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A taxonomic investigation of some rhizomatous species of the genus Muhlenbergia (Gramineal).

James Kurtz

A TAXONOMIC INVESTIGATION OF SOME RHIZOMATOUS SPECIES OF THE GENUS MUHLENBERGIA (GRAMINEAE)

A Thesis

Presented to the

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and the

Faculty of the Graduate College

University of Nebraska at Omaha

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

by

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Date

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A TAXONOMIC INVESTIGATION OF SOME RHIZOMATOUS SPECIES OF THE GENUS MUHLENBERGIA (GRAMINEAE)

INTRODUCTION

The genus Muhlenbergia, usually placed in the subfamily Eragrostoideae (Stebbins and Crampton, 1961; Gould, 1975) is a large, widely distributed, group of grasses, encompassing numerous species and various growth forms. The subgenus Muhlenbergia, comprised of mesic, broad-leaved, usually rhizomatous species, can easily be separated from the rest of the genus on the basis of growth habit and habitat preferences (Pohl, 1969). Species of the subgenus are widely distributed in North America but are most abundant in the deciduous forests of the eastern part of the continent.

Taxonomic Considerations:

Members of the subgenus Muhlenbergia are distinguished by small, one-flowered spikelets with the rachilla disarticulating above the glumes. Glume length varies from shorter than the lemma to much longer. The glumes are keeled on the back and acuminate or awned. The lemma is membranaceous, three-nerved, and sometimes awned. Inflorescences vary from a narrow, lobulate panicle to a slender loosely open panicle. All of the species included in this study are perennials and possess well-developed scaly rhizomes. Seven species native to eastern Nebraska and western Iowa were studies: M. Bushii Pohl, M. frondosa (Poir.) Fern., M. mexicana (L.) Trin., M. racemosa (Michx.) B.S.P., M. sobolifera (Muhl.) Trin., M. sylvatica (Torr.) Torr. and M. tenuiflora

(Willd.) B.S.P.

Bush (1919) published a key for the Missouri muhlenbergias and described several new species. M. brachyphylla Bush was first recognized by Bush; this name proved to be a homonym and the species was subsequently renamed M. bushii (Pohl, 1969). Following the example of earlier authors, Bush erroneously designated M. mexicana as M. foliosa (R. & S.) Trin. and treated M. frondosa as M. mexicana. Fernald (1943), after careful study of the type material, clarified the nomenclatural problems which had plagued this group. He restored the name M. mexicana to those plants erroneously designated M. foliosa by various authors and assigned the name M. frondosa (based on Agrostis frondosa Poir.) to those plants which had long been confused with M. mexicana. Fernald also designated several new nomenclatural combinations and named one new variety. Mitchell (1962) studied regional patterns of variation and ecotypic variation for several species of the subgenus Muhlenbergia. He suggested that introgression may occur between M. frondosa and M. racemosa and also between M. frondosa and M. bushii. Pohl (1969) published a detailed study of the subgenus which included a key to species, varieties, and forms; certain aspects of the anatomy, cytology, distribution, and ecology of the species were also considered. Pohl's key is an improvement over earlier treatments but is still inadequate since some of the species and forms cannot be consistently segregated.

Anatomical Considerations:

Until the 1930's, classification of the grasses was based primarily on the inflorescence and gross morphology. Recently, anatomical, cytological, and physiological characteristics have been extensively used to define probable phylogenetic relationships within the family. The use of leaf anatomy for grass systematics is over one-hundred years old, but its widespread application to taxonomic problems is relatively new. Anatomical characteristics of the lamina, both in transverse section and epidermal view, have been used in conjunction with other characteristics (1) to place genera within tribes, (2) to designate new subfamilies, and (3) to help clarify the evolutionary history of the family (Gould, 1968). Relatively little work on leaf anatomy at the species level has been done.

The leaf epidermis is distinguished by two regions or zones: (1) the costal zones, comprised of those cells positioned above the vascular bundles, and (2) the intercostal zones, comprised of those cells situated between the vascular bundles. Cells of the epidermis are classified as long-cells when horizontally elongate, or as short-cells when equidimensional or nearly so. Silica-cells are short-cells which contain a prominent silica body.

Dermal appendages are divided into three categories: (1) micro-hairs; very small, two-celled, thin-walled appendages, (2) prickle-hairs; thick-walled pointed cells with swollen bases, and (3) papillae; small knobs on the cell surface formed by protrusions of the cell wall (Metcalfe, 1960).

Transverse leaf anatomy of members of the genus Muhlenbergia places them in the chloridoid alliance (Brown, 1958). Species of this alliance are characterized by a thick-walled endodermis or mestome sheath around the vascular bundles and by a parenchyma sheath which possesses specialized plastids. The chlorenchyma of the mesophyll is radially arranged.

Morphological similarity among members of the subgenus Muhlenbergia makes them difficult to separate using conventional taxonomic characteristics. The intent of this study is to explore these taxonomic difficulties and to study the distribution of these species in the east-central Great Plains.

METHODS AND MATERIALS

The majority of the plants used in this study were collected from an area which included seven Nebraska counties and two Iowa counties; field collections were made from August through mid-October 1975. Additional specimens used were borrowed from the University of Nebraska-Lincoln herbarium.

All measurements of 10 mm or less were made with a stereoscopic binocular microscope with an ocular micrometer calibrated to 0.1 mm intervals. Lemma, glume, and anther measurements were obtained from mature spikelets. The larger basal leaves were chosen for ligule measurements and for making transverse sections of the blade and sheath. Blade sections were taken at a point midway between the tip of the blade and the ligule; sheath sections were taken from a point not more than 1.0 cm below the ligule. Sections were made freehand from both fresh material and herbarium specimens; dried leaves were soaked in a softening solution (Pohl, 1962). Hoyers solution was used to clear the sections and also as a mounting medium (Humason, 1972). Cellulose acetate casts were made to study epidermal characteristics (Payne, 1968). Pollen from suspected hybrids was mounted in lactophenol-cotton blue; a high percentage of shrunken or collapsed pollen was taken to indicate low fertility. Carbohydrate storage was determined by hand sections of mature grains stained with iodine (Tateoka, 1962).

RESULTS AND DISCUSSION

Anatomical Characters:

Transverse sheath anatomy provides a reliable character to separate M. mexicana and M. sylvatica, since it clearly shows the degree to which the sheath is keeled. M. mexicana (Fig. 1a) has prominently keeled sheaths in contrast to the rounded sheaths of M. sylvatica (Fig. 1b). The other species have sheaths which vary from rounded to abruptly keeled (Figs. 1-3). The anatomy of the sheath is similar to that of the blade.

Epidermal leaf anatomy is of limited taxonomic value. Only three differences are consistent enough to be mentioned: (1) M. bushii (Fig. 4b) has fewer prickle-hairs and bicellular micro-hairs on its adaxial surface than the other species, (2) M. mexicana (Fig. 5a) has a greater abundance of prickle-hairs over the vascular bundles on its adaxial blade than does M. Sylvatica (Fig. 5b), and (3) M. sobolifera (Fig. 8a) has a greater abundance of cross-shaped silica-cells than the other species. Aside from the above features, no species differences were noted in size and shape of the cells or in the abundance of the various dermal appendages either on the adaxial or abaxial surface (Figs. 4-9).

Transverse blade anatomy also proved to be of limited value, since most of the species studied were similar. Minor differences can be noted among the species illustrated (Figs. 10-12), but are not consistent enough to be of value. The leaves are organized into more or less circular units around the vascular bundles in all of the species, although this feature is not as prominent in M. tenuiflora (Fig. 12b).

Figure 1. a) M. mexicana - cross section of sheath

x. - xylem

p. - phloem

e. sh. - endodermal sheath

p. sh. - parenchyma sheath

s. - sclerenchyma

b) M. sylvatica - cross section of sheath

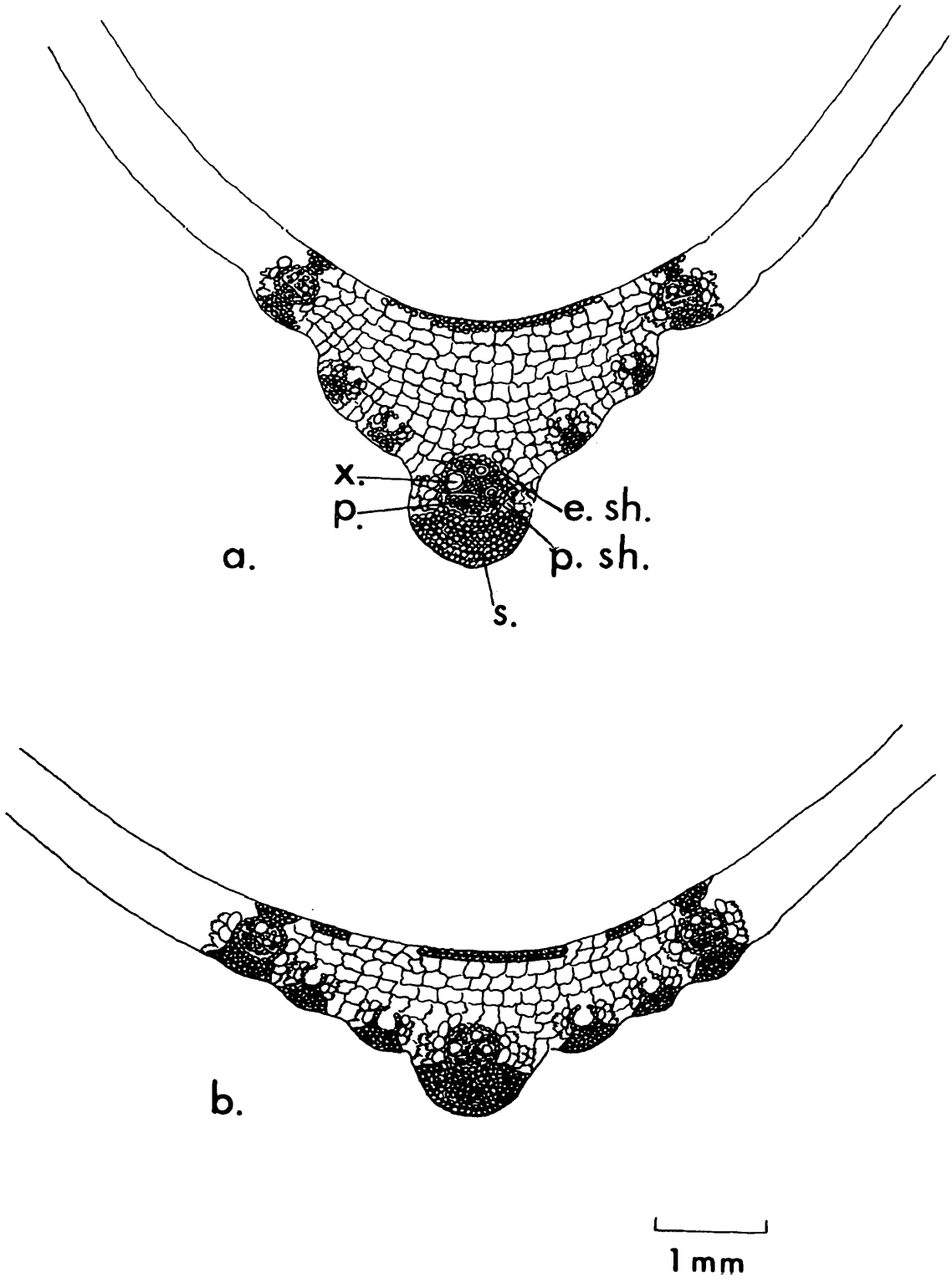

x.
p.
e. sh.
p. sh.
s.
a.
b.
1 mm

Figure 2. a) M. racemosa - cross section of sheath

b) M. frondosa - cross section of sheath

c) M. sobolifera - cross section of sheath

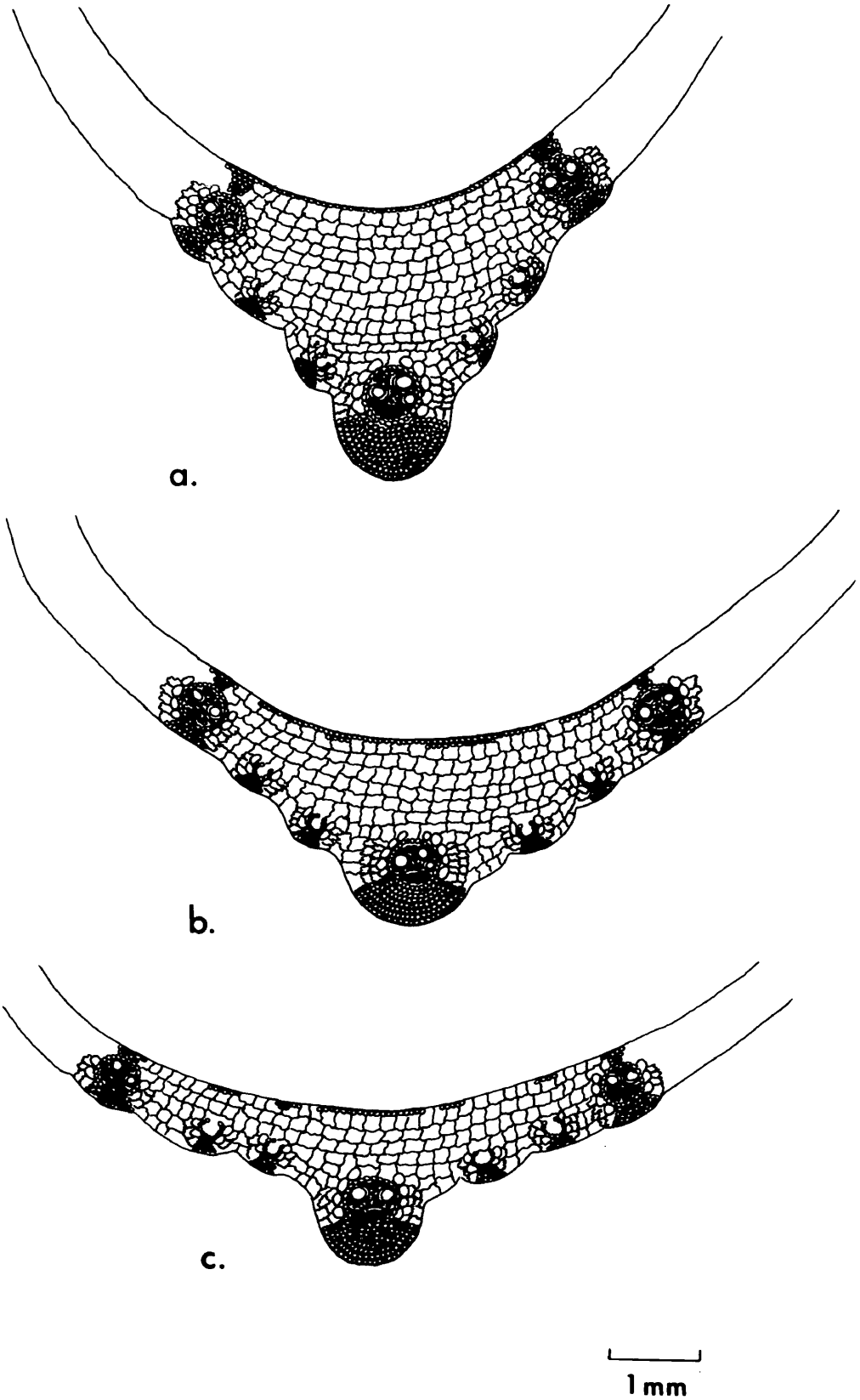

a.
b.
c.
1 mm

Figure 3. a) M. tenuiflora - cross section of sheath

b) M. bushii - cross section of sheath

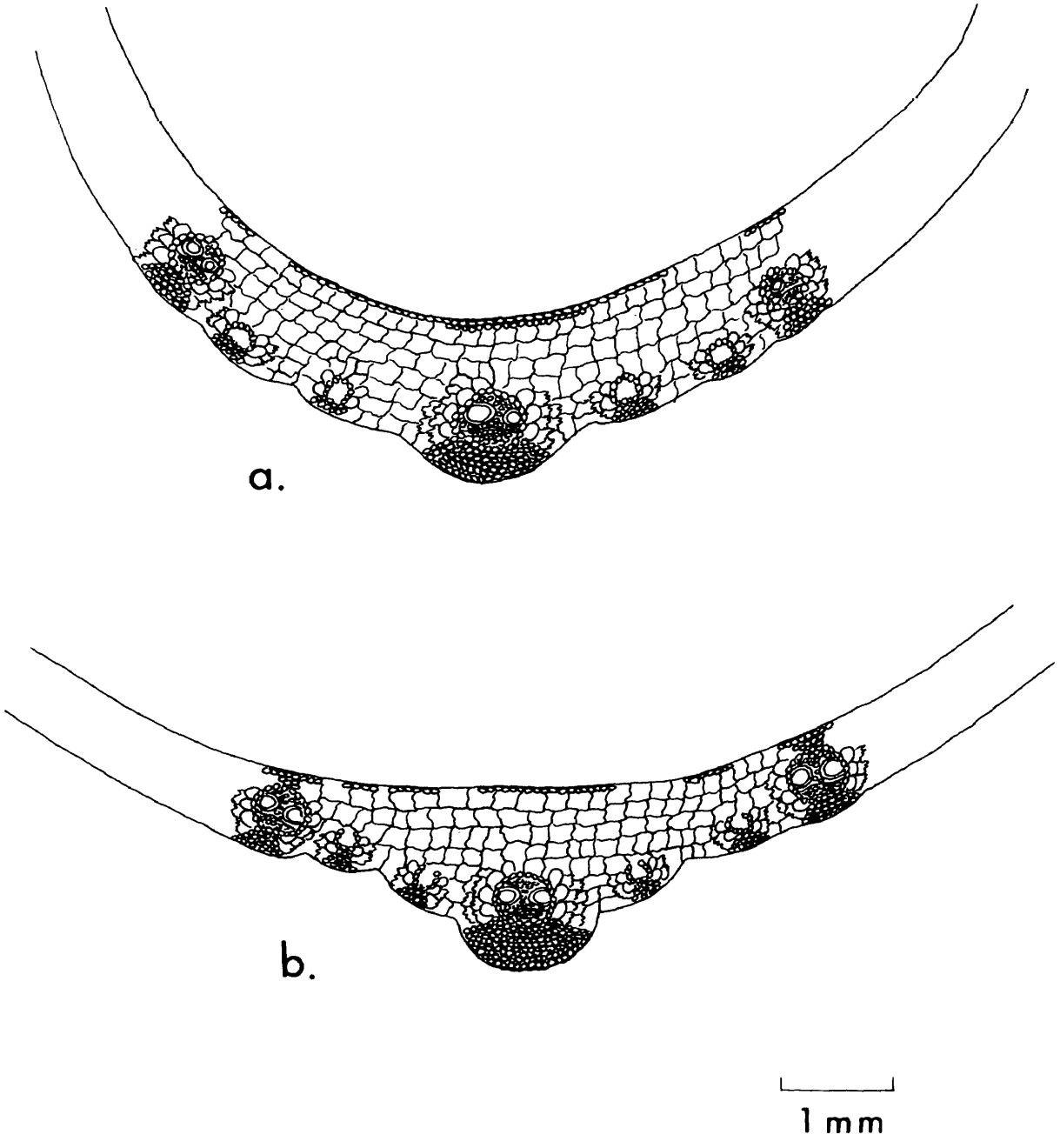

a.
b.
1 mm

Figure 4. a) M. racemosa - adaxial leaf surface

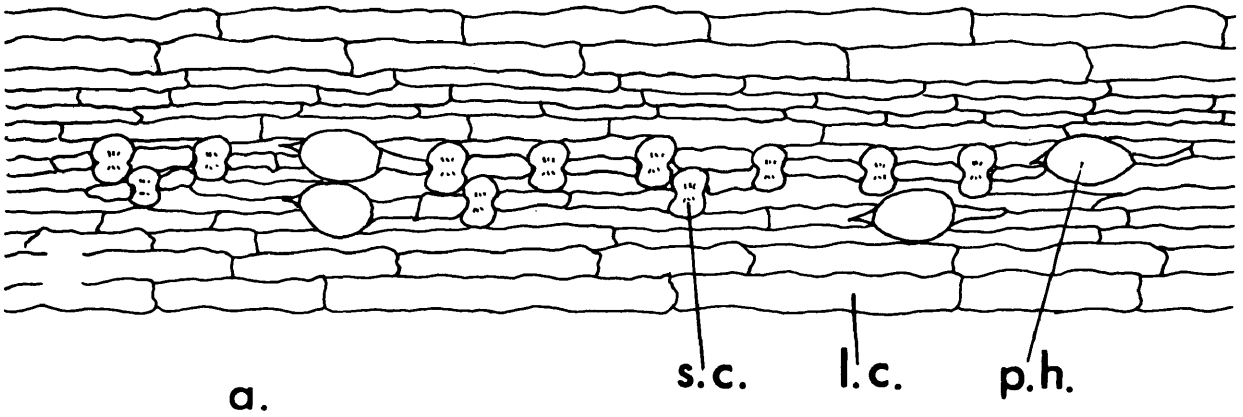
s.c. - silica-cell

l.c. - long-cell

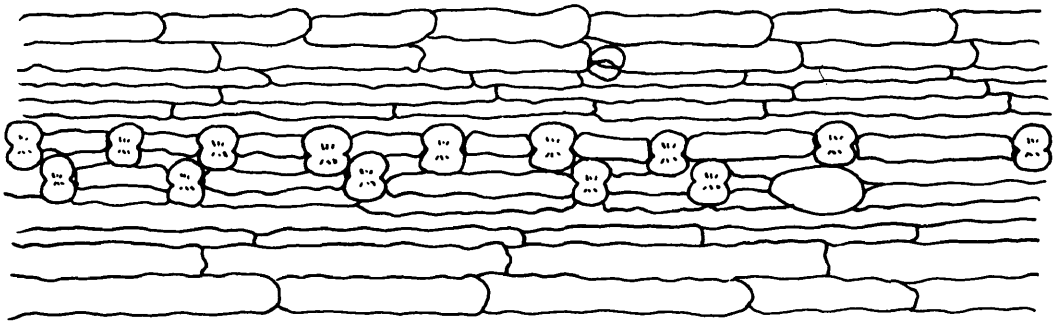
p.h. - prickle-hair

b) M. bushii - adaxial leaf surface

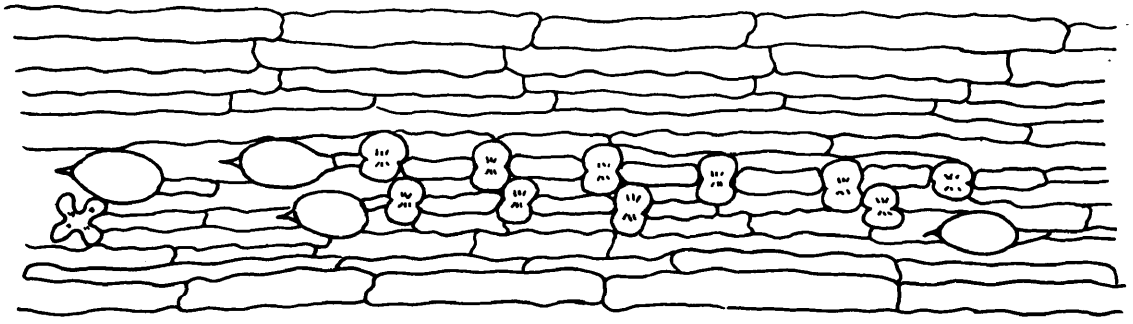
c) M. frondosa - adaxial leaf surface



a.



b.

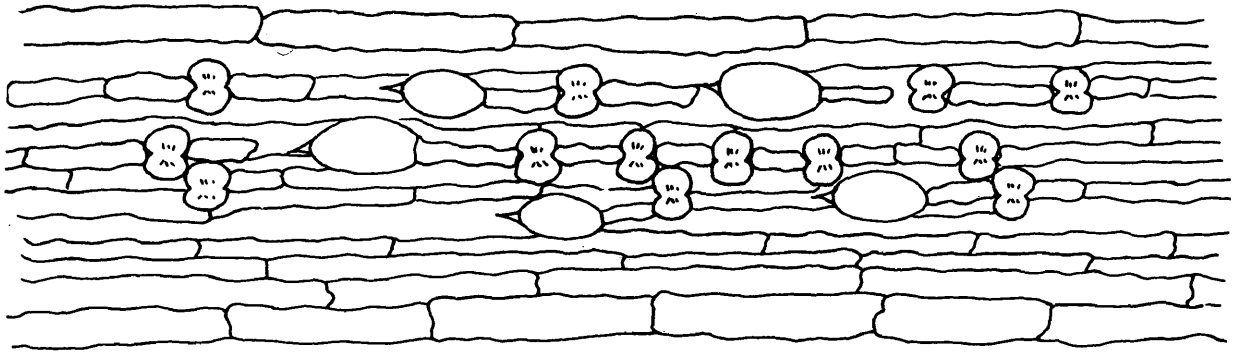


c.

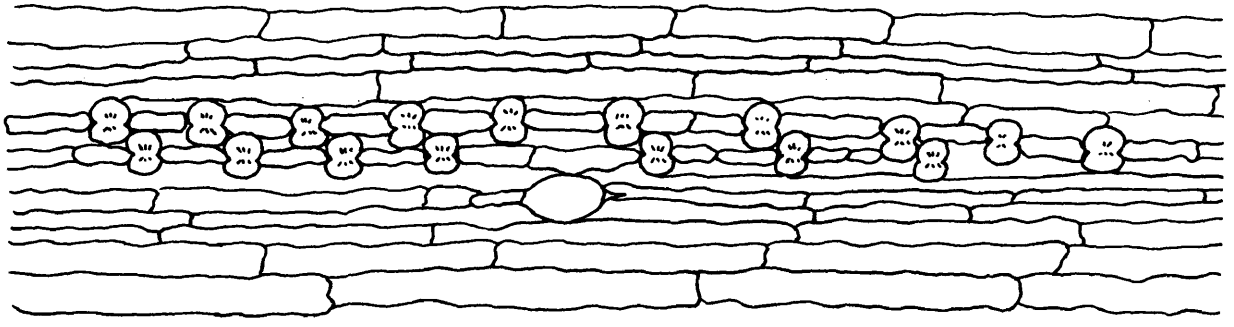
.1 mm

Figure 5. a) M. mexicana - adaxial leaf surface

b) M. sylvatica - adaxial leaf surface



a.

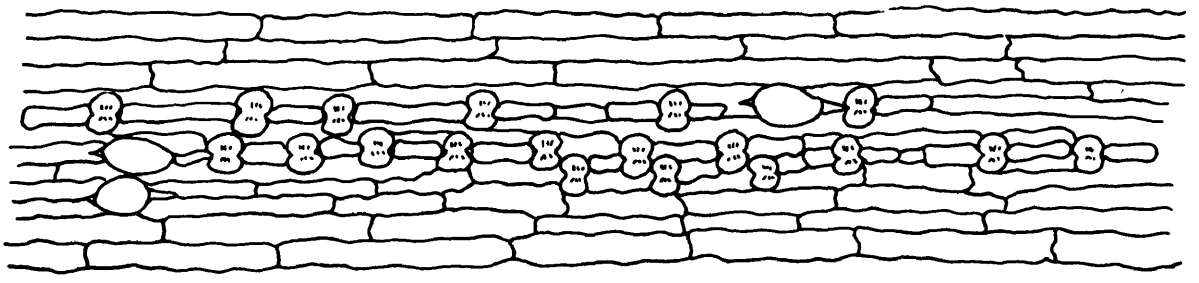


b.

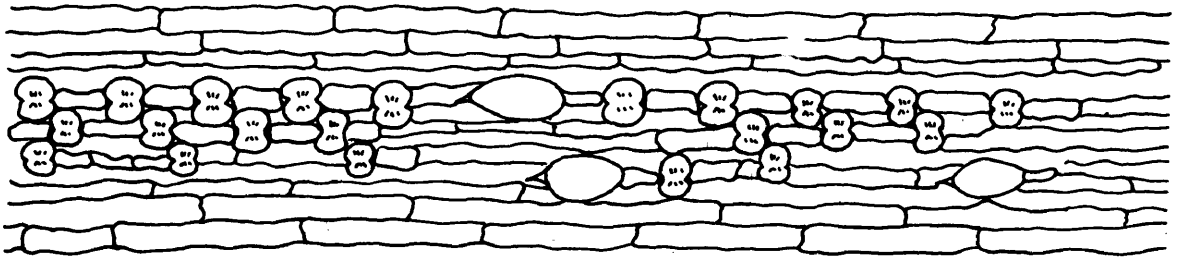
.1 mm

Figure 6. a) M. sobolifera - adaxial leaf surface

b) M. tenuiflora - adaxial leaf surface



a.



b.

.1 mm

Figure 7. a) M. racemosa - abaxial leaf surface

p.h. - prickle-hair

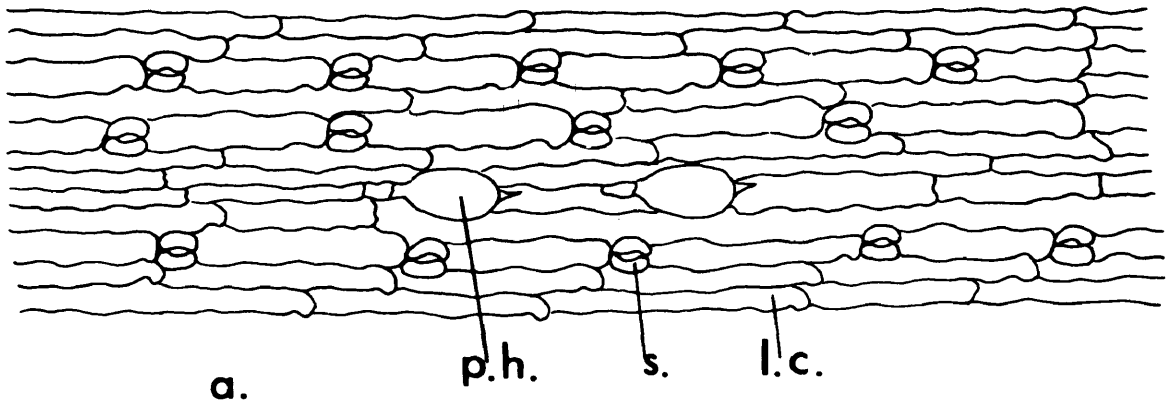
s. - stoma

l.c. - long-cell

b) M. bushii - abaxial leaf surface

m.h. - microhair

c) M. frondosa - abaxial leaf surface



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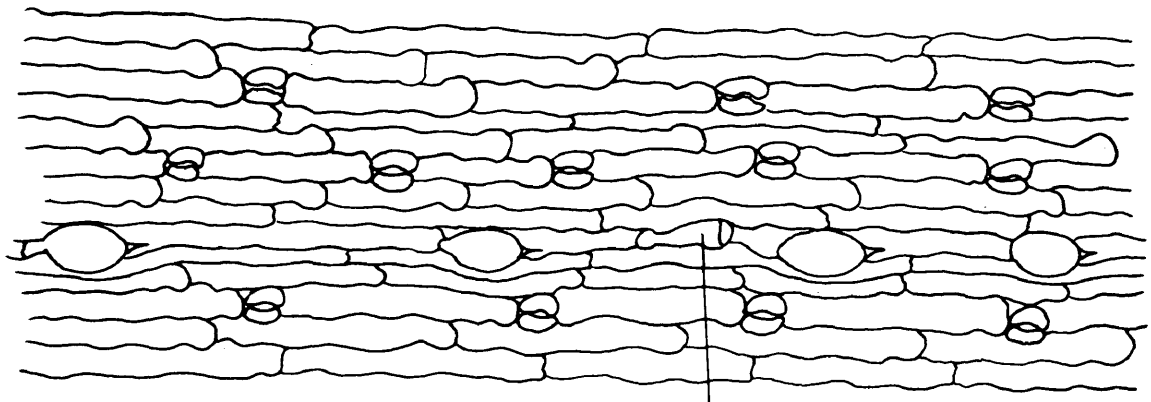
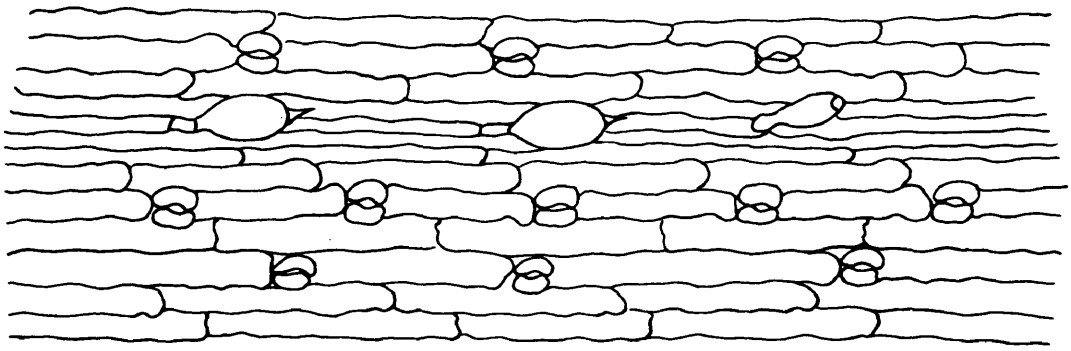


b.

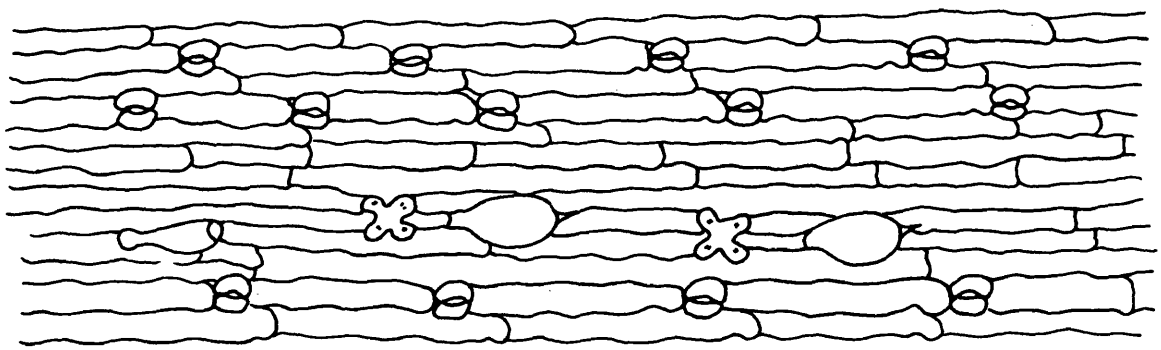


c.

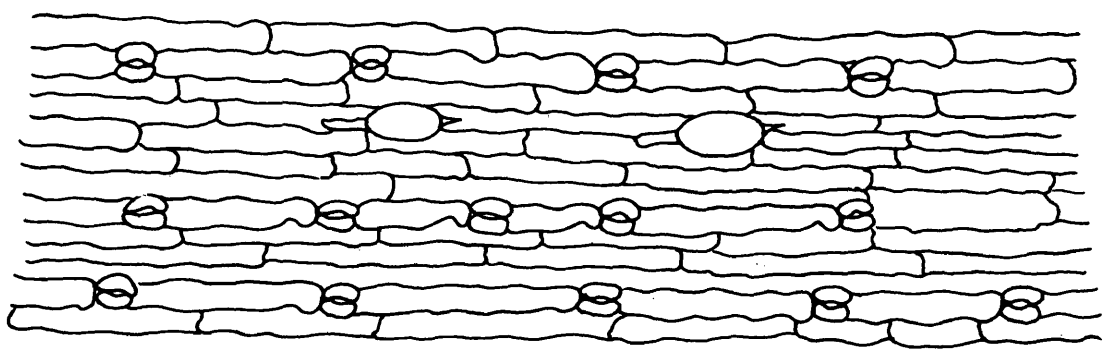
.1mm

Figure 8. a) M. sobolifera - abaxial leaf surface

b) M. tenuiflora - abaxial leaf surface



a.

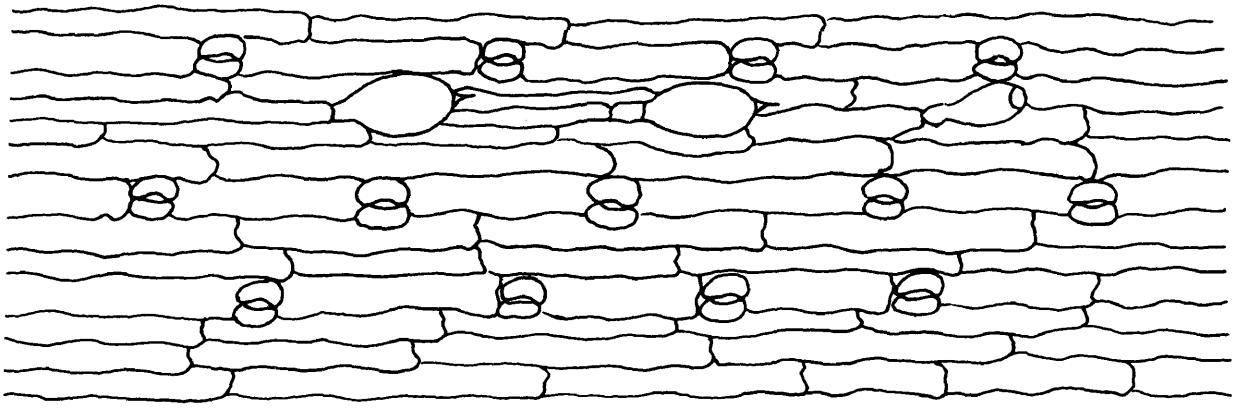


b.

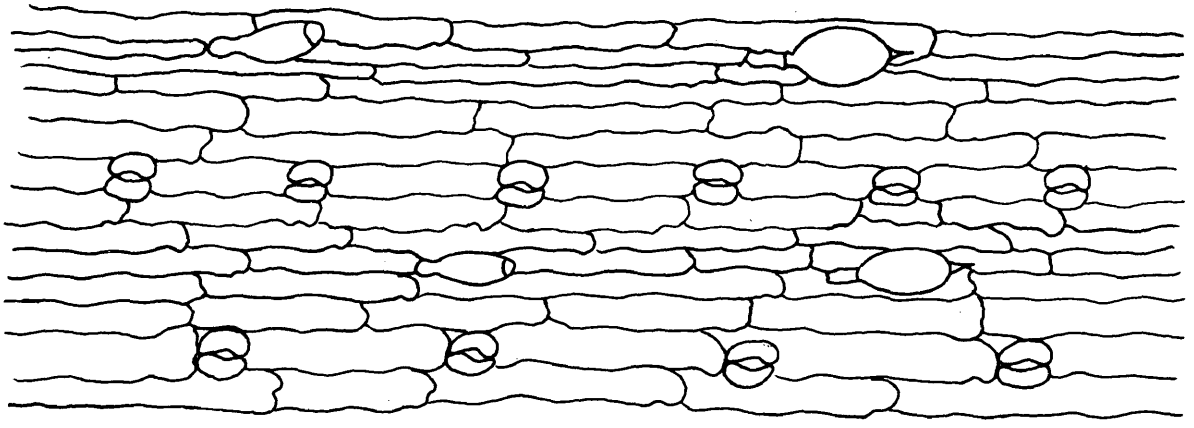
.1 mm

Figure 9. a) M. mexicana - abaxial leaf surface

b) M. sylvatica - abaxial leaf surface



a.



b.

.1 mm

Figure 10. a) M. racemosa - cross section of leaf blade

x. - xylem

p. - phloem

s. - sclerenchyma

e. sh. - endodermal sheath

p. sh. - parenchyma sheath

b. - buliform cell

b) M. bushii - cross section of leaf blade

c) M. sylvatica - cross section of leaf blade

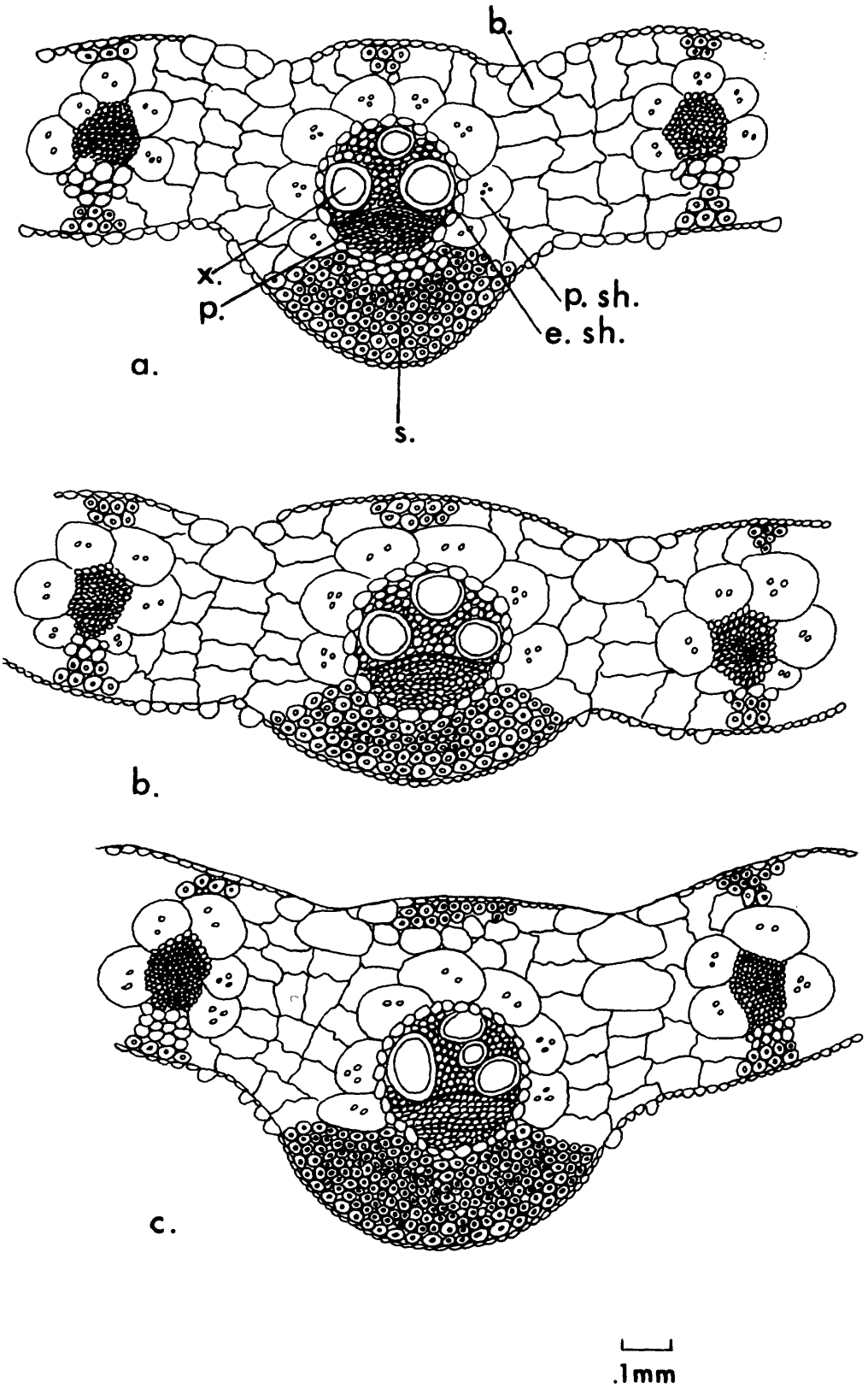
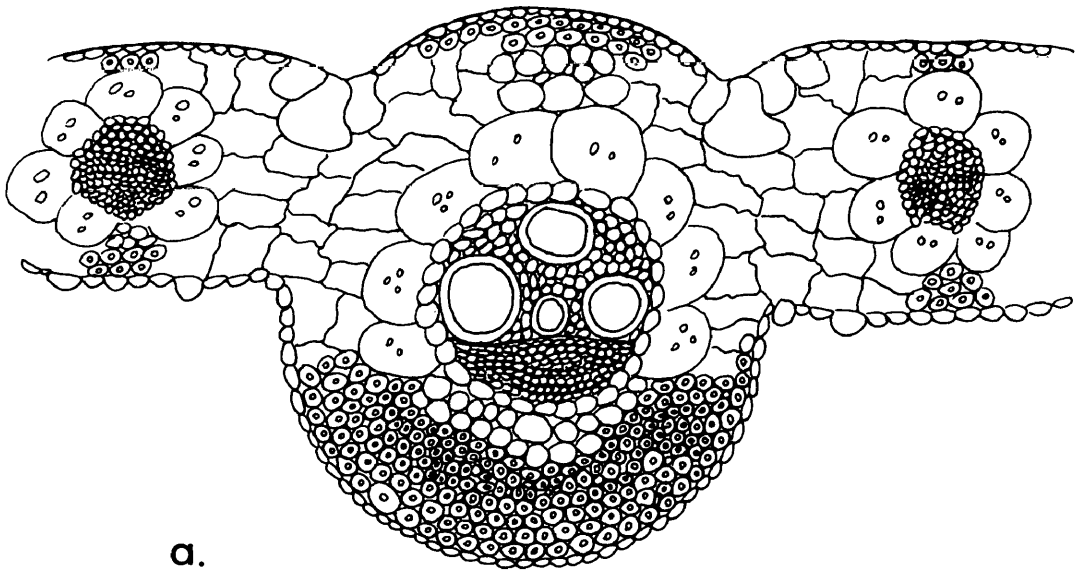
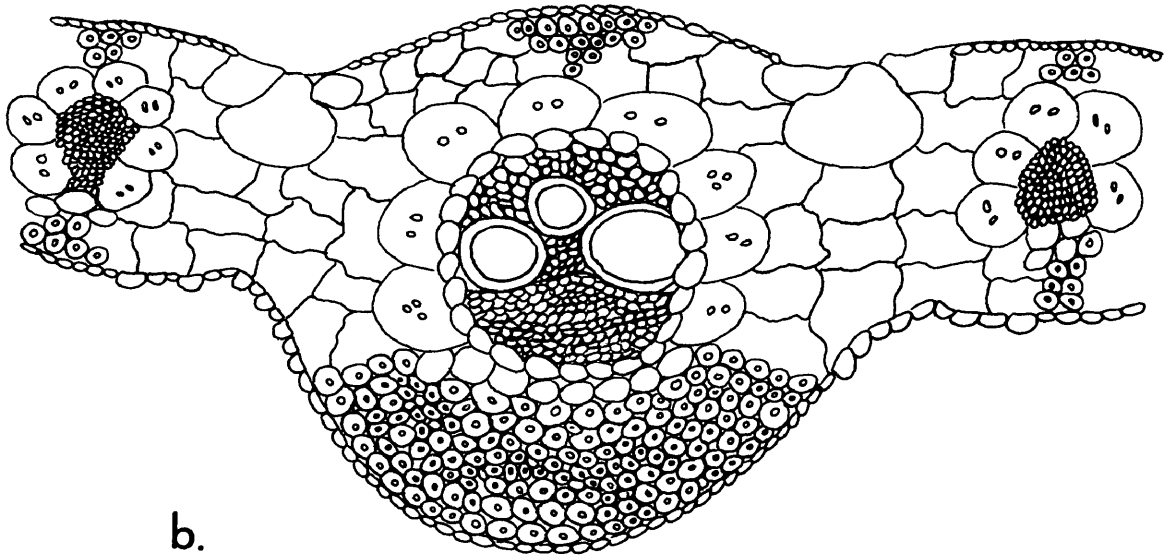

b.
x.
p.
p. sh.
e. sh.
a.
s.
b.
c.
.1mm

Figure 11. a) M. frondosa - cross section of leaf blade

b) M. sobolifera - cross section of leaf blade



a.

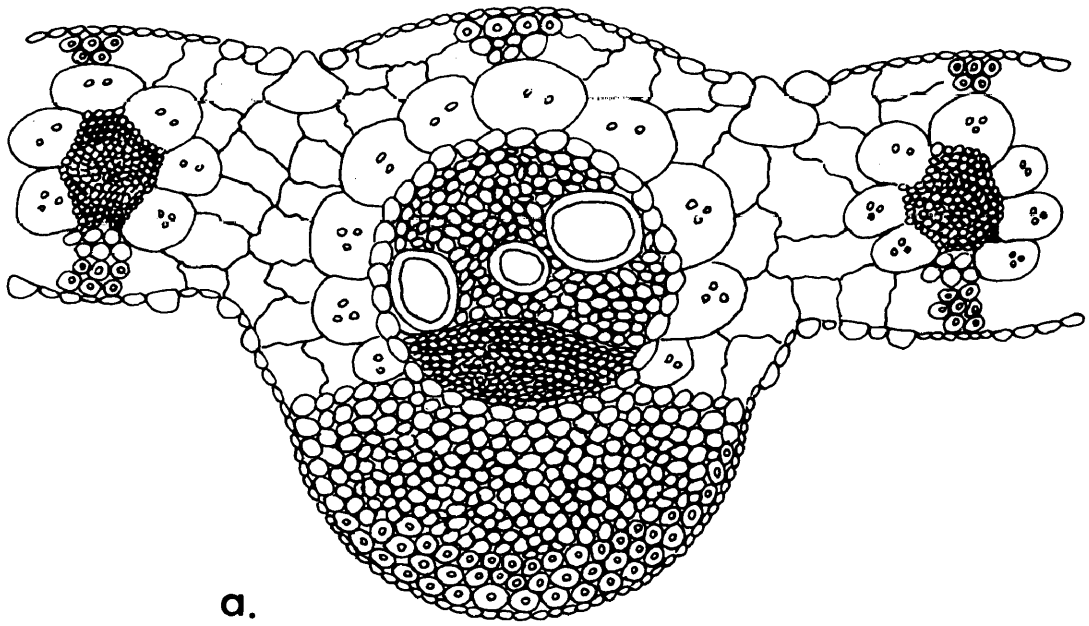


b.

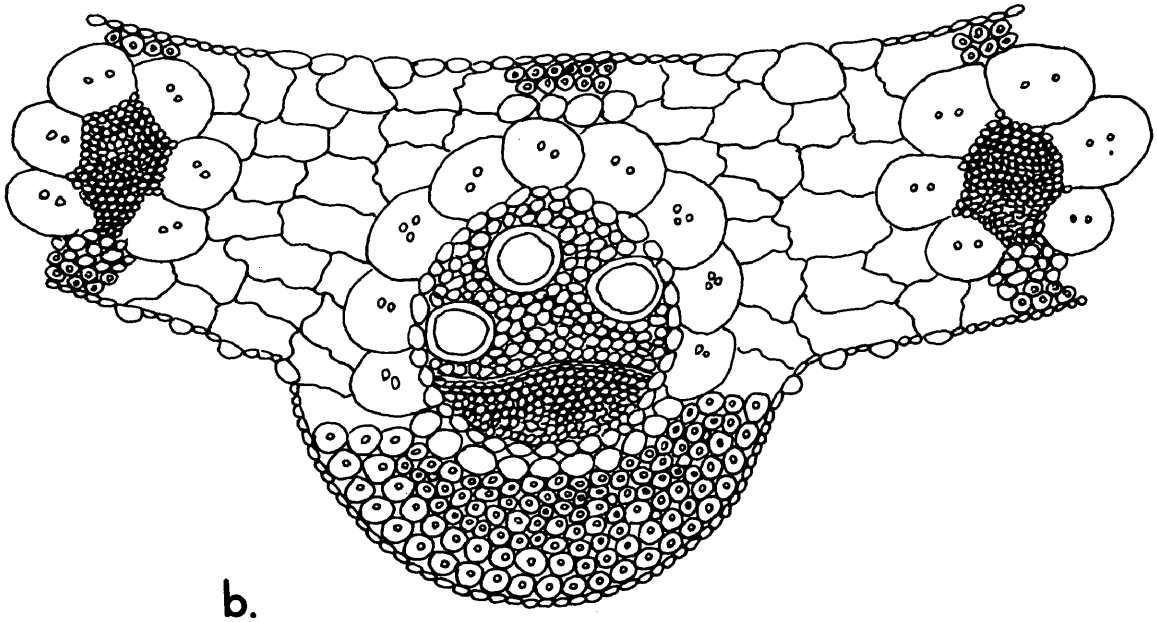
.1mm

Figure 12. a) M. mexicana - cross section of leaf blade

b) M. tenuiflora - cross section of leaf blade



a.



b.

.1 mm

Species Differences and Key Characters:

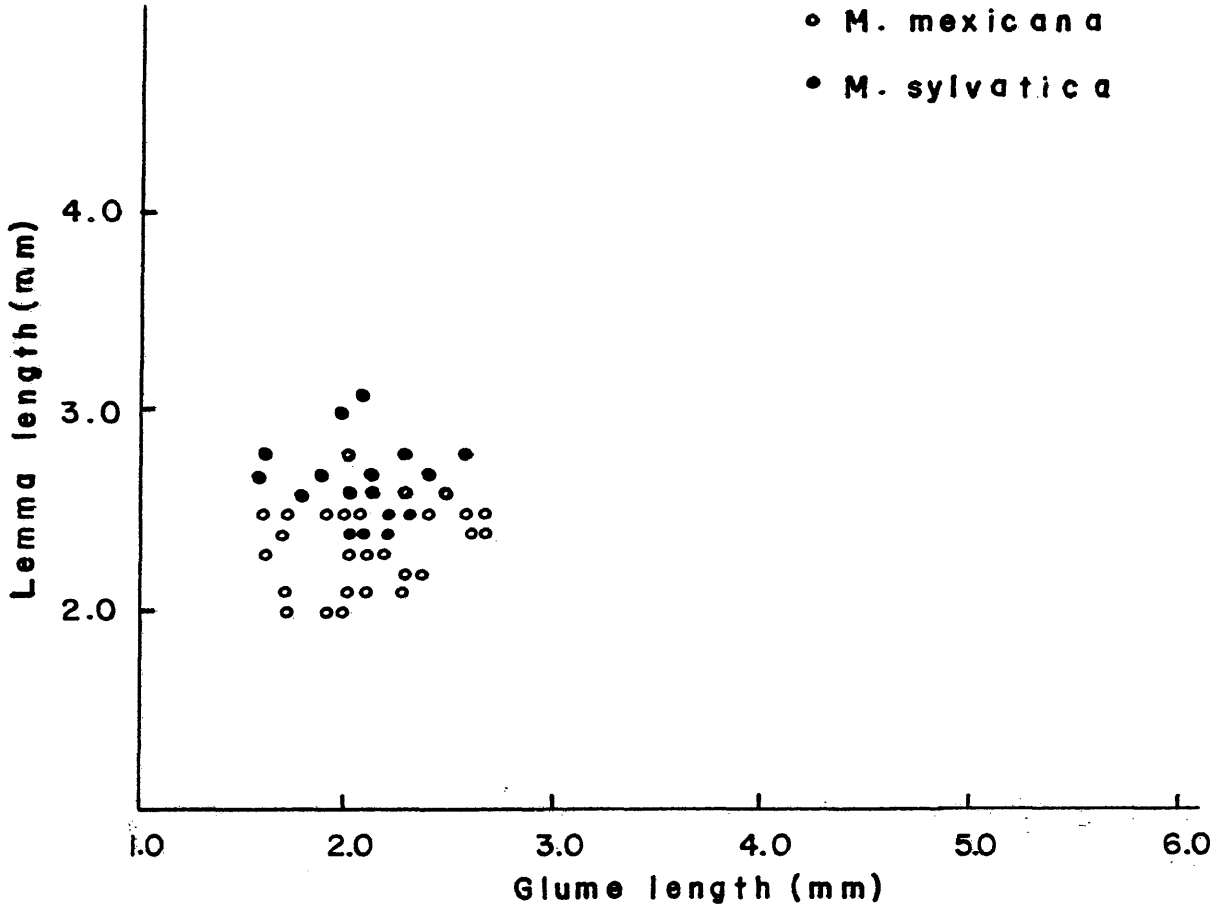
Comparisons between species were made using ligule, anther, lemma, and glume measurements. The species pairs selected for the scatter diagrams were chosen because of their similarity to each other or because they tend to be paired in the key. The individuals plotted were from different geographic areas where possible. M. tenuiflora is represented by a limited number of individuals because of its scarcity in the region.

M. mexicana - M. sylvatica (Fig. 13, Table 1):

These species are difficult to separate and have often been confused, probably because two distinct forms of M. mexicana exist. The form with slender elongate inflorescences, not unlike those of M. sylvatica, is common in eastern Nebraska while the typical form with dense lobulate inflorescences appears to be common in western Nebraska. Average ligule length of M. sylvatica is twice that of M. mexicana. The ligule of M. sylvatica also projects well above the summit of the sheath, in contrast to the ligule of M. mexicana which is barely visible from the side. Additional differences noted included (1) mean anther length which is fifty per cent greater in M. sylvatica than in M. mexicana and (2) an abruptly keeled leaf sheath in M. mexicana in contrast to the rounded sheaths of M. sylvatica. Glume and lemma length are not useful characters, although M. sylvatica tends to have longer lemmas.

M. mexicana - M. racemosa (Fig. 14, Table 1):

Several characters are needed to separate these species. Individuals were occasionally encountered which were intermediate between the



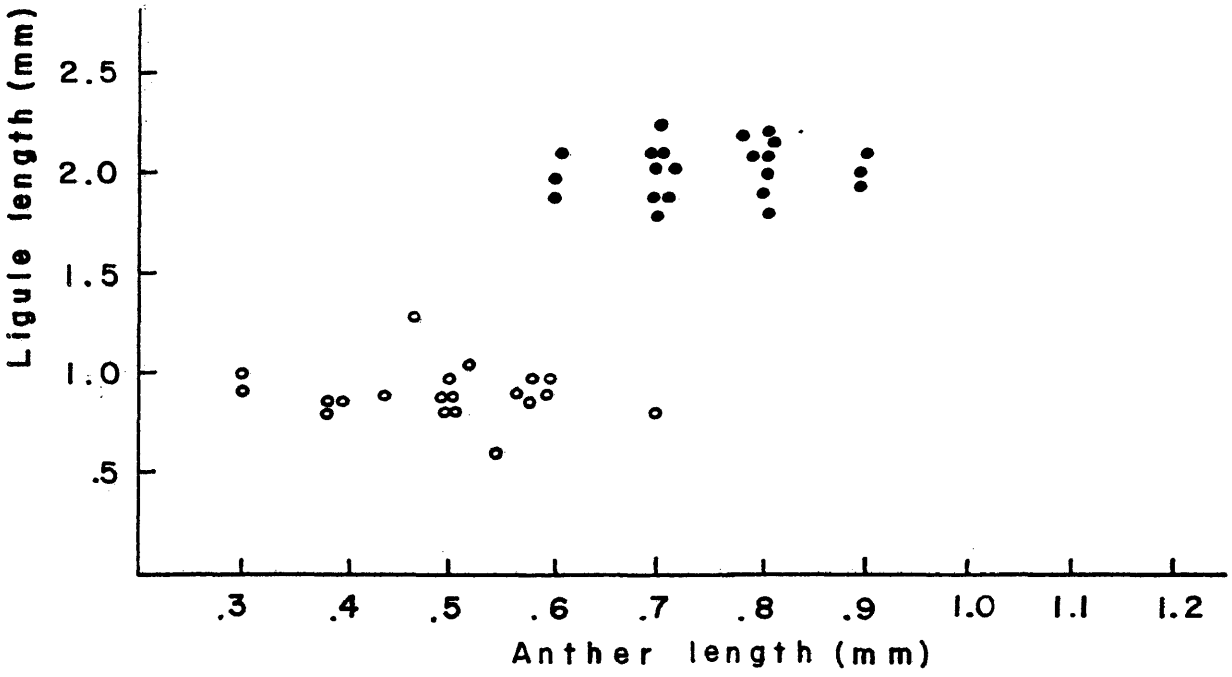


Figure 13. Scatter diagrams comparing M. mexicana and M. sylvatica

Table 1. Comparison of species using six key characters. Lengths are given in mm.

	LIGULE	ANTHER	LEMMA	GLUMES	INTERNODES	PANICLES
M. bushii	0.2-0.8 $\bar{x}$ = 0.6	0.3-0.6 $\bar{x}$ - 0.4	2.4-3.3 $\bar{x}$ = 2.8	1.5-2.4 $\bar{x}$ = 2.0	smooth and shining	numerous included panicles
M. frondosa	0.8-1.5 $\bar{x}$ = 1.1	0.3-0.6 $\bar{x}$ = 0.4	2.8-3.5 $\bar{x}$ = 2.9	1.9-3.2 $\bar{x}$ = 2.7	smooth and shining	numerous included panicles
M. tenuiflora	0.4-0.9 $\bar{x}$ = 0.6	1.1-2.2 $\bar{x}$ = 1.2	2.9-3.4 $\bar{x}$ = 3.1	1.5-3.0 $\bar{x}$ = 2.1	puber-ulent	panicles long exserted
M. sobolifera	0.4-1.0 $\bar{x}$ = 0.6	0.4-0.8 $\bar{x}$ = 0.7	1.7-2.1 $\bar{x}$ = 1.9	1.3-2.0 $\bar{x}$ = 1.6	smooth and shining	panicles long exserted
M. sylvatica	1.3-2.5 $\bar{x}$ = 2.0	0.5-0.8 $\bar{x}$ = 0.8	2.2-3.5 $\bar{x}$ = 2.6	1.6-3.0 $\bar{x}$ = 2.0	puber-ulent or glabrous	panicles long exserted
M. mexicana	0.4-1.2 $\bar{x}$ = 0.8	0.3-0.6 $\bar{x}$ = 0.5	2.0-3.1 $\bar{x}$ = 2.3	1.5-2.8 occasionally over 3.0 $\bar{x}$ = 2.1	puber-ulent	panicles long exserted
M. racemosa	0.6-1.5 $\bar{x}$ = 1.2	0.5-1.0 $\bar{x}$ = 0.6	2.3-3.5 $\bar{x}$ = 3.1	4.0-6.0 $\bar{x}$ = 4.7	glabrous to puber-ulent roughened	panicles usually exserted

two species with respect to internodal pubescence and glume length. Pohl's key indicates that M. racemosa invariably has smooth, shining internodes, but many individuals of this species were found to have puberulent, roughened internodes similar to those of M. mexicana. Furthermore, individuals of M. mexicana were encountered with relatively long awn-tipped glumes similar to those of M. racemosa. The following are valuable when atypical plants are encountered: (1) glumes of M. racemosa are much longer than the lemmas on all spikelets of a given plant; in M. mexicana glume length is more variable, not exceeding the lemmas in all of the spikelets; (2) the lemmas of M. racemosa are never awned in contrast to the occasionally awned lemmas of M. mexicana; (3) anthers and ligules of M. racemosa are longer than those of M. mexicana although some overlap occurs; (4) grains of M. racemosa are usually longer than 1.5 mm, while those of M. mexicana are less than 1.5 mm. If introgression between M. frondosa and M. racemosa occurs as Mitchell (1962) suggests, the introgressants might have relatively long glumes, dense panicles, and upright growth habit, similar to the intermediate plants discussed above. Since pollen stainability was normal, however, the putative hybrid origin of such plants was not verified.

M. bushii - M. frondosa (Fig. 15, Table 1):

Glumes and ligules of M. frondosa are much longer than those of M. bushii, but individuals were occasionally encountered which were intermediate with respect to these characters. Three other characters are valuable with such individuals (Mitchell, 1962): (1) the terminal panicle of M. bushii tends to be more exserted than in M. frondosa,

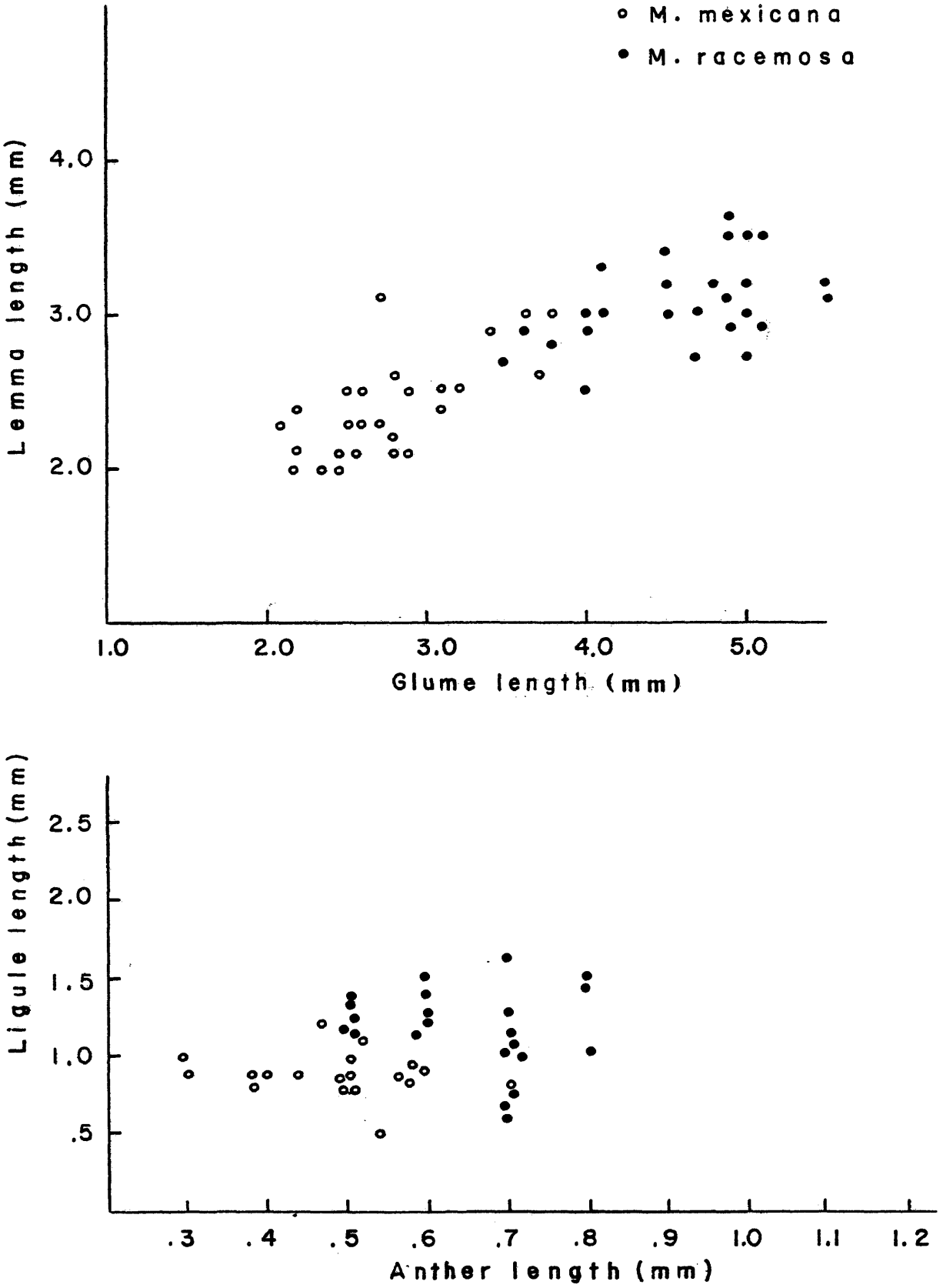


Figure 14. Scatter diagrams comparing M. mexicana and M. racemosa

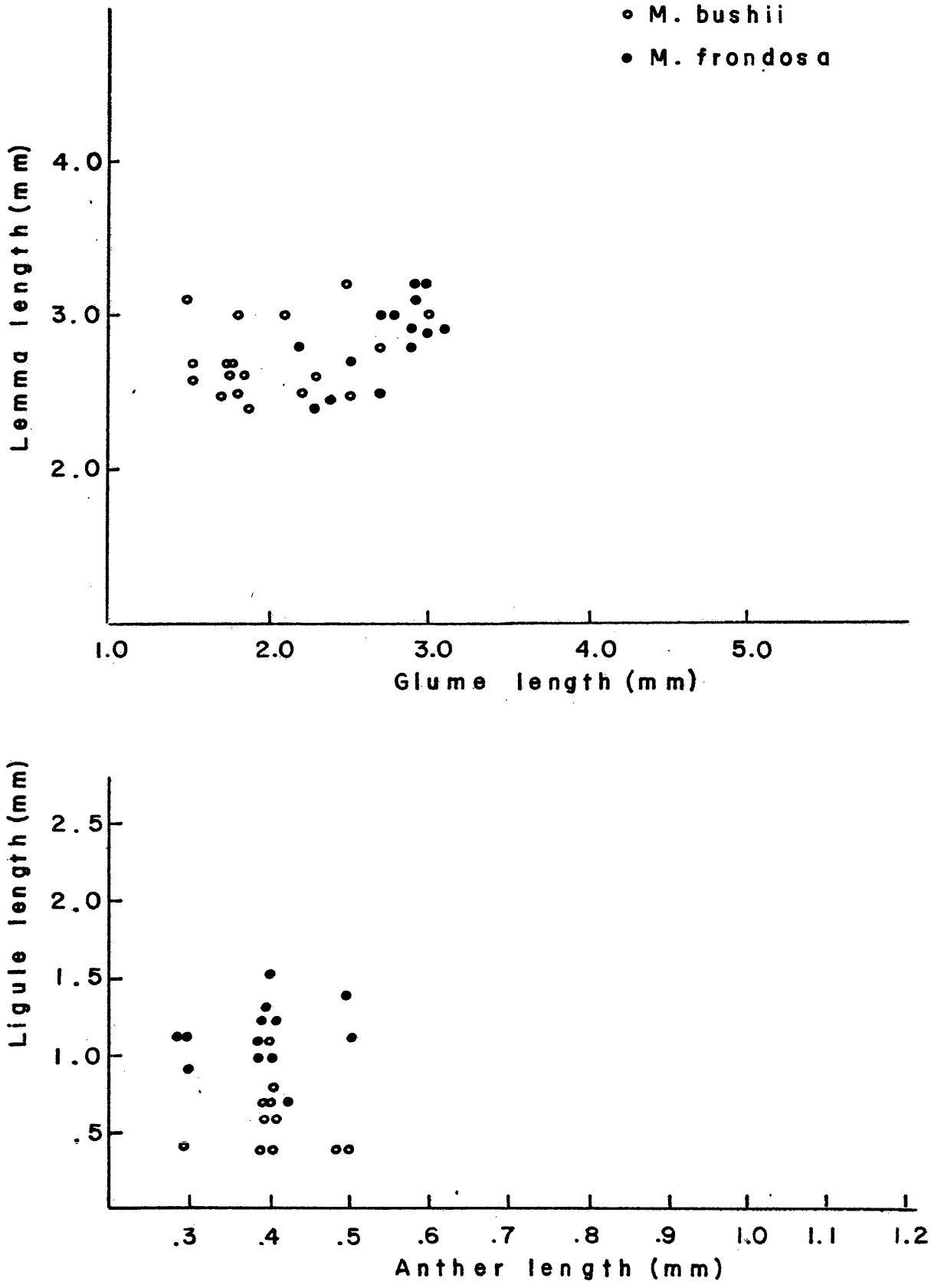


Figure 15. Scatter diagrams comparing M. bushii and M. frondosa

(2) the leaves of M. bushii tend to be positioned at right angles to the stem, unlike those of M. frondosa, (3) leaves of the side branches in M. bushii are relatively shorter and narrower than are the leaves of the main culm; such an obvious difference does not exist in M. frondosa. Introgression of M. bushii and M. frondosa in shaded habitats could account for intermediate plants encountered in this study (Mitchell, 1962) although pollen stainability of intermediate plants was normal.

M. sobolifera - M. tenuiflora (Fig. 16, Table 1):

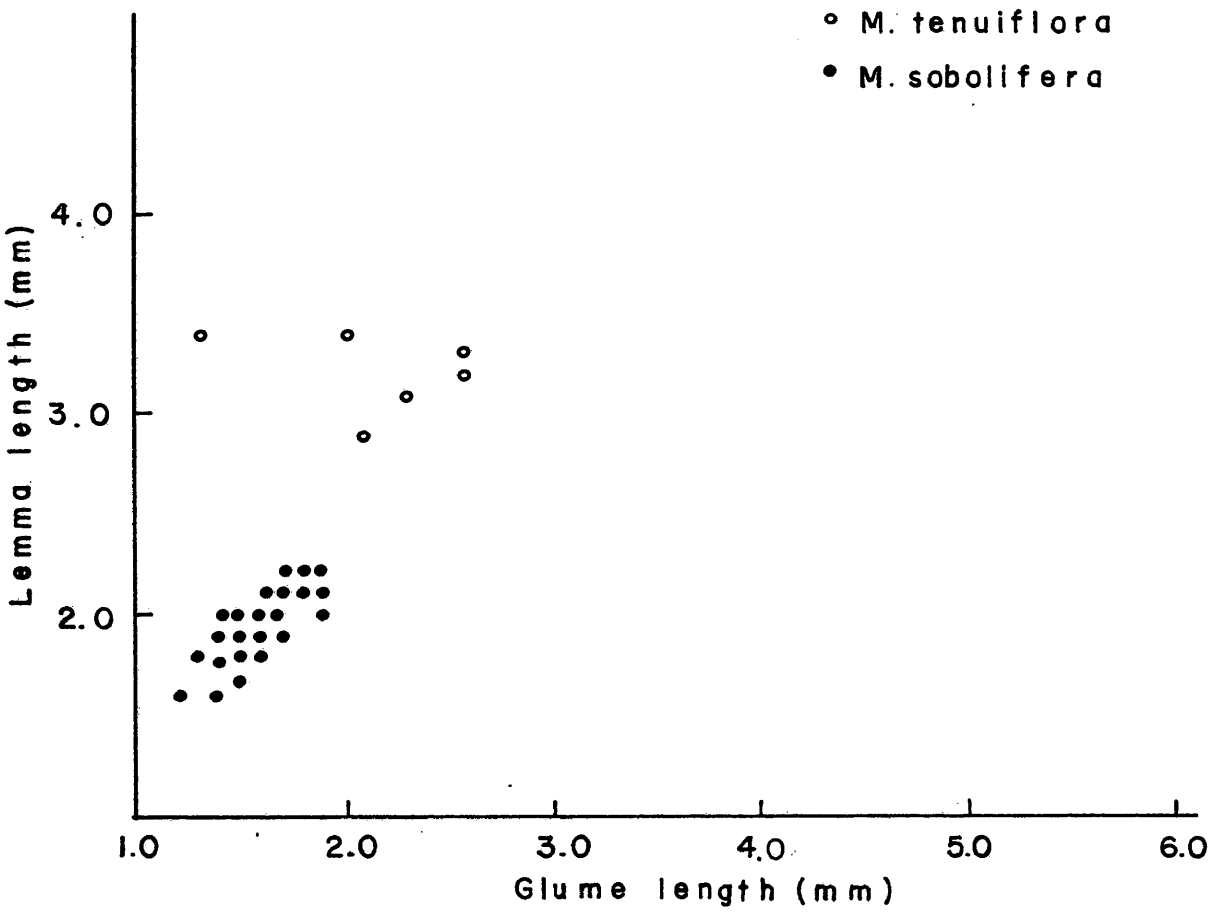
These two species are usually paired in keys because each has short, broadly ovate glumes. Lemma and anther length are sufficient to separate the two.

Carbohydrate Storage:

Tateoka (1975) indicated that the starch grains of the caryopsis can be of taxonomic value. His study indicated that members of the genus Muhlenbergia have compound starch grains. All of the species included in the present study were determined to possess compound starch grains with no differences being noted among the species (Fig. 17).

Distribution:

The wooded bluff region along the Missouri and Platte rivers appears to be the most favorable local habitat for members of the subgenus. Fontenelle Forest (Sarpy Co., Nebr.) and Indian Cave State Park (Nemaha and Richardson Cos., Nebr.) are especially rich in muhlenbergia species. The bluffs along the Nebraska side of the Missouri River have a greater abundance and diversity of species than



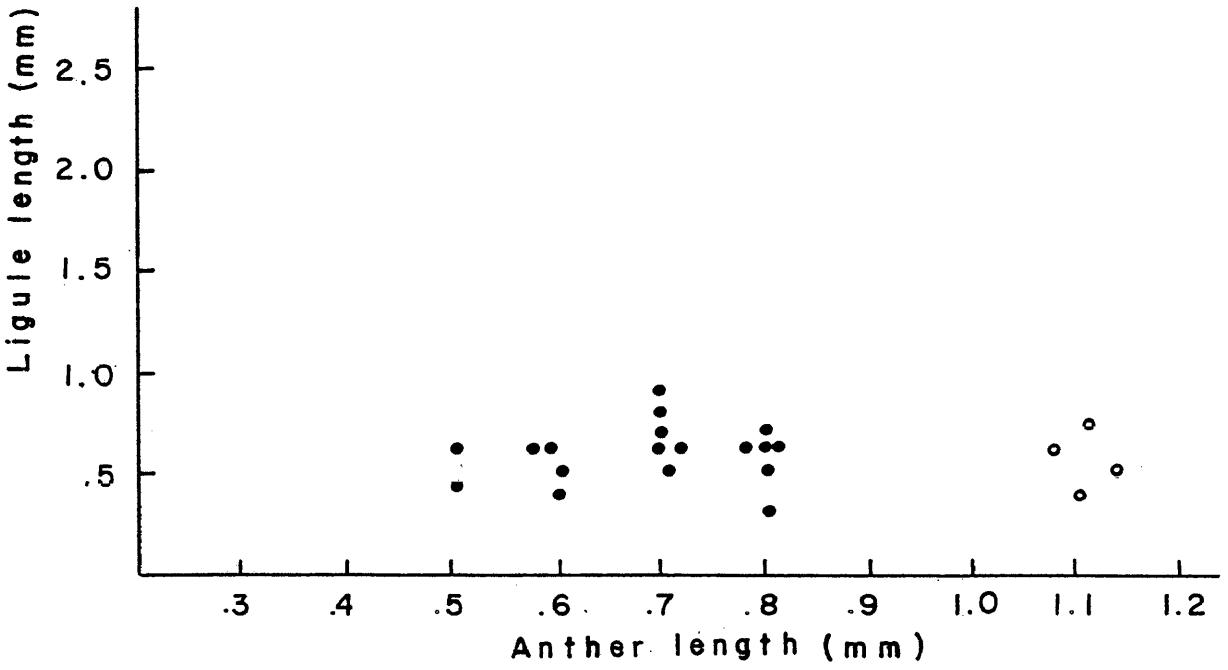


Figure 16. Scatter diagrams comparing M. temuiflora and M. sobolifera

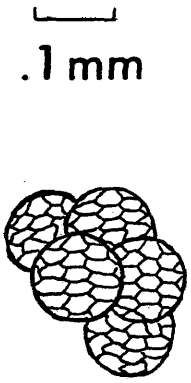


Figure 17. Starch grains from caryopsis of M. racemosa.

do those on the Iowa side.

M. tenuiflora is quite uncommon in this region; one small colony was encountered in an undisturbed upland woods (Sarpy Co., Nebr.). M. sobolifera, another species of upland forests is also scarce; its range extends from Missouri and Kansas into three southeastern Nebraska counties. The range of M. sylvatica (Fig. 18) is more restricted than distribution maps have indicated (McGregor et al., 1976) since two Nebraska collection sites (Hall and Webster Cos.) are based upon misidentifications; it is also restricted to upland woods. M. bushii (Fig. 19), a species of forest borders and lowland woods, is more common than distribution maps have indicated since it was collected in five additional Nebraska counties. M. mexicana is common and abundant both in upland and lowland woods. Only the slender form was collected during this study; the form with dense inflorescences apparently being more common in western Nebraska. M. frondosa and M. racemosa are both common in a variety of habitats and characteristically grow in disturbed sites.

Key:

The following key was constructed using observations made in the course of this study combined with some of those characteristics used by Pohl (1969), Gleason and Cronquist (1965), Fernald (1943), and Mitchell (1962).

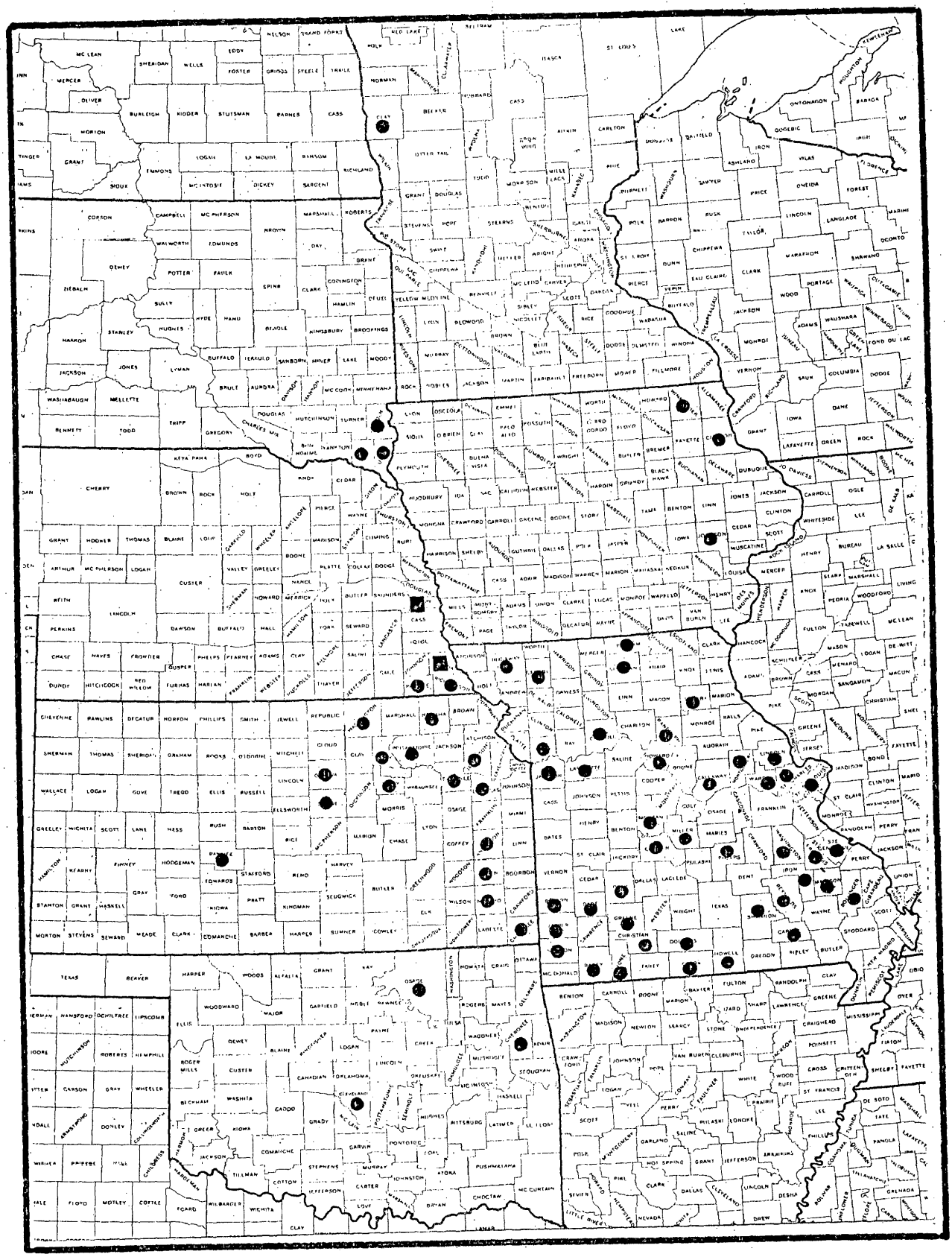


Figure 18. Distribution of M. sylvatica
■ county record, collected during this study
● previously collected in county

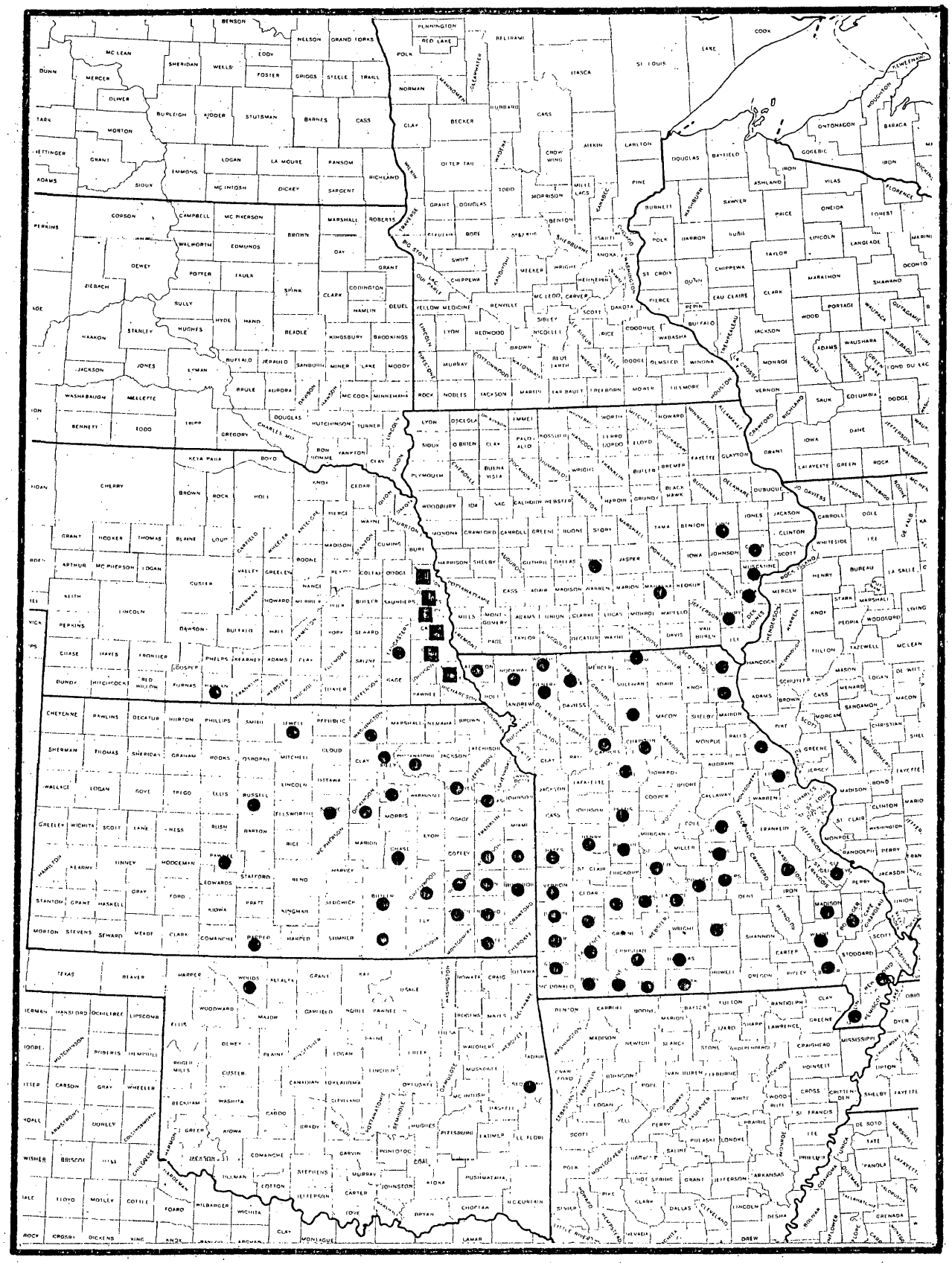


Figure 19. Distribution of M. bushii
■ county record, collected during this study
● previously collected in county

Glumes with stiff awn-tips, both one-third longer than the awnless lemma in the majority of the spikelets; anthers 0.5 mm or longer; grain usually longer than 1.5 mm; internodes often smooth and shining, occasionally puberulent-roughened

M. racemosa

Glumes awnless or awn-tipped, usually shorter than the lemma, occasionally longer; lemma awned or awnless; anthers, grain, and internodes variable

Internodes of culm glabrous, sometimes slightly puberulent near the summit

Plants with numerous axillary inflorescences, many of these included in the leaf sheath

Glumes much shorter than the lemma, mostly under 2.2 mm; ligules 0.7 mm or less; leaves positioned at right angles to the stem, those of the secondary branches often shorter and narrower than the leaves of the main culm; terminal panicle often well exserted

M. bushii

Glumes nearly as long as the lemma, the second sometimes exceeding the lemma; ligule 0.8 mm or more; leaves not conspicuously positioned at right angles to the stem and with little difference in size between the leaves of the branches and the main culm; terminal panicle not usually long exserted

M. frondosa

Plants with few axillary inflorescences, but if present their peduncles long and exserted

Ligules conspicuous, 1.4–2.5 mm, projecting above the summit of the sheath, lemma 2.4 mm or more

M. sylvatica

Ligules not conspicuous, 1.0 mm or less; lemma 2.2 mm or less

M. sobolifera

Internodes of culm puberulent, especially near the summit

Glumes much shorter than the lemma, broadly ovate and overlapping; anthers longer than 1.0 mm
M. tenuiflora

Glumes as long as the lemma (occasionally shorter), lanceolate, not overlapping; anthers 0.8 mm or less

Ligules conspicuous, 1.4-2.5 mm, projecting above summit of sheath; inflorescences slender; anthers 0.6-0.8 mm; leaf sheaths rounded
M. sylvatica

Ligules not conspicuous, 1.2 mm or less; inflorescences from very dense and lobulate to very slender; anthers 0.5 mm or less; leaf sheaths abruptly keeled
M. mexicana

SUMMARY AND CONCLUSIONS

Muhlenbergia is a large, widely distributed group of grasses. The subgenus Muhlenbergia is comprised of mesic, broad-leaved, usually rhizomatous species. Seven species of the subgenus, native to the east-central Great Plains were studied: M. bushii Pohl, M. frondosa (Poir.) Fern., M. mexicana (L.) Trin., M. racemosa (Michx.) B.S.P., M. sobolifera (Muhl.) Trin., M. sylvatica (Torr.) Torr. and M. tenuiflora (Willd.) B.S.P. Certain of these species are morphologically similar and difficult to separate by conventional taxonomic characteristics. This study is designed to clarify some of the taxonomic problems associated with the group and to study the distribution of the species.

Characteristics of leaf anatomy and carbohydrate storage were evaluated in addition to the usual floral and morphological characters. The anatomical criteria are of limited taxonomic value. Transverse sheath anatomy provides a clear picture of the degree to which the sheath is keeled and thus furnishes an additional character to separate M. mexicana and M. sylvatica. Transverse blade anatomy is of limited use, only one of the species can be segregated using this character. Epidermal leaf anatomy is also unrewarding with the exception of certain minor differences in the abundance of dermal appendages.

The traditional morphological characters provide the best means for separating members of the subgenus. Ligule, anther, lemma, and glume length along with internodal pubescence and presence of axillary panicles are the most useful characters, and are used to develop a key to the species.

M. tenuiflora is the least common species of the subgenus, being found in only one county. M. sobolifera is also scarce; its range extends from Kansas and Nebraska into three southeastern Nebraska counties. M. bushii is more common than previous records had indicated; five additional county records were collected. The range of M. sylvatica is more restricted than distribution maps have shown, since two collection sites are based upon misidentifications. M. mexicana is common and abundant; two distinct forms are present in the region. M. frondosa and M. racemosa are also common and abundant.

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