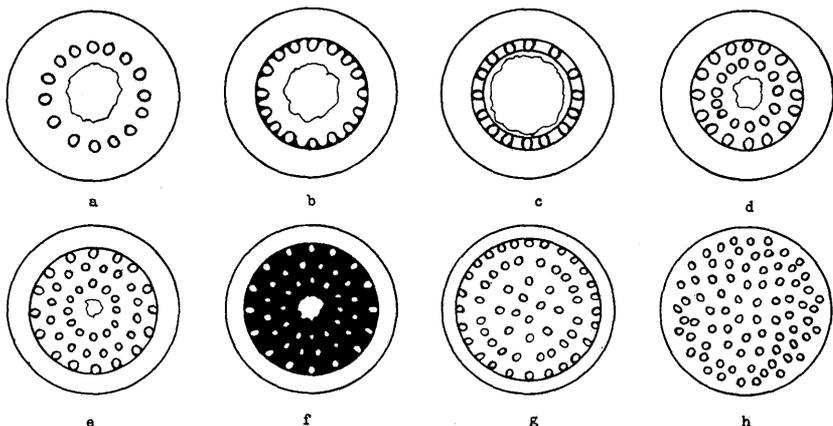
## INTRODUCTION.

The study of the anatomy of the vegetative organs of the grasses has been confined to the examination of the mature structures. The internal anatomy of the leaves has been studied by Duval-Jouve (10), Pee-Laby (15), Lewton-Brain (16), Schwendener (19), Arber (2), Guntz (12), Holm (13), and others with special reference to differences that show means of identification of species, and with reference also to the types of structure in relation to the various habitats (14, 16, 18, 24). The work on the stem structure of the Gramineae is confined mainly to a record of the occurrence of amphivasal bundles and to the theory of cambial activity in relation to the phylogeny of the group as stated by Van Teighem (23), Guillard (11), Crysler (8), and Holm (13).

The grasses have been described as hollow stemmed plants with scattered vascular bundles; and neither statement is definitive. Many of the grasses have solid stems, especially when grown in xerophytic situations; many of them do not have scattered vascular bundles, but have the bundles (Text Fig. 1, a, b, c) arranged in a circle between a central pith and an outer cortex (22). Many of the Festuceae and the Hordeae (Text Fig. 1, b) have a single circle of vascular bundles, while in the Agrostideae and Paniceae there are from one to three cycles of bundles (Text Fig. 1, d, e, f) in addition to the set in contact with the pericycle. Some of the Paniceae and all of the Andropogoneae have three or four cycles of vascular bundles (Text Fig. 1, e, f, g) in addition to those in contact with the pericycle, and the Tripsaceae (or Maydeae) have the vascular bundles in the scattered arrangement (Text Fig. 1, h). Some of the genera of the tribes present exceptions, but the general tendency is from vascular bundles in one circle to the arrangement scattered throughout the pith.

Most of the hollow stemmed grasses are those with only one or two cycles of vascular bundles around a large pith, and

most of the solid stemmed species are those with the scattered bundles or those with three or more cycles and a small pith. The first group is solid stemmed only when in slow-growing situations; the corn type is solid stemmed in any situation, and the Paniceae type of small pith is solid in xerophytic habitats. Canfield (6) reports that in the Jornada region of the southwest the hollow stemmed grasses are those that grow in more favored situations as to water supply and most of those that he reports as solid are members of the tribes that

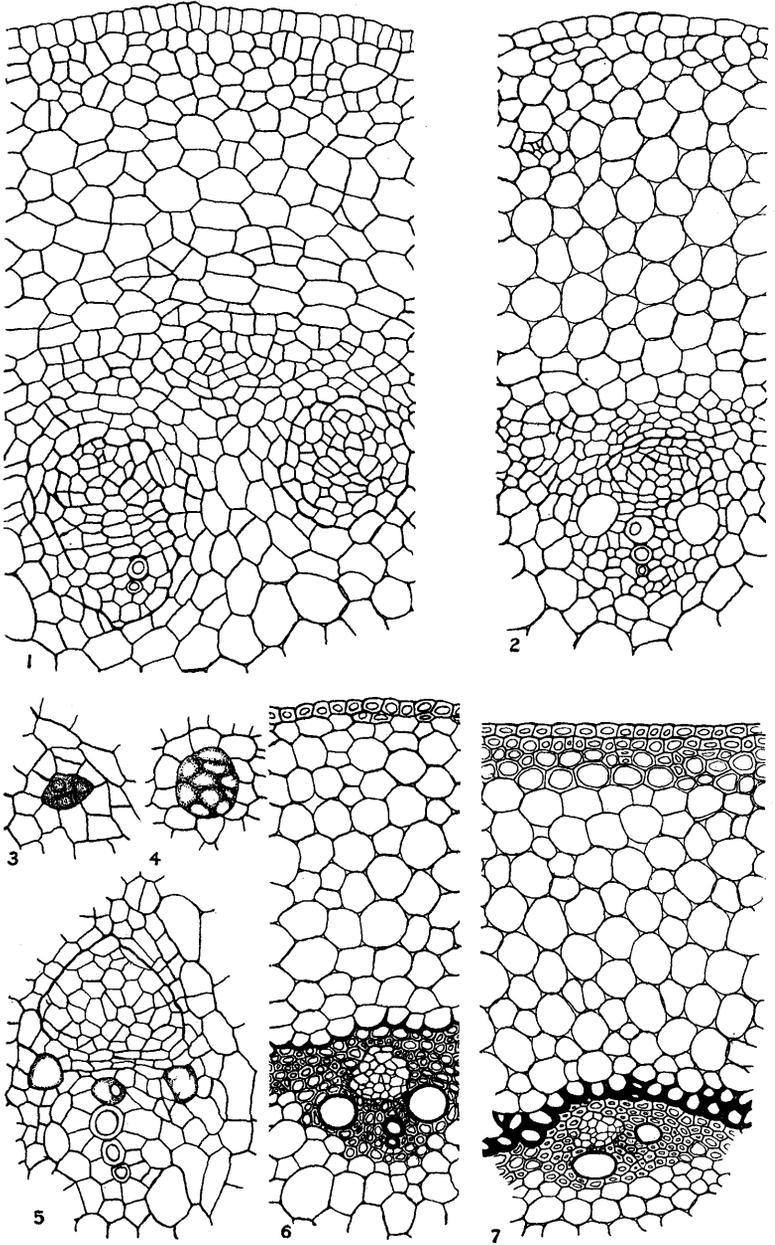


Text Fig. 1. Diagrammatic cross-sections of grass stems showing the arrangement of the vascular bundles of the stele. a, *Leerzia*; b, *Agropyron*; c, *Phragmites*; d, *Eragrostis* and *Phleum*; e, *Aristida* and *Setaria*; f, *Panicum*; g, *Andropogon*; h, *Zea*.

have the several cycles of bundles and small pith or those without pith and with scattered vascular bundles.

Duval-Jouve (10) states that the presence of a cortex and stele is the only thing about the stems that is common to all grasses. In the more primitive grasses the cortex is much thicker in proportion to the diameter of the stele than in the higher forms. The presence of a definite stelar pericycle in most of the tribes marks the limit of the stele and cortex, while in such genera as *Sorghum* and *Zea* the lack of a thickened pericycle fails to delimit these areas in the mature stem. The stem tips of *Zea*, however, do show a cortex.

This paper presents a study of the development and differentiation of tissues in four species of grasses whose mature structures show marked differences in the arrangement of the vascular strands. Serial sections through several nodes of the



FIGS. 1 TO 7, *Agropyron repens* (L.) Beauv.

stem tip were studied, and the arrangement and differentiation of vascular bundles of these were compared with the internodes of the mature stem, sectioned just below the node in the region where greatest lignification occurs, and also just above the node where the cells retain their meristematic activity longer. Sections of the rhizome and aerial stems of short and elongated internodes have been examined and found to show interesting relationships in structure, especially as to the character of the vascular bundles and the stelar and bundle pericycle.

The arrangement of vascular strands in grasses is of various types (22), but those chosen for this study are: (a) vascular bundles in a single circle as shown by *Agropyron*, (b) vascular bundles in two to five circles as in *Spartina* and *Calamovilfa*, and (c) vascular bundles scattered as in *Zea*. The first two always have a central pith although they may be hollow in maturity. This arrangement of bundles in a single circle has been shown by Holm (13) and by Duval-Jouve (10). The variations from the arrangement of bundles seen in *Agropyron* to the extreme scattered type in *Zea* seem to show a definite trend of vascular evolution with the scattered bundles as the highest type in the series.

#### DESCRIPTION.

##### *Agropyron repens* (L.) Beauv.

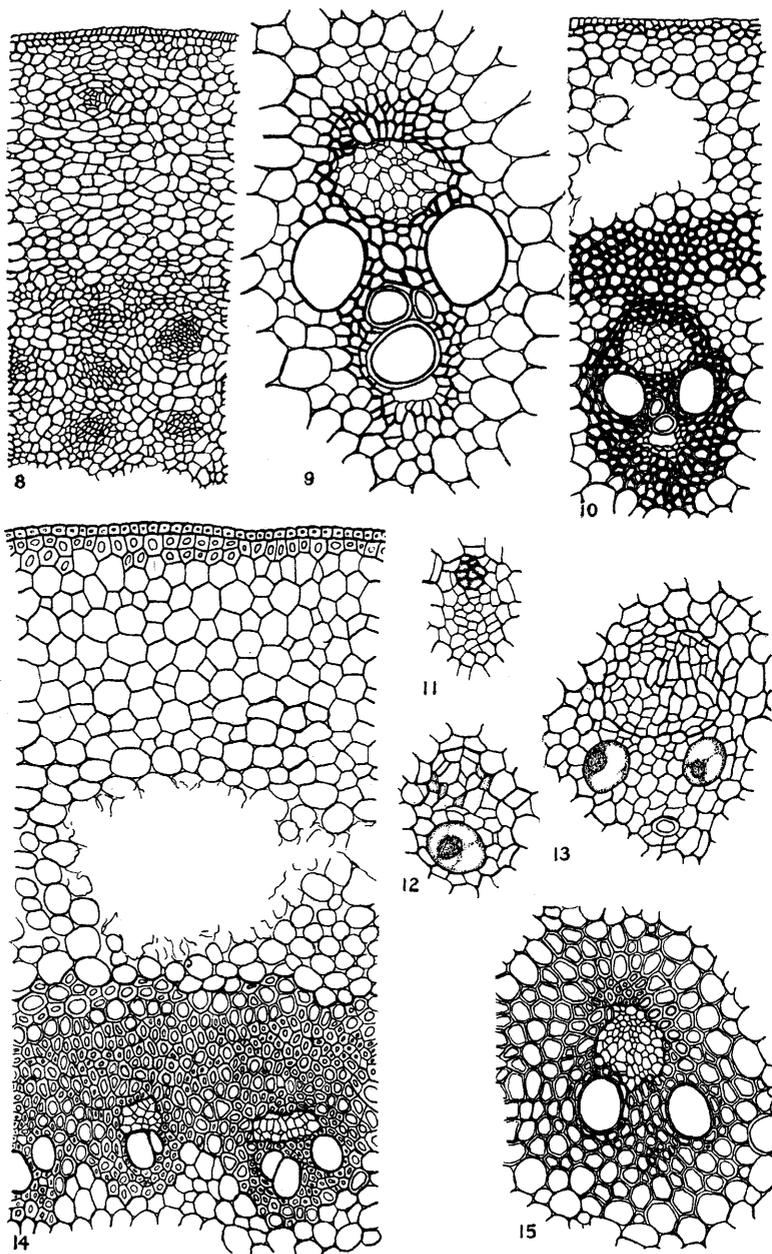
(Plate I)

The vascular strands of this grass arise in the stem tip in a circle that marks off a definite cortex and pith (Figs. 1, 2). No vascular strands are formed in the pith and those found in the cortex are leaf traces. Thus the arrangement in the meristem is the same as in the mature stem. The form of the mature bundle, however, varies as to the number of protoxylem vessels according to the degree of elongation (Figs. 5, 6, 7). The youngest bundle strand is recognized by the denser cytoplasm of two or three cells (Fig. 3). These rapidly divide until a cross section of the bundle shows from 25 to 30 cells (Fig. 1). This is

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#### EXPLANATION OF PLATE I.

- Fig. 1. Cross-section of young stem tip showing two young bundles of the circle.  
 Fig. 2. Older stage of the same stem tip.  
 Figs. 3 and 4. Cross-section of young bundles.  
 Fig. 5. Bundle from rapidly growing region showing cambium-like cells caused by pressure of xylem and phloem.  
 Fig. 6. Portion of rhizome of longer internode near surface of ground showing two protoxylem vessels and lignified endodermis and pericycle.  
 Fig. 7. Portion of rhizome showing heavy endodermis and vascular bundle without protoxylem. Epidermis and hypodermis are thick-walled and lignified.



FIGS 8 TO 15, *Spartina michauxiana* Hitchc.

followed by a general enlargement and division of the whole strand until the first protoxylem vessels are formed (Fig. 1), and then the cells of the phloem region continue to divide and enlarge so that they appear as a definite area of the bundle (Fig. 1). In the slow-growing internode only one or two small protoxylem vessels are formed, sometimes none at all (Figs. 6, 7); for example, in the rhizome the phloem is differentiated first and only one to three metaxylem vessels are formed (Fig. 7). In the aerial stem of long internodes from two to five protoxylem vessels are developed (Figs. 5, 6).

In the rhizome there is a pronounced endodermis and a pericycle (Fig. 7) which is of thick-walled lignified cells and almost surrounds the vascular strands that in turn become wholly lignified except for the phloem (Fig. 7). The cortex develops small air passages, and the epidermis and hypodermal layers become lignified. In this same stem the pericycle and endodermis gradually diminish as the culm becomes aerial and in some forms entirely disappear in the above-ground parts.

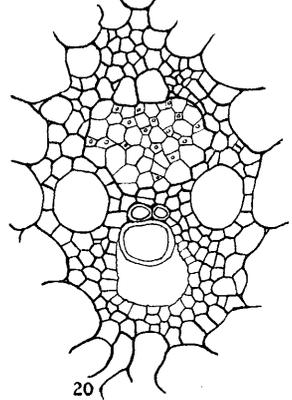
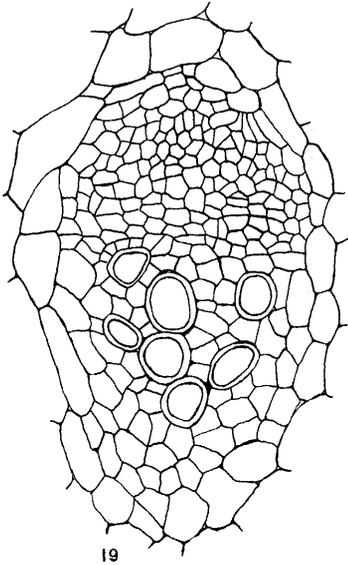
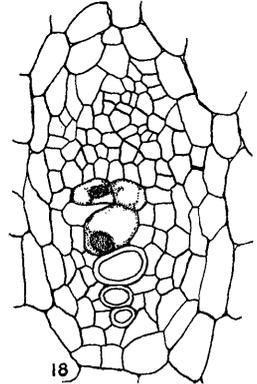
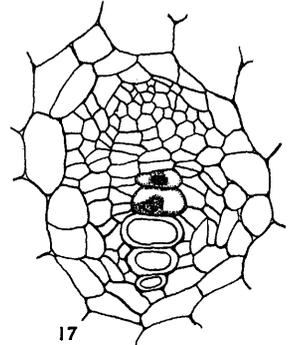
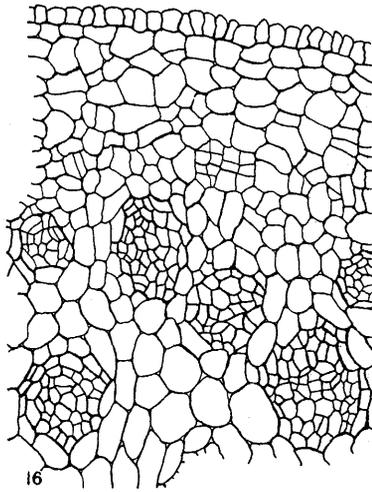
*Spartina michauxiana* Hitchc.

(Plate II)

In *Spartina* the vascular strands arise in a band of two or three circles with a definite cortex (Fig. 8). The bundles first appear as they do in the other forms, but the metaxylem vessels are the first water tubes to appear (Fig. 12). The sieve tubes and their companion cells form at approximately the same time. Similarly in the rhizome and slow-growing internodes of the aerial stem no protoxylem vessels are found, but in the elongated internodes of the aerial part there may be two or more (Figs. 9, 10). In the rhizome the outer circle of vascular bundles is imbedded in the lignified pericycle which is surrounded by an endodermis (Fig. 14). The inner circles are not connected to the pericycle except for an occasional bundle. This structure is in contrast to the aerial stem of *Spartina* where the endodermis and pericycle appear only in fragments. In both rhizome and aerial stems the epidermis and hypodermal layers become thick-walled and lignified, and in both the cortex enlarges and there appear numerous lysigenous air passages (Fig. 14).

EXPLANATION OF PLATE II

- Fig. 8. Portion of young stem tip showing young vascular bundles and cortex.  
 Fig. 9. Inner vascular bundle of the aerial stem.  
 Fig. 10. Portion of aerial stem showing cortex with air passages, and one of the outer circle of vascular bundles attached to a fragment of the pericycle.  
 Fig. 11. Young bundle showing beginning of phloem before any xylem tubes appear.  
 Fig. 12. Young bundle showing phloem with companion cells and a single metaxylem vessel.  
 Fig. 13. Cross-section of bundle showing a single spiral vessel which was formed after the metaxylem vessels were enlarged.  
 Fig. 14. Portion of cross-section of mature rhizome.  
 Fig. 15. A single vascular bundle of a short internode of rhizome without spiral vessels, all of the cells lignified except phloem.



FIGS. 16 TO 20, *Zea Mays* L.

- Fig. 16. Portion of cross-section of young stem tip.  
Fig. 17. Immature bundle of young plant with five spiral vessels and no metaxylem, and with cells pressed into cambium-like shapes.  
Fig. 18. Immature bundle from same region as Fig. 17 with lateral pressure showing complete lack of cambium-like cells.  
Fig. 19. Vascular bundle from young rapidly growing plant with seven protoxylem vessels and no metaxylem vessels.  
Fig. 20. Immature vascular bundle of normal type, no indication of cambium.

*Calamovilfa longifolia* (Hook.) Hack.

The stem structure of *Calamovilfa* (Text Fig. 1) is similar to that of *Spartina* except that in the mature rhizome all the vascular portion of the stele becomes very thick-walled and even the phloem cells become lignified. The vascular bundle originates from a single cell and develops as in *Agropyron* with protoxylem vessels only in the bundles of the longer internodes. In this highly lignified stem some of the bundles in the nodes and short internodes are amphivasal. In the aerial stem there is evident cortex, and a pith that finally breaks down in the center so that the stem has a small cavity.

*Zea Mays*.

(Plate III)

In the stem tip of corn the vascular strands develop at some distance from the epidermis and mark off a cortex (Fig. 16). This apparently disappears because there is no development of pericycle and endodermis, and therefore with the abundant leaf traces the mature stems have numerous scattered bundles without a definite marking to show the limits of the stele and cortex.

The vascular strands evidently begin with two or more cells, and the protoxylem vessels are the first cells of the bundle to be differentiated. In the rapidly growing young plants of the laboratory where there is little lignification the number of protoxylem vessels is larger than in any other form examined (Figs. 17, 18, 19), and in these bundles no metaxylem vessels are developed. This is a variation from normally grown plants where the vascular bundle develops as in *Agropyron* and *Calamovilfa* (Figs. 16, 20). As in the other grasses lignification in aerial stems is greatest just below the node. In the short internodes the bundles do not have lacunae, although practically all the strands of the average length of internode have lacunae by reason of the destruction of the protoxylem vessels by rapid elongation after their lignification (Fig. 20).

## CAMBIAL ACTIVITY.

Crysler (8), Van Teighem (23), Guillard (11), and Andersohn (1) have reported and figured a temporary cambium in several grasses. One does not find in their studies any figure of mitotic phases in these cells; and evidently all the figures were taken from either mature or nearly mature aerial stems, or from the meristematic region of the lower part of the internode. The present study has not revealed any cell division in the area between xylem and phloem after these areas are differentiated except for occasional cells. Cells divisions do occur in the xylem and phloem areas of the vascular strand and not in the cells between them where the cambium would originate. The number of cells that occur on a line from the

inner portion of the phloem to the innermost cell of the xylem is within one or two cells of being a constant number, regardless of the size of the bundle. Apparently this number does not change after the xylem vessels begin to be lignified. The explanation of the appearance of cambial cells—and this is very striking—is that the rapid enlargement of the phloem and xylem presses the intervening cells into the shape of cambium cells (Figs. 1, 2, 5, 17). In those bundles where the pressure is lateral, although several protoxylem vessels are formed, no semblance of cambium appears (Figs. 18, 19).

The meristematic condition of all cells of the vascular bundle in growing regions is evident from the continued differentiation of protoxylem vessels in such bundles (Figs. 17, 18, 19). The appearance of a cambial arrangement of cells in a relatively small number of bundles and its absence in other bundles of the same size in the same meristematic area, (Figs. 18, 19), the absence of observed mitosis, and the constancy of number of cells mentioned above, all seem to demonstrate that there is not even a temporary cambium in the grass bundle (Fig. 21).

#### DISCUSSION.

If a complete study of the comparative anatomy of the grass tribes is made it now seems possible to the writer that some of the questions regarding the position of the tribes in a developmental series may be solved. The scattered vascular bundle type is certainly the top of the series, as it is now placed, and the writer believes that the single circle of bundles between cortex and pith is the lowest form of the series (22). The relationship of genera and their proper places within the tribes may be made clear also by the study of the vascular anatomy. The question of species must take into account the effect of environment of stem structures, since the development of tissues shows such definite variations in response to the rates of growth (Figs. 5, 6, 7, 10, 14, 18, 19, 20). The cortex, endodermis, and pericycle vary in amount and degree of lignification depending not only on the inherited type of bundle arrangement in the series pointed out but also on the rate of growth. The marked differences in the development of the xylem strands is directly related to the rate of growth, and there seems to be very little variation in the structure of the individual bundle phylogenetically except as to the amount and character of the bundle pericycle.

Various authors have figured and labeled a proto-phloem as distinct from the mature phloem. It is evident from the figures shown in this paper that there is no such distinction. The xylem and phloem develop by cell divisions in the inner and outer portions of the vascular bundles and there is no further development after their differentiation except the thickening and lignification of the cell walls of the water tubes and bundle pericycle.

## SUMMARY.

1. All the stem tips of the grasses studied show a stele and a cortex even though they are not delimited in the mature stem.

2. The vascular bundles of the grasses are not all arranged as in *Zea*, for the arrangement varies from a single circle through a series of forms to the scattered vascular bundle type.

3. The hollow stem or solid stem in the grasses depends first upon the arrangement and number of the vascular bundles and second upon the rate of growth.

4. There is a tendency for both the stelar and bundle pericycle to become less pronounced as the scattered vascular bundle type is approached.

5. In the vascular bundles:

*a* The number of the protoxylem vessels varies with the amount of elongation and the duration of the meristematic condition.

*b* There is no distinction of proto-phloem and meta-phloem.

*c* There is no temporary cambium.

## REFERENCES.

1. **Anderssohn, Miss S.** Uber d. Entwickel d. primaren Gefassbunzelstrange d. Monokotylen. Bihang. till K. Svenska. Vetenska Akad. Handl. 12: 188-197. 1899.
2. **Arber, Agnes.** Studies in the Gramineae. IX. 1. The Nodal Plexus. 2. Amphivasal Bundles. Annals of Botany 44: 593-620. 1930.
3. **Artschwager, Ernest.** Anatomy of the vegetative organs of sugar cane. Jour. Agric. Res. 30: 197-221. 1925.
4. **Bugnon, P.** Origine des faisceaux liberoligneux transverses forment un lacis aux noeuds des Graminees. Compt. Rend. 170: 671-673. 1920.
5. ———. Causes du parcours transversal des faisceaux liberoligneux aux noeuds des Graminees. Compt. Rend. 171: 673-675. 1920.
6. **Canfield, R. H.** Solid and hollow stemmed grasses of the Jornada experimental range. Science 78: 342. 1933.
7. **Carrier, Lyman.** The identification of grasses by vegetative characters. U. S. Dept. of Agri. Bull. 461. 1917.
8. **Cryslor, M. A.** The nodes of grasses. Bot. Gaz. 41: 1-16. 1906.
9. **Evans, Arthur T.** Vascularization of the node in *Zea mays*. Bot. Gaz. 85: 97-103. 1928.

10. **Duval-Jouve, J.** Histotaxie des feuilles de Graminees. *Ann. Sci. Nat. Bot.* (vi) 1: 294-371. 1875.
11. **Guillard, A.** Anatomie de la tige des Monocotyledons. *Am. Sci. Nat. Bot.* 5: 6e ser. 1878.
12. **Guntz.** Untersuchungen uber die anatomische structure der Gramneenblätter. Inaug. dissert. Leipsig, 1886.
13. **Holm, Theo.** Studies in the Gramineae. IX. The Gramineae of the alpine region of the Rocky Mts. in Colorado. *Bot. Gaz.* 46: 422-444. 1908.
14. **Johanson.** The anatomy of the stolons of the Gramineae. *Kgl. Svenska Vetensk. Akad. Hdlgr.* 23, No. 2. Review by Theo. Holm in *Bot. Gaz.* 17: 121-122. 1892.
15. **Pee-Laby, E.** Etude anatomique de la feuille des Graminees de la France. *Am. Sci. Nat. Bot.* 8: 8e ser. 227-346. 1898.
16. **Lewton-Brain, L.** On the anatomy of the leaves of British grasses. *Trans. Linn. Soc. London. Bot.* 6: ser. 2, 315-359. 1904.
17. **Rosler, Paul.** Histologische Studien am Vegetationspunkt von *Triticum Vulgare*. *Zeitschr. wiss. Biol. Abt. e. Planta.* 5: 28-69. 1928.
18. **Sabnis, T. S.** The physiological anatomy of the plants of the Indian desert. *Gramineae. Jour. Ind. Bot.* 2: 222-227. 1921.
19. **Schwendener, S.** Mestomschleiden der Gramineenblätter. *Sitzungber. K. Acad. Berlin*, 405. 1890.
20. **Solereder, Hans. and Meyer, Fritz J.** Systematische Anatomie der Monocotyleden. *Glumiflorae. Heft. 2*, 176 pp. 1929.
21. **Stover, E. L.** The vascular anatomy of *Calamovilfa longifolia*. *Ohio Jour. Sci.* 24: 169-179. 1924.
22. ———. Studies in the comparative anatomy of the grass tribes. (Paper read before Section G, A. A. A. S., at Cleveland.) Unpublished.
23. **Van Tieghem, Pb.** Recherches sur la structure des feuilles de monocotyledons. *Compt. Rendu. Ac. Sc. Paris*, 48: 981. 1869.
24. **Volkens, G.** Die Flora der Aegyptisch-Arabischen. Wurste, Berlin. 1887.

#### Invertebrate Zoology.

This, the most recent of the many zoological textbooks written by the author, is stated to be a revision and expansion of his first, the *Introduction to Zoology*, published in 1910. It is well planned and organized, and in the same general style as his previous books. The classification is, on the whole, conservative. Short, but comprehensive descriptions of representative types are given, in which both structural and functional aspects are stressed. Illustrations are numerous, and for the most part clear and well selected, although there are a few serious omissions and some poor selections. The only strictly original illustrations are the eight excellent full-page stereograms by Mrs. Root.

Careful examination and several months' use as a textbook in the reviewer's classes have disclosed a number of defects. Typographical errors are far too frequent for a book of this character. Drawings borrowed from other authors have usually been redrawn and relabeled; and while the redrawing has been good, the relabeling has in several cases been careless and confused. (For example, figures 71, 252, 254, 256.) The life history of *Gonionemus* is not given as fully as it might have been; the author does not seem to be familiar with Joseph's 1925 paper on this subject. In the chapter on Mollusca there is no discussion of the lamellibranch gill as a feeding mechanism, and no adequate description of its structure or its ciliation.

Similar omissions may be noted in other chapters also. The discussions of the comparative anatomy and phylogeny of the invertebrates seem inadequate for an advanced textbook of invertebrate zoology.—W. J. KOSTER.

*Invertebrate Zoology*, by Robert W. Hegner. xiii + 570 pp. New York, The Macmillan Co., 1933.