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Anatomical Study of the Grass Tribe Festuceae

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ANATOMICAL STUDY OF THE GRASS

TRIBE FESTUCEAE

(TITLE)

BY

MARIANNE MORGAN

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YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
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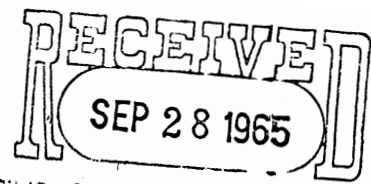
27 September, 1965

Dear Dear Hamand:

Because my advisor and I plan to publish my thesis in the near future, I am not signing the enclosed form.

Yours truly,

Marianne Morgan



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ACKNOWLEDGMENTS

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ANATOMICAL STUDY OF THE GRASS TRIBE FESTUCEAE

In recent years the taxonomic importance of anatomical characteristics has been realized in the family Gramineae. Using one or more of these characteristics, a few new attempts have been made at establishing a phylogenetic classification of this group. In many of these studies, however, only one or two species from each genus were examined.

In this study, the lodicule, leaf anatomy, and leaf epidermis from each species of the classical tribe Festuceae found growing in Illinois were examined as was the embryo from most genera and subgenera. In general, the results were in agreement with those obtained by Decker (1964) and Reeder (1957); however, some discrepancies did occur which will be discussed later in the paper. Only the Illinois species which Jones (1963) includes in the classical tribe Festuceae were studied.

METHODS AND MATERIALS

Most of the specimens used in this study were from herbarium material that was obtained from the herbaria of Eastern Illinois University and the University of Illinois. When available, living specimens were used, particularly for studying leaf anatomy.

Embryos were prepared for study similar to techniques outlined by Reeder (1957) and later by Decker (1964). The

caryopses were boiled for approximately five minutes, placed in a three per cent solution of potassium hydroxide until the endosperm was soft, and the embryo was then removed. It was then oriented in agar, stained with basic fuschin to fascilitate handling, dehydrated in the standard Tertiary Butyl Alcohol series, and embedded in paraffin. Sections were cut at ten microns and stained with safranin and fast green.

Leaf material for cross sections was selected from two to three centimeters above the ligule. The material was boiled in water until softened, dehydrated in the standard Tertiary Butyl Alcohol series, and embedded in paraffin. Sections were cut at twenty microns and stained with safranin.

The leaf epidermis was obtained by first boiling leaf sections until softened. The leaf was then placed on a glass slide where the leaf tissue was scraped off leaving only the epidermis next to the slide. This procedure was followed for both the upper and lower epidermis. These epidermal sections were placed in a watch glass containing water, and then into a solution of two per cent alum containing two to four drops of a one per cent solution of methylene blue. The sections were counterstained in a solution of ruthenium red, passed through an alcohol dehydration series, and mounted in permount.

Lodicules were prepared by boiling the grass spikelets in water for five to seven minutes, dissecting out the lodicules, and mounting them on a slide with petroleum jelly.

RESULTS AND DISCUSSION

For convenience and easy comparison, the classification of the grass tribe Festuceae as outlined by Decker (1964) is used in Table I. Only the species placed in the traditional tribe Festuceae by Jones (1953) are included in this table. For each species information with regard to the type of lodicule, leaf cross section, leaf epidermis, and embryo is tabulated.

Lodicule - Lodicules, which are thought to be reduced perianth parts, are small scales found at the base of the ovary in the grass floret. Very little systematic importance was attributed to these until Stebbins (1956) showed that they may be indicators of taxonomic relationship. Since that time, four distinct lodicule types have been described (Decker, 1964).

In examining the lodicules of the Illinois grasses of the tribe Festuceae, three of these four types were observed. These types, the festucoid, panicoid, and eragrostoid, are distinguished by shape and by the presence or absence of vascularization. The festucoid type is relatively long, pointed, membranous, lacks vascularization, and often has a thickened base (Fig. 1 & 2). The panicoid type is short and truncate, thickened throughout and with heavy vascularization (Fig. 3), while the eragrostoid type is similar to the panicoid type but lacks vascularization (Fig. 4).

All species of the genera Briza, Bromis, Dactylis, Diarrhena, Festuca, Poa, and Puccinellia included in this study have

festucoid (F) type lodicules (Fig. 1 & 2). Though all species have this type of lodicule, some variation does exist as to texture, size, shape, and the presence or absence of hairs. Most members of the genus Bromus lack the small lateral lobe (Fig. 2), while it is common in most species of Festuca. The latter species also have a more delicate lodicule. In some species of Bromus, hairs are commonly found on the lodicules.

The panicoid (P) type lodicule was found in all members of the genera Distichlis, Eragrostis, Phragmites, Redfieldia, Tridens, and Triplasis included in this study (Fig. 3). Again, a great deal of variation exists in shape and size, but all are generally truncate and have vascularization. Phragmites communis (Fig. 5) has an apical point that is membranous, and extremely thickened vascularized areas in the basal region. Although this species does not display the typical panicoid type shape, it does have heavy vascularization. Therefore, it is considered to be panicoid.

Only three genera (Schizachne, Melica, and Uniola) included in this study consistently have eragrostoid (T) type lodicules (Fig. 4). In these genera, the lodicules are fused, truncate, and lack vascularization. Of the six species of Glyceria studied, five have the typical eragrostoid lodicules while one species, Glyceria pallida has the festucoid type. Numerous specimens of this species were examined, and in all, the festucoid type of lodicule was observed. Uniola latifolia (Fig. 6) is listed as

having a panicoid type of lodicule by Decker (1963), but no vascularization was found in the specimens examined in this study.

Leaf cross section - Variation in the anatomy as revealed by transverse sections has been emphasized as a fundamental character by Hubbard (1948), Stebbins (1956), Brown (1958), and others for determining relationships in the Gramineae. Important characters used include the nature of the two sheaths that surround the vascular bundle, the arrangement of the chlorenchyma tissue, the presence or absence and position of the bulliform cells, and the distribution of the schlerenchyma tissue between the vascular bundles and the epidermis.

According to Brown (1958) six groups can be found, based on leaf anatomy using some of the characteristics listed above. Brown states that the criteria used to distinguish these groups are the presence or absence of the endodermis (inner bundle sheath); the structure and function of the parenchyma sheath (outer bundle sheath); and the arrangement of the cells immediately outside the parenchyma sheath.

In studying the Festucoid grasses of Illinois, four of the six types of leaf anatomy outlined by Brown (1958) were found. The festucoid (F) type has a well developed, thick-walled endodermis; an indistinct parenchyma sheath which is thin-walled and contains chloroplasts similar to those of the chlorenchyma; and loose, irregularly arranged, spongy mesophyll (Fig. 7). The eragrostoid (E)

type has an endodermis, at least around the large bundles; a well developed parenchyma sheath with cells containing specialized plastids; and a chlorenchyma of long, narrow, radially arranged cells with very few chloroplasts (Fig. 8). The bambusoid (B) type has a well developed endodermis; a parenchyma sheath with thick-walled, rounded cells that contain typical chloroplasts; and a tightly packed chlorenchyma (Fig. 9). The arundinoid (A) type has a poorly developed endodermis; a greatly enlarged, thick-walled parenchyma sheath in which the cells lack chloroplasts; and densely packed chlorenchyma cells (Fig. 10). Most of the traditional Festucoid grasses of Illinois are placed into the Festucoid (F) or Eragrostoid (E) groups using leaf anatomy characteristics (Table I).

Of the genera studied, all of the species in the genera Briza, Bromus, Dactylis, Festuca, Glyceria, Malica, Poa, Diarrhena, Puccinellia, and Schizachne have festucoid type leaf anatomy (Fig. 7). However, some variation does exist. In some, the parenchyma sheath is nonexistent, while in others, a weak sheath is present. In most cases, the cells are very thin and chloroplasts are present, but usually they are not as numerous as in the cells of the spongy mesophyll. The leaf anatomy of Festuca elatior (Fig. 11) shows many similarities to that of the bambusoid type; the endodermis is present, the parenchyma sheath is well developed, thick-walled, and chloroplasts are present. The chlorenchyma is loosely arranged, however, and not tightly

packed as in the bambusoid.

Using leaf anatomy characteristics, all Illinois species of the genera Distichlis, Eragrostis, Redfieldia, Tridens, and Triplasis are placed in the Eragrostoid group (Fig. 8). In all species examined the endodermis is usually found surrounding the larger bundles but is not as well developed as in the Festucoid group; the parenchyma sheath is large, has thickened walls with the cells containing numerous specialized chloroplasts; and the chlorenchyma cells are radially arranged.

The two remaining genera, Uniola and Phragmites, are the only genera not placed in the Festucoid or Eragrostoid groups. Uniola, with its well developed endodermis, thickened parenchyma sheath with chloroplasts in the cells, and a compact chlorenchyma is placed in the Bambusoid group (Fig. 9). Phragmites, in contrast, has a weak endodermis and an extremely large parenchyma sheath that lacks chloroplasts, indicating a relationship with the Arundinoid group (Fig. 10).

Decker (1964) suggested that the presence or absence and extent of bulliform cells may be important for showing relationships. It was found, however, that the variation of this characteristic is too great to be usable. In some of the genera studied a few of the species lacked bulliform cells altogether, while in others the bulliform cells were well developed. In the genus Festuca the variability of these cells can be seen. Festuca ovina lacks bulliform cells (Fig. 12) while

these were present in Festuca obtusa (Fig. 13) and extremely well developed in Festuca elatior (Fig. 14).

Leaf epidermis - The significance of the leaf epidermis in the classification of grasses was pointed out by Prat (1932) when he found that by using the shape and structure of siliceous cells and stomata and the presence or absence of bicellular hairs, the Festucoid and Panicoid grasses could be distinguished. The importance of bicellular hairs was shown by Tateoka, Inoue, and Kawano (1959).

Decker (1964) used three characteristics of leaf epidermis to distinguish the various groups of grasses. He found that the stomata were rectangular (festucoid) or oval (panicoid) in shape; the bicellular hairs were absent (festucoid), linear bicellular (panicoid), or bulbous bicellular (eragrostoid); and the siliceous cells were rectangular (festucoid), dumbbell-shaped (panicoid), saddle-shaped (eragrostoid), or a mixture of siliceous cells with no type being predominant (M).

Using the criteria mentioned above, four basic groups can be recognized in the classical tribe Festuceae of Illinois (Table I). In the Festucoid group (Fig. 15) the stomata are rectangular in shape (F), no bicellular hairs are present (F), and siliceous cells are predominantly rectangular in outline (F). Most species of the genera Briza, Bromus, Dactylis, Diarrhena, Festuca, Glyceria, Melica, Poa, Puccinellia, and Schizachne

have the F-F-F type of epidermis. Some variation in characters does occur among these genera. The stomata of Festuca elatior varies from the typical festucoid type to almost panicoid in shape (Fig. 16), but the rectangular type predominates. Though bicellular hairs are generally not found in the Festucoid group, eragrostoid type hairs are found on Poa autumnalis giving it an F-E-F epidermis. Siliceous cells vary extensively throughout the genera. Rectangular types are most common, but dissected rectangular occur in many species of Glyceria, and nearly round ones are found in Festuca elatior.

In the Eragrostoid group, which is composed of the genera Distichlis, Eragrostis, Redfieldia, Tridens, and Triplasis, most species display the P-E-E or P-E-P type of epidermis (Fig. 17). Here again, some variation exists in the shape of the siliceous cells. In the genera Eragrostis and Tridens, both panicoid and eragrostoid type siliceous cells are present, and the type is often difficult to distinguish. In Table I, the third letter in the epidermis column indicates the predominant type of siliceous cell that was found. Variation also exists in the number of bicellular hairs present on the epidermis. Some species of Eragrostis have few hairs while in Eragrostis poaeoides, no hairs are found (P-F-E).

The Centothecoid group of Decker (1964) is represented in our area by the single species Uniola latifolia. This species has oval stomata, linear bicellular hairs, and dumbbell-shaped

siliceous cells giving it a P-P-P type of epidermis (Fig. 18).

The fourth group, Arundinoid, is represented in Illinois by Phragmites communis. In this species a P-P-E type of epidermis is found (Fig. 19). Decker (1964) does not indicate the type of bicellular hairs found, but numerous linear hairs were found in the specimens examined.

Embryo - The work of Reeder (1957) pointed out the importance of the grass embryo in classification when he examined the embryo in median sagittal section and in transverse section through the coleoptile. Decker (1964) repeated the work of Reeder and extended it to include many other grass genera.

Important characters revealed in median sagittal section are the course of the vascular tissue and whether an internode is absent (F) or present (P), the presence (+) or absence (-) of an epiblast, and the absence (F) or presence (P) of a cleft between the scutellum and the coleorhiza. In transverse section, the shape of the embryonic leaf can be observed. If the margins of this leaf meet it is festucoid (F), and if they overlap it is panicoid (P). The festucoid type also has fewer vascular traces in the embryonic leaf than the panicoid type.

Six basic groups of embryos can be recognized using the above characteristics, four of which are found in the embryos included in this study. In the Festucoid group, there is no internode present in the vascular tissue (F), an epiblast is

usually present (+), there is no cleft between the scutellum and the coleorhiza (F), and the margins of the embryonic leaf merely meet and do not overlap (F). The genera found to have the F+FF type embryo include Briza, Dactylis, Festuca, Glyceria, Melica, Poa, Puccinellia, and Schizachne (Fig. 20 & 21). Bromus is also placed in this group even though it has no epiblast and therefore is F-FF (Fig. 22 & 23).

The genera Distichlis, Eragrostis, Redfieldia, Tridena, and Triplasis have the eragrostoid type embryo. It was found that an internode is present in the vascular system (P), an epiblast is present (+), a cleft is present between the scutellum and coleorhiza (P), and the first embryonic leaf meets but does not overlap (F). The embryo, therefore, has the F+PF configuration (Fig. 24 & 25).

Reeder (1957) considered the Bambusoid group to have a F+PP embryo. After further study Reeder (1962) found that the correct formula should be F+PP. In this study, the only genus found to have this formula was Diarrhena (Fig. 26 & 27). In studies by Decker (1964) and Reeder (1957), this genus was assigned the formula F+FF.

Uniola is the only genus of the Illinois grasses of the classical tribe Festuceae to have a F+PP embryo (Fig. 28 & 29). It has an internode in the vascular system (P), an epiblast (+), a cleft between the scutellum and coleorhiza (P), and an overlapping embryonic leaf (P), and is therefore a member of the Centothecoid

group.

Embryos of Phragmites communis are not included in the study because mature caryopses could not be obtained.

CONCLUSIONS

In most cases, the results of this study agree with those obtained by previous authors. Several exceptions have been found, however, which indicates that numerous species should be analyzed before a genus is placed in a particular group. The exceptions found during this study are analyzed below.

In Phragmites communis a type of lodicule occurs which has not been discussed in previous literature. Decker (1964) considered the lodicule of this species to be panicoid because of the vascularization. In the present study, the panicoid vascularization was observed, but the lodicule shape was festucoid. Because of the vascularization, it is tentatively being considered as panicoid.

Uniola latifolia is listed by Decker (1964) as having an arundinoid type leaf anatomy. Using the criteria of Brown (1958), Uniola displays the bambusoid type and not the arundinoid. It has a well developed endodermis and a thick walled parenchyma sheath containing chloroplasts, both typical of the bambusoid type.

Variation in the presence and type of bicellular hairs occurs in the classical tribe Festuceae in Illinois. Poa autumnalis, given an F-F-F epidermis formula by Decker (1964), was found to have eragrostoid type bicellular hairs. Furthermore, no bicellular hairs

were found in Eragrostis poseoides, while Decker (1964) states that eragrostoid type hairs are present. In several other species of Eragrostis, the bicellular hairs were very sparse and difficult to find. The presence of bicellular hairs appears not to be a good criterion for this genus.

All species of the genus Glyceria have an eragrostoid (T) type lodicule with the exception of Glyceria pallida, which has a lodicule with the typical festucoid shape (F). This probably indicates that some variation exists in this characteristic, making it unreliable for consistently separating the various groups.

Instead of having a festucoid embryo as thought previously, Diarrhena americana seems to have a bambusoid type (F+PP). Reeder (1957) and Decker (1964) assigned this genus a formula of F+FF. However, the margins of the embryonic leaf distinctly overlap, and there is a small cleft between the scutellum and the coleorhiza. Further studies should be undertaken with this species to determine its true relationship in the Gramineae.

Though there are exceptions to the criteria used in anatomical investigations existing in the Illinois species of the classical tribe Festuceae, the anatomical traits seem, in most cases, to be consistent.

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- Fig. 1. Festucoid: lodicule of Bromus inermis (F).
- Fig. 2. Festucoid: lodicule of Poa pratensis (F)
- Fig. 3. Panicoid: lodicule of Eragrostis cilianensis (P).
- Fig. 4. Eragrostoid: lodicule of Glyceria striata (T).
- Fig. 5. Lodicule of Phragmites communis (P).
- Fig. 6. Lodicule of Uniola latifolia (T)
- Fig. 7. Festucoid: leaf cross section of Poa pratensis (F).
en, endodermis; ps, parenchyma sheath.
- Fig. 8. Eragrostoid: leaf cross section of Distichlis stricta. (E).
ch, chlorenchyma.
- Fig. 9. Bambusoid: leaf cross section of Uniola latifolia (B).
- Fig. 10. Arundinoid: leaf cross section of Phragmites communis (A).
- Fig. 11. Festuca elatior cross section.
- Fig. 12. Epidermis of Festuca ovina lacking bulliform cells.
- Fig. 13. Bulliform cells of Festuca obtusa.
- Fig. 14. Bulliform cells of Festuca elatior.

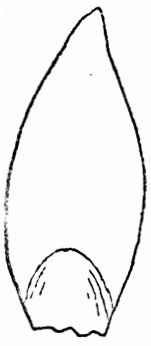


Fig. 1



Fig. 2



Fig. 3



Fig. 4

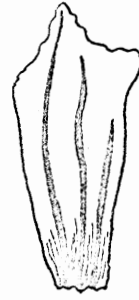


Fig. 5



Fig. 6

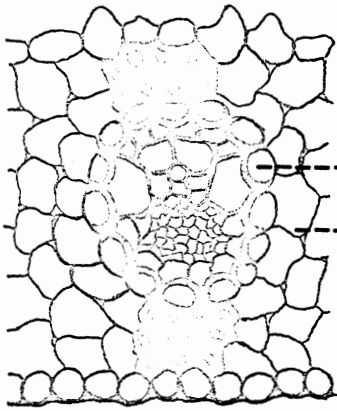


Fig. 7

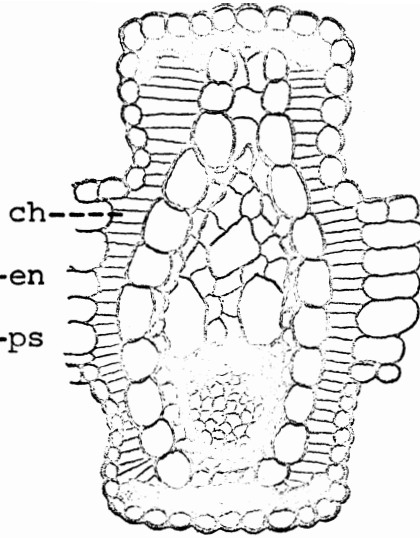


Fig. 8

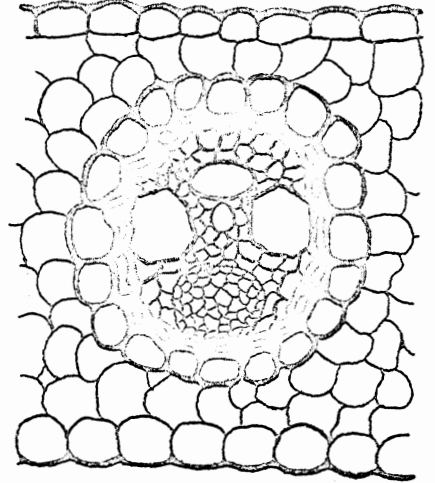


Fig. 9



Fig. 12

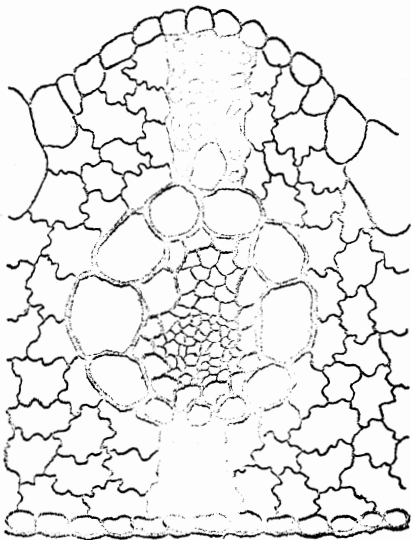


Fig. 10

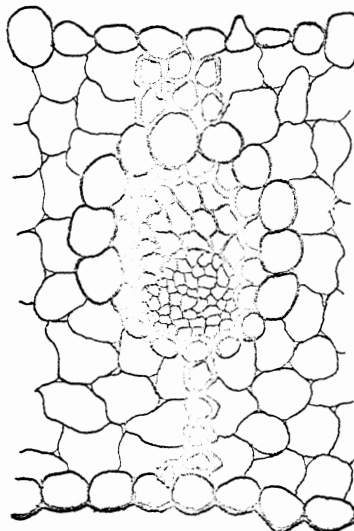


Fig. 11

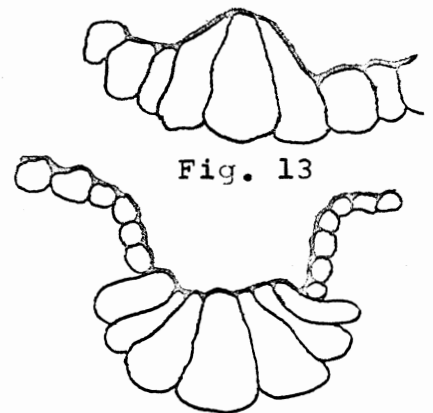


Fig. 13

Fig. 14

- Fig. 15. Festucoid: epidermis of Bromus inermis (F-F-F).
- Fig. 16. Festuca elatior epidermis with stomata and eragrostoid siliceous cells.
- Fig. 17. Eragrostoid: epidermis of Eragrostis cilianensis (F-E-E).
- Fig. 18. Centothecoid: epidermis of Uniola latifolia (P-P-P).
- Fig. 19. Arundinoid: epidermis of Phragmites communis (P-P-E).
- Fig. 20-21. Festucoid: cross and longitudinal section of embryo of Briza maxima (F+FF).
- Fig. 22-23. Festucoid: cross and longitudinal section of embryo of Bromus latiglumis (F+FF).
- Fig. 24-25. Eragrostoid: cross and longitudinal section of embryo of Tridens flavus (P+FF).
- Fig. 26-27. Bambusoid: cross and longitudinal section of embryo of Diarrhena americana (F+PP).
- Fig. 28-29. Centothecoid: cross and longitudinal section of Uniola latifolia embryo (P+PP).

Fig. 15. st, stomate; si, siliceous cell.

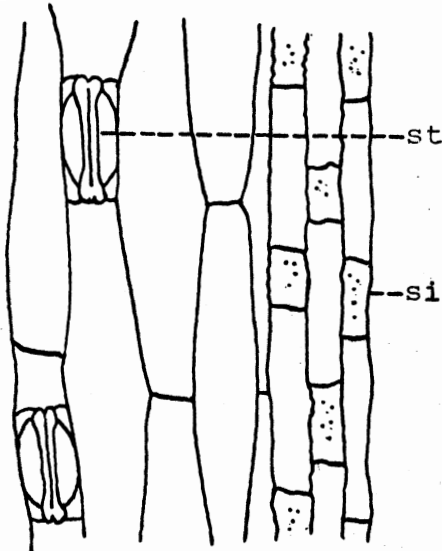


Fig. 15

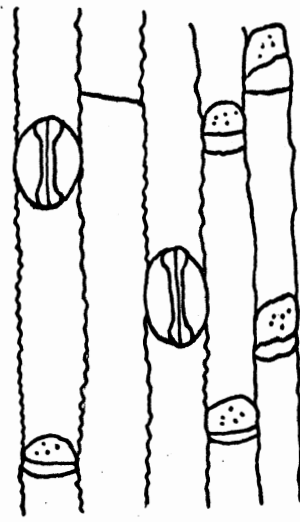


Fig. 16

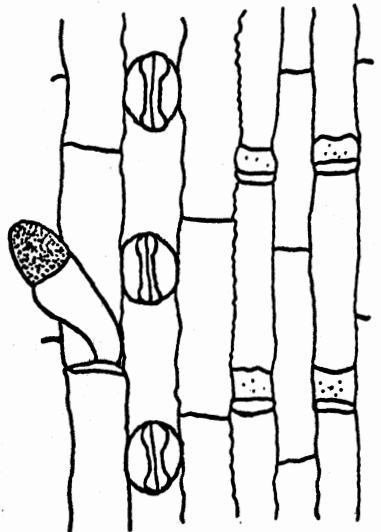


Fig. 17

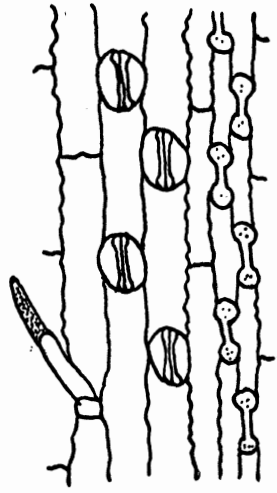


Fig. 18

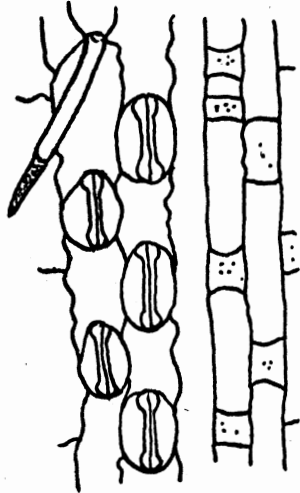


Fig. 19



Fig. 20



Fig. 21



Fig. 22



Fig. 24



Fig. 26



Fig. 28



Fig. 23



Fig. 25



Fig. 27



Fig. 29

Table I - Summary of the Characteristics and New Taxonomic Relationships of the Genera from the Classical Tribe Festuceae of Illinois.

	Leaf			
	Lodicule	Leaf x.s.	epidermis	Embryo
GROUP 1. ANUNDINOID				
<u>Phragmites communis</u>	P	A	P-P-E	
GROUP 2. CENOTHECOID				
<u>Uniola latifolia</u>	T	B	P-P-P	P+PP
GROUP 3. ERAGNOSTOID				
<u>Dactyloctenium stricta</u>	P	E	P-E-E	P+FF
<u>Eragrostis capillaris</u>	P	E	P-E-E	
<u>cilianensis</u>	P	E	P-E-E	
<u>Frankii</u>	P	E	P-E-E	
<u>hypnoides</u>	P	E	P-E-E	
<u>pectinacea</u>	P	E	P-E-P	
<u>roseoides</u>	P	E	P-F-P	
<u>rustana</u>	P	E	P-E-P	
<u>spectabilis</u>	P	E	P-E-E	
<u>trichodes</u>	P	E	P-E-E	P+FF
<u>Redfieldia flavosa</u>	P	E	P-E-E	P+P?
<u>Tridens flavus</u>	P	E	P-E-E	P+FF
<u>strictus</u>	P	E	P-E-E	
<u>Triploasis purpurea</u>	P	E	P-E-P	P+FF
GROUP 4. FESTUCOID				
<u>Brisa maxima</u>	F	F	F-F-F	F+FF
<u>Bromus arvensis</u>	F	F	F-F-F	
<u>brissiformis</u>	F	F	F-F-F	
<u>ciliatus</u>	F	F	F-F-F	
<u>convolutus</u>	F	F	F-F-F	
<u>inermis</u>	F	F	F-F-F	
<u>ispanicus</u>	F	F	F-F-F	F+FF
<u>kalni</u>	F	F	F-F-F	
<u>latiglumis</u>	F	F	F-F-F	F+FF
<u>marrinatus</u>	F	F	F-F-F	F+FF

Table I - cont'd

	Lodicule	Leaf x.s.	Leaf epidermis	Embryo
<u>Bromus Mollis</u>	F	F	F-F-F	
<u>nottowayanus</u>	F	F	F-F-F	
<u>purgans</u>	F	F	F-F-F	
<u>racemosus</u>	F	F	F-F-F	F+FF
<u>secalinus</u>	F	F	F-F-F	F+FF
<u>sterilis</u>	F	F	F-F-F	
<u>tectorum</u>	F	F	F-F-F	F+FF
<u>willdenowii</u>	F	F	F-F-F	
<u>Dactylis glomerata</u>	F	F	F-F-F	F+FF
<u>Diarrhena americana</u>	F	F	F-F-F	F+PP
<u>Festuca capillata</u>	F	F	F-F-F	
<u>elatior</u>	F	F	F-F-F	
<u>obtusa</u>	F	F	F-F-F	
<u>octoflora</u>	F	F	F-F-F	F+FF
<u>ovina</u>	F	F	F-F-F	
<u>paradoxa</u>	F	F	F-F-F	
<u>Glyceria borealis</u>	T	F	F-F-F	F+FF
<u>canadensis</u>	T	F	F-F-F	F+FF
<u>grandis</u>	T	F	F-F-F	F+FF
<u>pallida</u>	F	F	F-F-F	
<u>septentrionalis</u>	T	F	F-F-F	
<u>striata</u>	T	F	F-F-F	
<u>Melica mutica</u>	T	F	F-F-F	
<u>nitens</u>	T	F	F-F-F	F+FF
<u>Poa annua</u>	F	F	F-F-F	
<u>autumnalis</u>	F	F	F-F-F	
<u>chapmaniana</u>	F	F	F-F-F	
<u>compressa</u>	F	F	F-F-F	
<u>languida</u>	F	F	F-F-F	
<u>palustris</u>	F	F	F-F-F	
<u>pratensis</u>	F	F	F-F-F	
<u>sylvestris</u>	F	F	F-F-F	F+FF
<u>trivialis</u>	F	F	F-F-F	
<u>wolffii</u>	F	F	F-F-F	
<u>Puccenellia distans</u>	F	F	F-F-F	F+F?
<u>Schizachne purpurascens</u>	T	F	F-F-F	F+FF