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A Study of the Subfamily Classification in the Gramineae

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A STUDY OF THE SUBFAMILY CLASSIFICATION IN THE GRAMINEAE

(TITLE)

BY

Jimmy L. Carlen
B.S. in Ed., Eastern Illinois University, 1969

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
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I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
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INTRODUCTION

In the past 25 years, the use of new anatomical, morphological, and cytological criteria have been very significant in the separation of the Gramineae into 6 distinct subfamilies. External morphological characteristics are still, however, the prime criteria employed in the differentiation of genera, species, subspecies, and varieties.

At present, some of the most commonly used of these "new" taxonomic characteristics are those concerning the epidermis in the root hair region, the cell types in the leaf epidermis, the structure of the vascular bundle sheath and mesophyll of the leaf, the vascularization and structure of the embryo, the shape and vascularization of the lodicule, and the number and size of the chromosomes. Due to the extensive work of Brown (1958) on the leaf anatomy of the Gramineae and the work of Reeder (1957, 1962) on embryo structure in the Gramineae, these two criteria are the most important and reliable of the above mentioned characteristics. In addition, however, several minor characteristics which have not been studied in detail may prove to be of significance in determining phylogenetic relationships. Among these minor characteristics are certain structures associated with the grass stem. Stem characteristics that appear to have some taxonomic significance are the presence or absence of culm and sheath pulvini, whether the stem is hollow or solid, the presence or absence of branches and/or lateral buds at the upper nodes of the stem, and the number of rings of vascular bundles present in the internode region. An extensive study of Illinois grasses has been made in an effort to determine the taxonomic significance of the stem characteristics listed above.

MATERIALS AND METHODS

Ninety species of grasses were collected and analyzed for the characters listed in the following tables. Most of these species occur naturally in Illinois, although a few cultivated forms were also examined. In nearly all cases fresh material was employed though some species were examined using dried herbarium specimens. When this was done, the dried culms were boiled in water in an effort to restore the material to as near its original condition as possible.

The presence or absence of lateral buds and branches was determined by removing the leaf sheath from each node. The nodes were numbered starting with the inflorescence and the condition was recorded for each node. Usually 3 or 4 culms of each species were examined.

The presence or absence of the sheath and culm pulvinus was determined by making longitudinal sections with a razor blade of the nodal region. If a sheath pulvinus was present a definite swelling could be detected at the base of the leaf sheath (Figure 1). A culm pulvinus (Figure 2) showed up as a swelling of the culm itself. Both of these pulvini were situated directly above the actual node.

For the determination of the arrangement of the vascular bundles in the stem and of the internal internode structure (hollow vs. solid), the stem was boiled in water and left overnight to soften the sclerified tissue. Diagonal slices were then made with a razor blade and dipped in safranin.

In the following discussion of the subfamilies, Tables 1, 2, and 3 are used to summarize the stem characteristics of the species examined.

In columns 1 and 2 of these tables the presence or absence of a sheath pulvinus or a culm pulvinus has been indicated by a + or - respectively while an "I" indicates the pulvinus is indefinite. The culm internode condition, being either solid or hollow, has been represented in column 3 by an S or H respectively. In column 4 the average number of nodes directly below the inflorescence which lack both a lateral bud and a lateral branch of all the specimens examined has been indicated. Column 5, labeled "Extent of Branching", has been subdivided into two columns. The two columns show the incidence of branching out of the total number of nodes examined. The position of branching in column 6 has been determined by the relative positioning along the length of the culm.

The nomenclature of this paper follows that of Jones (1963) while the arrangement of the species into tribes and subfamilies is from Gould (1968).

DISCUSSION

Following mainly the classification of Stebbins (1956), Stebbins and Crampton (1961), and Gould (1968) the family Gramineae is presently divided into six subfamilies. In Illinois, as well as throughout the United States, the subfamilies Bambusoideae, Oryzoideae, and Arundinoideae are poorly represented. As a result, these three subfamilies have been omitted and only the subfamilies Festucoideae, Panicoideae, and Eragrostoideae are included in this study. Although not part of the present research, the characteristics of the root, leaf epidermis, leaf anatomy, lodicule, embryo, and cytology are discussed according to work published in these areas. The stem morphology and anatomy of each subfamily are then discussed by comparing results of previous studies with results obtained in the present study. The morphology and anatomy are discussed concerning the culm and sheath pulvini, culm internode condition, bud and branch position, and vascular bundle arrangement of the stem.

Subfamily Festucoideae

The subfamily Festucoideae in the United States is composed of 9 tribes, 41 genera and 391 species, which represent 36 percent of all United States species of the Gramineae (Gould, 1968). This subfamily has reached its maximum diversity in the cool climate of the northwestern United States and most species are found in regions with abundant moisture during the growing season. In general, the species of the Festucoideae are adapted to cool and cold, humid climates, although a few are found in tropical areas. Species of Bromus, Poa, Festuca, Agropyron, and other typical Festucoideae do grow well at high elevations in the tropics.

The subfamily Festucoideae as treated by Gould (1968) and others in recent floristic works represents a combination of grasses that have a number of morphological, anatomical, cytological, and physiological characteristics in common. Most of the important characteristics discussed below are used to separate the Festucoideae from the other subfamilies in the Gramineae.

Roots

Studies by Row and Reeder (1957) indicate that in the festucoid grasses the epidermal cells in the region of root hairs are alternately long and short, with only the short cells giving rise to root hairs. Furthermore, in most genera the root hairs arise from near the root tip end of the cells and angle toward the root tip.

Leaf Epidermis

Work on the leaf epidermis of true festucoid grasses has shown that the stomata are rectangular shaped; the silica cells are usually rounded, elliptical, long and narrow, or crescent-shaped; the short cells over the veins are usually solitary or paired, seldom if ever in long rows and bicellular microhairs are absent (Decker, 1964 and Gould, 1968).

Leaf Anatomy

Studies by Brown (1958) indicate that the grasses may be divided into six groups based on their internal leaf structure. In the Festucoideae the vascular bundle sheath is typically double, with an inner sheath of small, thick-walled cells and an outer sheath of large parenchyma cells which is frequently interrupted on one or both sides by sclerenchyma tissue. The chloroplasts of the parenchyma sheath and the mesophyll are similar and the mesophyll is loosely and irregularly arranged, with many large intercellular air spaces.

Lodicule

In all festucoid grasses studied by Decker (1964) the lodicules were elongated, pointed, thick at the base and membranous above, with little or no vascularization.

Embryo

Reeder (1957) and later Decker (1964) undertook a detailed study of the embryo anatomy of many grasses. Their studies show that festucoid grasses have characteristic embryos which differ significantly from those of other grass subfamilies. Reeder (1957) classified this embryo as the F+FF type. This means that in the embryo of festucoid grasses the vascular traces to the scutellum and coleoptile diverge at approximately the same point (F), an epiblast is usually present (+), the lower part of the scutellum is fused to the coleorhiza (F), and the embryonic leaf has few vascular bundles and its margins do not overlap (F).

Cytology

The basic chromosome number in the subfamily Festucoideae is X=7 and the chromosomes are comparatively large (Gould, 1968).

Stem Morphology

Of the 24 species of festucoid grasses examined, 21 lacked a definite culm pulvinus. Only *Brachyelytrum erectum* (Schreb.) Beauv. exhibited a definite culm pulvinus while an indefinite culm pulvinus was observed in *Oryzopsis racemosa* (Sm.) Ricker and *Agropyron repens* (L.) Beauv. Brown, Pratt, and Mobley (1959) in a study of 33 festucoid species found that none possessed a definite culm pulvinus; however, 7 were reported as indefinite. This lack of a culm pulvinus appears to be quite consistent character among the members of this subfamily.

All the festucoid grasses examined had a definite sheath pulvinus. Similar results were obtained by Brown, Pratt, and Mobley (1959) in their study. In most cases the sheath pulvinus was well developed and a very obvious characteristic (Figure 1). It could usually be observed without cutting a longitudinal section of the stem.

A study by Brown, Harris, and Graham (1959) listed 36 of 43 festucoid species studied as possessing either a hollow or small hollow internode. A small hollow condition may be described as a culm with comparatively thick walls and a small hollow center. The normal hollow condition noted by Brown et. al. (1959) may be interpreted as having relatively thin walls and a large portion of the central culm being devoid of tissue. In the present study, it was determined to be quite difficult to separate small hollow from hollow. Therefore, culm conditions in the present study have been treated as hollow or solid only. To make a comparison between the work of Brown et. al. (1959) and the present study small hollow and hollow were listed as hollow. In the present study culms of 24 festucoid species were examined concerning internode condition. Nineteen of the 24 examined were determined to be hollow.

Stebbins and Crampton (1961) in a review of grass characteristics suggested that in festucoid grasses the 3 or 4 nodes below the inflorescence never bear buds or branches. Present studies indicate that this is generally true. In column 5 of Table 1 the number of nodes lacking buds or branches is indicated. The number in this column indicates the average number of nodes below the inflorescence which lacked buds or branches. In 19 of the festucoid species studied, an average of 2 or more nodes below the inflorescence lacked buds or branches. Only in 2 species of *Agrostis*, 3 of *Poa*, and *Phalaris arundinacea* L. did the upper nodes have buds. In no specimens were buds observed at the first node below the inflorescence.

The position and extent of culm branching has been considered by Stebbins and Crampton (1961) to have some possible taxonomic significance. They indicate that the 3 or 4 nodes below the inflorescence never bear branches in festucoid grasses while in the eragrostoid and panicoid grasses all the nodes but the uppermost one immediately below the inflorescence either bear branches or can be induced to do so by decapitation. As would be expected, branching was not found to be very prevalent in the Festucoideae. In fact, branching was altogether lacking in 10 of the 24 festucoid representatives examined. Branching in the remaining 14 species was entirely restricted to the basal portions of the culm. In most cases the basal branching occurs at those nodes at or near the ground level, thereby acting as an asexual means of reproduction.

According to Gould (1968), the vascular bundles of the culm internodes of members of the subfamily Festucoideae are arranged in one to few rings at the inner margin of the cortex. The results of the present study somewhat agreed in that all species examined possessed more than 1 but never more than 4 rings of vascular bundles. It was also noted that none of the 24 festucoid species examined possessed just 1 ring of vascular bundles.

TABLE 1.--Stem Characteristics of the Species Studied in the Subfamily Festucoideae. (For an explanation of symbols see the Material and Methods section of this paper.)

SPECIES	Culm Pulvinus	Sheath Pulvinus	Culm Internode	Avg. No. of Nodes From Top Lacking Buds or Branches	Extent of Branching		Position of Branching
					Incidence	Total	
Tribe Aveneae							
Agrostis alba L.	-	+	H	3	3	19	Basal
A. hyemalis (Walt.) BSP.	-	+	H	3	2	13	Basal
Ammophila breviligulata Fern.	-	+	H	7	3	20	Basal
Avena sativa L.	-	+	H	12	0	12	Absent
Cinna arundinacea L.	-	+	H	16	0	21	Absent
Phalaris arundinacea L.	-	+	H	3	1	14	Basal
Phleum pratense L.	-	+	H	15	1	18	Basal
Tribe Brachyelytreae							
Brachyelytrum erectum (Schreb.) Beauv.	+	+	S	12	0	15	Absent
Tribe Diarrheneae							
Diarrhena americana Beauv.	-	+	H	7	4	11	Basal
Tribe Festuceae							
Bromus inermis Leyss.	-	+	H	12	0	14	Absent
Bromus purgans L.	-	+	H	10	1	13	Basal
Dactylis glomerata L.	-	+	H	5	1	9	Basal
Festuca elatior L.	-	+	S	7	0	13	Absent
Poa annua L.	-	+	S	3	5	10	Basal
Poa compressa L.	-	+	H	5	0	21	Absent
Poa pratensis L.	-	+	H	2	4	9	Basal
Tribe Meliceae							
Glyceria striata (Lam.) Hitchc.	-	+	H	10	0	14	Absent
Tribe Stipeae							
Oryzopsis racemosa (Sm.) Ricker	I	+	H	10	0	10	Absent
Tribe Triticeae							
Agropyron repens (L.) Beauv.	I	+	H	14	6	21	Basal
Elymus canadensis L.	-	+	H	23	3	30	Basal
Elymus villosus Muhl.	-	+	S	11	1	14	Basal
Elymus virginicus L.	-	+	H	16	1	20	Basal
Hordeum jubatum L.	-	+	H	12	0	13	Absent
Hystrix patula Moench.	-	+	H	25	0	30	Absent

Subfamily Panicoideae

The subfamily Panicoideae is represented in the United States by 2 tribes, 29 genera, and 365 species, representing approximately 33 percent of all United States grass species (Gould, 1968). Members of the Panicoideae have been more successful in the moist, subtropical areas of Southeastern United States and least successful in the Northwest. In general, members of the Panicoideae are limited in geographical distribution primarily by temperature and secondarily by moisture.

The Panicoideae are a distinct taxonomic group because modern morphological, anatomical, and cytological criteria hold quite true throughout this subfamily. The characteristics listed below are representative of the subfamily Panicoideae and may be used to distinguish this group from the other subfamilies of the Gramineae.

Roots

Reeder and Row (1957) found that the panicoid grasses differed significantly from festucoid grasses in root hair development. In the panicoid species examined all of the epidermal cells in the region of root hair development were similar size and all of these cells were capable of giving rise to root hairs. Also, most of the root hairs develop from near the middle of the cells and extend out at nearly a 90 degree angle from the root.

Leaf Epidermis

According to Gould (1968), the panicoid epidermis has dumbbell, or saddle-shaped silica cells, the stomata have triangular or tall, dome-shaped subsidiary cells giving the stomata a rounded appearance, the short cells over the veins are usually in rows of more than 5 cells, and bicellular microhairs are present. These hairs are usually linear and elongated.

Leaf Anatomy

Studies by Brown (1958) and Gould (1968) show that the leaf of typical panicoid grasses have a single sheath of large parenchyma cells around the vascular bundle that is continuous or interrupted on only one side by sclerenchyma tissue. In most genera, the chloroplasts of the parenchyma sheath cells are starch storage sites because of the loss of storage ability in the plastids of the mesophyll chlorenchyma. Also, the mesophyll chlorenchyma cells have reduced intercellular air spaces around the vascular bundles and are usually somewhat radially arranged.

Lodicule

Decker (1964) found the Panicoideae lodicule to be short and truncate, thickened throughout and heavily vascularized.

Embryo

Reeder (1957), described the panicoid embryo as P-PP by his abbreviated, 4-character description of embryos. This formula is interpreted to mean the embryo has "panicoid vascularization" with a definite internode between the coleoptile and the scutellum (P), no epiblast (-), a definite cleft between the coleorhize and scutellum (P), and the primary leaf possesses many bundles and the margins overlap (P).

Cytology

The basic chromosome number for most species is X=9 or X=10 and the chromosomes are small to medium in size (Gould, 1968).

Stem Morphology

The presence or absence of a culm pulvinus is highly variable in the panicoid grasses examined. A culm pulvinus was present in 14 species, absent in 16 species, and indefinite in 2 species. Brown, Pratt, and

Mobley (1959) reported the presence of a culm pulvinus in 36 of 49 species examined, and concluded that a culm pulvinus was typically present in members of this subfamily. Present information, however, indicates that this characteristic is highly variable and not reliable as a diagnostic characteristic of the subfamily.

Among the panicoid grasses studied, it was found that the presence of a sheath pulvinus was the most consistent culm characteristic studied. A definite sheath pulvinus was found in all species examined with the exception of Panicum huachucae Ashe. and Panicum microcarpon Muhl. Brown, Pratt, and Mobley (1959), however, concluded that a sheath pulvinus in the subfamily Panicoideae was either poorly developed or entirely lacking. This conclusion, however, is not supported by their data since they list 37 of 49 Panicoideae as possessing a sheath pulvinus. Proper interpretation of their data shows a definite consistency with the results of the present study.

The culm internode was hollow in 16 of the 32 species examined. This is similar to the results of Brown, Harris, and Graham (1959) where 30 of 56 panicoid grasses were found to have solid stems and 26 were found to possess a hollow or small hollow condition.

Stebbins and Crampton (1961) indicated that in panicoid grasses all nodes except the one immediately below the inflorescence bears a bud or branch. Present studies indicate that this is generally true. In 22 of the 32 panicoid species studied the first node below the inflorescence usually lacked a bud or branch. Of these species, 5 lacked buds or branches at the first 2 or 3 nodes below the inflorescence, while in one of these species, Miscanthus sacchariflorum (Maxim.) Hack., all of the nodes lacked buds and branches. The remaining 10 species were found to possess a lateral bud or branch at all nodes.

As indicated by Stebbins and Crampton (1961) branching was common in most of the panicoid species examined. The extent of branching (Table 2, column 5) varied from zero in 6 species to over 25 percent in most of the remaining grasses examined. In the species that were extensively branched the branching was usually throughout the stem, or at least some of the branches were from the upper part of the stem (Table 2, column 8). This differs from festucoid grasses where branching is usually absent, but when present, the branches arise from near the base of the culm (Table 1).

Gould (1968) has indicated that members of the subfamily Panicoideae have the vascular bundles scattered in the ground tissue or arranged in two to few rings at the inner margin of the cortex. Of the 32 panicoid species examined, 25 were found to have from 2 to 4 rings of vascular bundles. It was also found that *Panicum clandestinum* L. displayed only one ring of vascular bundles while in 6 other species the vascular bundles were scattered throughout the stem.

TABLE 2.--Stem Characteristics of the Species Studied in the Subfamily Panicoideae. (For an explanation of the symbols see the Material and Methods section of this paper.)

SPECIES	Culm Pulvinus	Sheath Pulvinus	Culm Internode	Avg. No. of Nodes From Top Lacking Buds or Branches	Extent of Branching		Position of Branching
					Incidence	Total	
Tribe Andropogoneae							
Andropogon furcatus Muhl.	+	+	S	3	12	47	Upper
Andropogon scoparius Michx.	+	+	S	1	15	38	Upper
Erianthus alopecuroides (L.) Ell.	-	+	S	3	0	6	None
Erianthus ravennae	-	+	S	3	0	17	None
Miscanthus sacchariflorus (Maxim.) Hack.	-	+	H	32	0	38	None
Sorghastrum nutans (L.) Nash.	-	+	H	3	1	13	Basal
Sorghum halepense (L.) Pers.	+	+	S	2	3	13	Basal
Sorghum vulgare Pers.	+	+	S	0	0	17	None
Tripsicum dactyloides L.	+	+	S	2	8	22	Upper & Basal
Tribe Paniceae							
Cenchrus pauciflorus Benth.	I	+	S	3	20	29	All
Digitaria ischaemum (Schreb.) Muhl.	-	+	H	1	26	34	All
Digitaria sanguinalis (L.) Scop.	-	+	H	3	19	26	All
Echinochloa crusgallii (L.) Beauv.	-	+	H	3	8	39	All
Panicum agrostoides Spreng.	+	+	H	0	10	13	All
Panicum anceps Michx.	-	+	H	0	8	10	All
Panicum boscii Poir.	-	+	S	1	5	6	All
Panicum clandestinum L.	-	+	H	0	21	24	All
Panicum dichotomiflorum Michx.	-	+	H	2	5	15	Upper & Basal
Panicum huachucae Ashe.	+	I	S	2	5	11	Upper & Basal
Panicum latifolium L.	+	+	S	0	19	24	Upper & Median
Panicum microcarpon Muhl.	+	I	H	2	14	23	Upper & Basal
Panicum oligosanthes Schult.	+	+	H	2	9	12	All
Panicum polyanthes Schult.	+	+	H	2	6	15	Upper & Basal

TABLE 2.--Continued.

SPECIES	Culm Pulvinus	Sheath Pulvinus	Culm Internode	Avg. No. of Nodes From Top Lacking Buds or Branches	Extent of Branching		Position of Branching
					Incidence	Total	
Panicum virgatum L.	-	+	H	3	0	17	None
Panicum xalepense HBK.	-	+	S	2	3	7	Upper & Basal
Paspalum ciliatifolium Michx.	-	+	S	0	4	11	Upper
Paspalum geminum Hash.	+	+	S	4	1	21	Median
Paspalum pubescens Muhl.	-	+	H	0	9	15	Upper & Basal
Paspalum stramineum Nash.	-	+	S	0	4	14	Upper
Setaria faberi Herm.	+	+	S	1	7	18	Median & Basal
Setaria lutescens (Weigel) F. T. Hubb.	I	+	I	7	0	23	None
Panicum capillare L.	+	+	H	1	64	69	All

Subfamily Eragrostoideae

In the United States the subfamily Eragrostoideae is represented by 8 tribes, 42 genera, and 309 species, approximately 28.5 percent of the United States Gramineae (Gould, 1968). Although well distributed over North America, the eragrostoids are most prevalent in the southwestern United States and in northern Mexico. The climate throughout this region is warm and dry and the Eragrostoideae species account for more than 50 percent of the grass vegetation.

Proposed in 1954 by Pilger, the subfamily Eragrostoideae had previously had its genera classified in the festucoid tribes Festuceae and Chlorideae by Hitchcock (1951). However, most modern taxonomic characters of anatomy, morphology and cytology reveal a tremendous similarity of this group to the subfamily Panicoideae. Although the new taxonomic characters found in the Eragrostoideae are not as clear-cut as those of the Panicoideae or Festucoideae, there is nevertheless definite patterns which differentiate the members of the Eragrostoideae from any other subfamily.

Roots

In their study of root hair development, Row and Reeder (1957) found panicoid characteristics most prevalent among the eragrostoid species studied. The epidermal cells of the root hair region were similar in size and all capable of root hair initiation.

Leaf Epidermis

The epidermis is similar to panicoid grasses (Gould, 1968) since the silica cells are saddle-shaped, the stomata have triangular or tall, dome-shaped subsidiary cells, which gives the stomata a rounded appearance, the short cells over the veins are usually in rows of more than 5 cells and bicellular microhairs are present. These are usually bullet-shaped or clavate in most eragrostoid grasses.

Leaf Anatomy

According to Brown (1958), eragrostoid grasses usually have vascular bundles with an outer sheath made up of large, well-developed parenchyma cells and an inner sheath of small, thick-walled sclerenchyma cells and this sheath may surround the bundle or be interrupted on one side by sclerenchyma cells. The mesophyll cells surrounding the vascular bundles and their associated ring of chlorenchyma cells are commonly separated from neighboring bundles by colorless cells which are continuous with the bulliform cells of the leaf epidermis.

Lodicule

According to Decker (1964), the lodicules of this subfamily are panicoid in characteristics since they are short and truncate, thickened throughout, and heavily vascularized.

Embryo

Reeder (1957) described the eragrostoid embryo as being P+PF by his abbreviated 4-character description of embryos. This formula may be interpreted to mean that the embryo has a "panicoid vascularization" with a definite internode between the coleoptile and the scutellum (P), an epiblast (+), a cleft separating the coleorhiza and scutellum (P), and the embryonic leaf has few vascular bundles and its margins do not overlap (F).

Cytology

The chromosomes of the Eragrostoideae are small and tend to be in basic numbers of X=9 or X=10 (Gould, 1968).

Stem Morphology

The presence or absence of a culm pulvinus is variable in the eragrostoid grasses examined. This structure was present in 6 species, indefinite in 6 species and absent in 16 species. Brown, Pratt, and Mobley (1959) in a study of stem characteristics reported that 16 of 45 species of eragrostoid grasses possessed a definite culm pulvinus. Later interpretation of this data by Gould (1968) characterized the eragrostoids as having "well-developed" culm pulvini. The present study, as well as those by Brown, Pratt, and Mobley (1959), indicates that a culm pulvinus is present in only about one-third of the eragrostoid species examined.

Of the stem characteristics studied, the most consistent among the species of the subfamily Eragrostoideae was the presence of a sheath pulvinus. Of the 28 species examined 25 exhibited a definite sheath pulvinus and in one species, *Spartina pectinata* Link., it was indefinite. A sheath pulvinus was absent in *Aristida oligantha* Michx. and *Eragrostis spectabilis* (Pursh.) Steud. Of the eragrostoid species studied by Brown, Pratt, and Mobley (1959) 42 of 45 species possessed a definite sheath pulvinus.

In general, most eragrostoid species appear to have a solid internode, and 28 species examined had this characteristic. Brown, Harris, and Graham (1959) obtained similar results in that of the 79 species they examined, 63 had a solid internode.

Stebbins and Crampton (1961) indicated that the eragrostoid grasses have similar branching patterns to that found in the subfamily Panicoideae. They suggest that in most eragrostoid genera all nodes but the uppermost one bear branches or can be induced to do so by decapitation. Of the 28 eragrostoid species examined in this study 6 did not have any branching

(Table 3, columns 6 and 7) while most of the remaining species had extensive branching. Though the extent of branching varied, in 17 species branching was relatively common and either median or throughout the stem. This branching pattern is similar to that found in the subfamily Panicoideae.

An examination of the stems of 28 Illinois eragrostoid grasses indicates that the culms of members of this subfamily typically lack a definite culm pulvinus, possess a definite sheath pulvinus, usually have a solid internode, possess lateral buds or branches at nearly all nodes, branches throughout have vascular bundles scattered in the ground tissue or in two to a few rings at the inner margin of the cortex (Table 3). These stem characteristics are very similar to those found in the subfamily Panicoideae.

According to Gould (1968), the subfamily Eragrostoideae may have its vascular bundles scattered in the ground tissue or in two to few rings at the inner margin of the cortex. The arrangement of the vascular bundles of the eragrostoid grasses examined were found usually to possess 2 to 4 rings of vascular bundles. However, in one species the condition was that the bundles were many and scattered.

TABLE 3.--Stem Characteristics of the Species Studied in the Subfamily Eragrostoideae. (For an explanation of symbols see the Material and Methods section of this paper.)

SPECIES	Culm Pulvinus	Sheath Pulvinus	Culm Internode	Avg. No. of Nodes From Top Lacking Buds or Branches	Extent of Branching		Position of Branching
					Incidence	Total	
Tribe Aristideae							
Aristida dichotoma Michx.	-	+	S	0	9	11	All
Aristida intermedia Scribn. & Ball	-	+	S	1	3	8	Median
Aristida longespica Poir.	+	+	S	0	14	17	All
Aristida oligantha Michx.	+	-	S	0	13	23	Median & Basal
Aristida purpurascens Poir.	-	+	S	1	1	18	Median
Tribe Chlorideae							
Bouteloua curtipendula (Michx.) Torr.	+	+	S	5	2	14	Basal
Eleusine indica L.	-	+	S	5	11	22	All
Leptochloa filiformis (Lem.) Beauv.	I	+	S	6	3	10	Basal
Spartina pectinata Link.	-	I	H	16	0	21	None
Tribe Eragrosteae							
Calamovilfa longifolia (Hook.) Scribn.	-	+	S	6	0	7	None
Eragrostis cilianensis (All.) Lut.	I	+	S	9	16	37	All
Eragrostis frankii C.A. Mey.	I	+	S	1	15	19	All
Eragrostis hypnoides (Lam.) BSP.	I	+	S	12	11	23	All
Eragrostis pectinacea (Michx.) Nees.	-	+	S	0	12	14	All
Eragrostis spectabilis (Pursh.) Steud.	I	-	H	3	0	22	None
Eragrostis trichodes (Nutt.) Wood	-	+	S	2	0	18	None
Muhlenbergia frondosa (Peir.) Fern.	+	+	H	0	39	48	All
Muhlenbergia mexicana (L.) Trin.	+	+	H	4	7	27	Median
Muhlenbergia racemosa (Michx.) BSP.	-	+	S	3	16	36	Upper & Median

TABLE 3.--Continued.

SPECIES	Culm Pulvinus	Sheath Pulvinus	Culm Internode	Avg. No. of Nodes From Top Lacking Buds or Branches	Extent of Branching		Position of Branching
					Incidence	Total	
Muhlenbergia schreberi J.F. Gmel.	I	+	S	3	23	43	All
Muhlenbergia tenuiflora (Willd.) BSP.	+	+	H	0	32	42	All
Sporobolus asper (Michx.) Kunth	-	+	S	0	6	23	Upper
Sporobolus cryptandrus (Torr.) A. Gray	-	+	S	2	4	18	Basal
Sporobolus heterolepsis A. Gray	-	+	S	9	0	14	None
Sporobolus neglectus Nash.	-	+	H	0	8	13	All
Sporobolus vaginiflorus (Torr.) Wood.	-	+	S	1	10	12	All
Tridens flavus (L.) Hitchc.	-	+	H	7	1	25	Basal
Tribe Unioleae							
Uniola latifolia Michx.	-	+	H	7	0	17	None

SUMMARY

The purpose of this study was to attempt to determine whether or not pulvinus condition, culm internode condition, branching, and vascular bundle arrangement might be used to separate the subfamilies of the family Gramineae. The stems of 85 Illinois species belonging to the Festucoideae, Panicoideae, and Eragrostoideae were examined in an effort to determine their value as taxonomic characters.

A comparison of the results of vascular bundle arrangement of grass culms has revealed that there seems to be a great similarity in the three subfamilies. Because of this similarity, virtually no importance can be attributed to this anatomical character.

Members of the Festucoideae have been observed to: lack a culm pulvinus, possess a sheath pulvinus, have a hollow stem internode, lack a lateral bud at the uppermost node, and have basal branching if branching occurs (Table 4). All of the characters were found to be quite consistent with the exception of "the number of nodes below the inflorescence which lack buds." As can be seen by the data presented in Table 1, column 5, all of the species examined lacked a bud or branch at the first node below the inflorescence; however, the number of nodes below the inflorescence that lacked buds or branches varied from 1 to 9.

Like the Festucoideae, the Panicoideae exhibit quite consistently a definite sheath pulvinus. A culm pulvinus and solid culm internode were observed with about a 50 percent frequency in comparison to their alternatives. The characteristics of branching showed considerable variation from that of the Festucoideae. In the Festucoideae, it was found that in all cases at least one node below the inflorescence lacked a lateral bud or branch. In 28 percent of the panicoid species examined, however, a lateral bud or branch was found to be present at the first node below the inflorescence. Lateral branches were also much more prevalent (Tables 1 and 2) in the panicoids. In only two instances was the branching limited to the basal region of the culm as it was observed in the subfamily Festucoideae.

In the Eragrostoideae, as in the Festucoideae and Panicoideae, a sheath pulvinus was nearly always present. A culm pulvinus was absent in 16 species and present in only 6 species. The culm internode was found to be solid 60 percent of the time. Branching characteristics resemble closely those of the subfamily Panicoideae in that the first node often possesses a lateral bud or branch, the extent of branching is usually high, and branching occurs at all levels of the culm length (Table 3).

The morphological and anatomical characteristics examined will not consistently distinguish the three subfamilies from each other. It may be possible, however, on a limited scale, to separate members of the subfamily Festucoideae from the Panicoideae and Eragrostoideae.

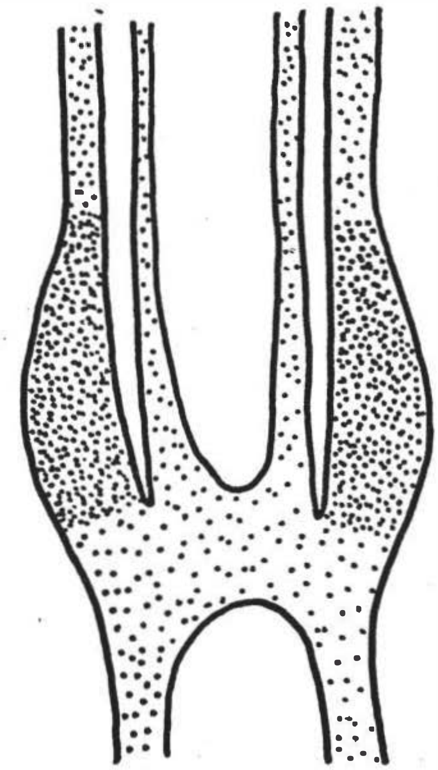
Branching may offer a means of separating the Festucoideae from the Panicoideae and Eragrostoideae. Festucoids tend to exhibit branching only at the bottom 10 percent of the culm nodes or to be absent altogether (Table 4). Panicoids were observed to have branching limited to the basal region 6 percent of the time or in only two species examined. Eragrostoid members were found to have branching limited to the basal region only 14 percent of the time or in 4 species examined. Extent of branching also showed that 45 percent of the nodes of panicoids and 58 percent of eragrostoid nodes exhibited branches, while only 9.4 percent of the nodes in Festucoid grasses had branches.

Although the absence of a culm pulvinus, the presence of a sheath pulvinus and a hollow internode occur with a high frequency in the Festucoideae, these characters also occur with substantial frequency in the Panicoideae and Eragrostoideae (Table 4). Therefore, characters concerning pulvinus and culm internode condition cannot be used to separate members of these three subfamilies.

TABLE 4.--Summary of Stem Characteristics in the Three Subfamilies of the Gramineae. The percentage figures indicate the occurrence of that trait.

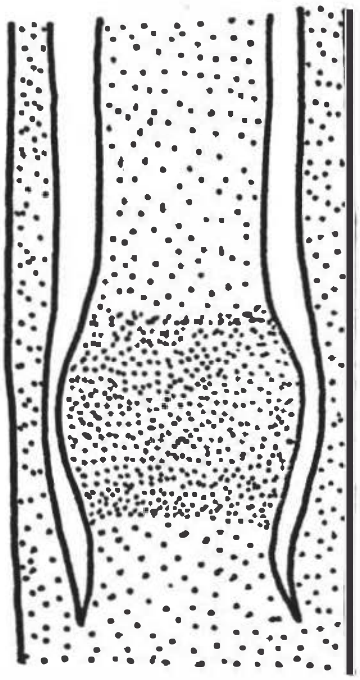
	Subfamily Festucoideae	Subfamily Panicoideae	Subfamily Eragrostoideae
Culm Pulvinus	96.0% Absent	50.0% Present	57.0% Absent
Sheath Pulvinus	100.0% Present	100.0% Present	90.0% Present
Culm Internode	83.0% Hollow	50.0% Hollow	71.0% Solid
Avg. No. of Nodes From Top Lacking Buds or Branches	10.2 Nodes	2.8 Nodes	3.7 Nodes
Extent of Branching	9.4% of Nodes were Branched	45.0% of Nodes were Branched	58.0% of Nodes were Branched
Position of Branching	100.0% Basal or Absent	6.0% Basal	14.0% Basal

Figure 1



SHEATH PULVINUS

Figure 2



CULM PULVINUS

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