

TAXONOMIC STUDY OF SUBGENUS  
PODOSEMUM AND SECTION EPICAMPES  
OF MUHLENBERGIA (GRAMINEAE)

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Introduction

Within the genus *Muhlenbergia* (Gramineae) is a group of tall, rather robust perennials that some botanists have treated as a distinct genus, *Epicampes*. Since Presl (1830) proposed *Epicampes*, many species have been added. All are found in the Western Hemisphere, the majority occurring in northern and central Mexico, the center of distribution.

The characters originally employed to delimit *Epicampes* have been interpreted by botanists in different ways. Some have placed considerable emphasis on the dorsal position of the awn of the lemma, while others have regarded the relatively long glumes of the spikelet as particularly characteristic. Another feature of value is the compressed-keeled nature of the basal sheaths. No one character has been found to distinguish all species of *Epicampes* from all other genera. Authors who have described species in the group have had different concepts of the genus, to the extent that *Epicampes* has never been clearly circumscribed. Unfortunately, no recent author has listed the species considered to comprise the genus *Epicampes*, and not only is the generic status and affinities of the group a problem, there is also no general agreement regarding the number of species.

Traditionally, the classification of grasses has been based on characters of gross morphology, with special reference to the structure of the spikelet. In such a classification *Epicampes* has been treated as a member of the tribe Agrostideae, which includes grasses with single-flowered spikelets, with close affinities to such genera as *Agrostis* and *Cinna*.

Starting before the turn of the century, but more particularly within the last decade, studies of features other than gross morphology have shed much light on the true relationships within the Gramineae. These studies have included investigation of the structure of the grass embryo, lodicules, chromosomes, and the anatomy of the leaf and epidermis. The results of these investigations are correlated remark-

ably and demonstrate that in many cases the characters of the spikelet and other features of gross morphology are not reliable indexes to the natural relationships of grasses. These studies for the most part have dealt with representative species of genera, in an attempt to find their natural affinities within the grass family. Relatively little effort has been made to utilize these studies at the infrageneric level to clarify relationships among the species within a single genus.

The first phase of the present study was to determine the relationship of the *Epicampes* group at the genus level, and studies of the embryo, lodicules, and leaf anatomy and epidermis were useful in this regard. The results of these investigations provide strong evidence that *Epicampes* is not related to such genera as *Agrostis* and *Cinna* of the Agrostideae but rather to grasses of the "chloridoid" alliance, which includes many grasses traditionally placed within the tribe Chlorideae.

The second phase was a taxonomic survey of the species belonging to the *Epicampes* group. Field studies were made in Mexico in 1959 and 1960 and herbarium specimens examined included the majority of type specimens or fragments of types of the species involved.

In addition to the large series of specimens studied at Yale University (YU) and the U.S. National Herbarium (US), collections were borrowed from the following herbaria: University of Arizona (ARIZ); California Academy of Sciences (CAS); Escuela Nacional de Agricultura, Chapingo, Estado de México (CHAP); Stanford University (DS); Field Museum of Natural History (F); Gray Herbarium of Harvard University (GH); University of Illinois (ILL); Instituto Politécnico Nacional, México, D.F. (IPN); Texas Research Foundation (LL); Universidad Nacional de México (MEXU); University of Michigan (MICH); Missouri Botanical Garden (MO); New York Botanical Garden (NY); Pomona College (POM); Naturhistoriska Riksmuseum, Stockholm (S); Southern Methodist University (SMU); A.&M. College of Texas (TAES); University of Texas (TEX); University of California (UC); University of New Mexico (UNM); and Instituto Botánico, Ministerio de Agricultura y Cría, Caracas (VEN); The abbreviations of herbarium names are those of Lanjouw and Stafleu (*Index Herbariorum*, ed. 5, 1964) except for CHAP and IPN which are the author's.

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### Historical Considerations

The description of the genus *Epicampes* by Jan S. Presl (1830) was based on a single collection from southern Mexico. In K. B. Presl's introduction is the statement (translated): "In the month of November Thaddaeus Haenke went alone to the capital city of Mexico, and returned in December to Acapulco." It was on this trip in 1791 that Haenke collected the type specimen of *Epicampes*. Although no locality other than "Mexico" is given, Presl's description and illustration of the specimen resemble most closely other specimens of *Epicampes* from the central Mexican plateau. Furthermore, Haenke's specimen was probably collected higher on the plateau in the state of Morelos or México, rather than in the lower and more tropical elevations of Guerrero, of which Acapulco is the main port of entry on the Pacific.

The name *Epicampes* may have been derived from the classical Greek word "*kampes*," an adjective meaning "curved." It is unclear why Presl chose a word with such a meaning as a name for this genus. Unfortunately, he gives no indication of its etymology in the original description.

The type species, *Epicampes strictus* Presl (*Muhlenbergia robusta* [Fourn.] Hitchc.), is widely distributed in the higher elevations from the state of Jalisco southward into Central America. His description of the genus, translated from the Latin, follows:

Panicle contracted, in the form of a spike, with alternate solitary branches. Glumes two, ovate, convex, nerveless, subequal, obtuse, entire. Floret a little longer than the glumes. Glumes two, convex, ovate, the lemma surrounding the palea at its base, entire, with the median nerve extending into a straight awn from beneath the apex, the palea 2-nerved, very obtuse, enclosing the genitalia. Stamens 3. Ovary ovate, emarginate at apex. Styles 2. Stigmas divided into dense branchlets. Lodicules . . . caryopsis. . . . It seems to differ enough from *Agrostis* by the entire lemma and palea, with a straight awn neither twisted nor plicate, from *Apera* by the awned lemma. To this genus belong also *Agrostis pubescens* and *A. lanata*.

Of the several features that Presl enumerated for *Epicampes*, the nerveless condition of the glumes and the awn rising from just be-

low the tip of the lemma have been regarded by subsequent authors as important diagnostic characters for the genus.

As originally proposed, *Epicampes* comprised three species. Besides *E. strictus*, Presl included *Agrostis lanata* H. B. K. and *A. pubescens* H. B. K. These species had been described by Humboldt, Bonpland, and Kunth (1815) from specimens collected by Humboldt in the state of Guanajuato, north of where Haenke had collected. Three other species described in the same work, *Crypsis macroura*, *C. phleoides*, and *Podosaemum distichophyllum*, were later included in *Epicampes* by other workers. Thus, the species assigned to *Epicampes* had been described under the genera, *Agrostis*, *Crypsis*, and *Podosaemum*.

Kunth, who originally named the two Humboldt collections from Guanajuato as species of *Agrostis*, later accepted Presl's contention that they belonged to *Epicampes*. In 1833, Kunth's *Agrostographia* was published in Germany, where *Epicampes* was included in the Agrostideae, a tribe established by Kunth in 1815. Incorporated in this tribe were all grasses characterized by single-flowered spikelets:

V. Agrostideae. Spikelets single-flowered, rarely with a rudimentary subulate flower above the other. Glumes 2, lemma and palea, membranaceous-herbaceous; lower often awned. Stigmas mostly spreading. Through *Muhlenbergia* affinities with *Stipa*.

Although recent research has demonstrated the unnaturalness of the Agrostideae as interpreted by Kunth, many contemporary taxonomists still recognize the tribe and place in it *Muhlenbergia*, including the *Epicampes* group.

Kunth's description of *Epicampes* was similar to Presl's. He placed the genus between *Cinna* L. and *Sporobolus* Brown, mentioning that it "differs from *Cinna* principally by its convex, non-keeled glumes." The genus *Muhlenbergia*, in which many recent authors have incorporated *Epicampes*, evidently was not considered by Kunth to be as closely allied, for he separates the two by several genera.

Trinius (1841) recognized *Epicampes* essentially as Presl and Kunth had before him but described the species in more detail and added one new species, *E. gracilis* (*Muhlenbergia lindheimeri* Hitchc.). He described the glumes as 1-nerved, in contrast to Presl's and Kunth's statements that the glumes are nerveless. Yet, in his description of *E. strictus* and *E. pubescens*, Trinius noted that the glumes are nerveless. The new species Trinius described was from Texas, the first of the group from the United States.

Until 1874 *Epicampes* was treated as comprising only four species, *E. strictus*, *E. lanatus*, *E. pubescens*, and *E. gracilis*, all with a habit and panicle similar to the first species that Presl described, and as a

genus ranging from southwestern United States (Texas) to southern Mexico. This concept of *Epicampes* was expanded by Grisebach (1874) in a description and discussion of the collections of Argentine plants of Professor Lorentz. In this work Grisebach described a new species, *E. coeruleus* (*Muhlenbergia angustata* [Presl] Kunth), with spikelike panicles, 1-nerved, awn-tipped glumes, and a long acute ligule. At the same time he transferred two other species with spikelike panicles to *Epicampes*: *Cinna phleoides* Kunth (based on *Crypsis phleoides* H. B. K.) and *C. stricta* Kunth (based on *Crypsis stricta* H. B. K.). By incorporating these species from Argentina into *Epicampes*, the range of the genus was considerably extended.

George Bentham (1881) in the first really critical comments concerning the generic limits of *Epicampes* recognized four subtribes within the Agrostideae, one, the Euagrostae, included *Epicampes*. About 16 genera comprised this subtribe, of which he concluded:

. . . the general character is a dorsal usually twisted awn on the flowering glume, the grain neither so closely enveloped in the fruiting glume as in Stipeae, nor so readily exposed as in Sporoboleae, and the spikelets usually small, loosely paniculate, very rarely condensed into a head as in Phleoideae; but there are exceptions to every one of these characters, and the limits of the larger genera are so vague as to render this portion of the genera of Gramineae the least satisfactory of the whole series.

Bentham stated that *Epicampes* was composed of "about 16 species,"<sup>1</sup> but that this number was possibly too large and most probably reducible by one-third, and that it "is a genus most embarrassing to the systematist; for it seems to connect *Muhlenbergia* and *Sporobolus* with *Agrostis*." One of the characteristics he regarded as distinctive of *Epicampes* was the long, narrow, dense panicle composed of numerous small spikelets. He differentiated *Epicampes* from *Muhlenbergia* by the awns on the lemmas which, when present in the former, are short and not quite terminal, while in the latter are longer and terminal. The dorsal position of the awn was one of the chief distinguishing features recognized by Presl in establishing the genus. Bentham distinguished *Epicampes* from *Sporobolus* by the fact that in the former the glumes are thinner and more membranous than the lemma and palea but in the latter they are thicker and less membranous. Bentham admitted his unfamiliarity with many of the

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<sup>1</sup> A survey of the literature reveals only 9 published species of *Epicampes* up to and including those described in Bentham's paper. For his estimate of 16 species, Bentham doubtless relied on Fournier's treatment of the group in *Mexicanas Plantas*. Although the title page was not printed until 1886, Fournier had sent copies to several botanists as early as 1880. In the first part of his "Notes" (p. 20) Bentham stated that Fournier had supplied him with a copy, remarking, "I feel bound, insofar as I am concerned, to treat it as having already taken date."

published species, adding that, "a further study may require considerable modification of the generic character and limits."

Following the example of Grisebach, Bentham included in *Epicampes* additional species with spikelike panicles. He transferred Fournier's *Crypsinna* and Kunth's *Cinna macroura* and *C. stricta* to *Epicampes macroura* (*Muhlenbergia macroura* [H.B.K.] Hitchc.). *Cinna macroura* Thurber was placed in *Epicampes* to become *Epicampes rigens* Benth. (*Muhlenbergia rigens* [Benth.] Hitchc.), a species closely related to *E. macroura*. The genus *Bauchea* Fourn., represented by a single Mexican species, *B. karwinskyi*, which Bentham had not seen, was also considered by him to be an *Epicampes* (although later synonymized with *Sporobolus wrightii* Munro ex Scribn.).

In Bentham and Hooker (1883)<sup>2</sup> four subtribes of the tribe Agrostideae are listed, with the genera enumerated under each. The four subtribes are: Stipeae, Phleoideae, Sporoboleae, and Euagrostaeae. *Epicampes* was placed within Euagrostaeae and *Muhlenbergia* in Stipeae. *Sporobolus*, considered by some as closely allied to *Epicampes*, was the basis of subtribe Sporoboleae.

Of the four subtribes listed, the Sporoboleae, containing the single genus *Sporobolus*, is distinctive in that the grain is not a true caryopsis but rather the seed is loose from the ovary wall (pericarp). Furthermore, the fruit is loosely enclosed within the lemma and palea and drops out easily; for this reason the popular name "dropseed" has been applied to the genus. The chief distinction of the Euagrostaeae appears to be the position of the awn on the lemma, dorsal in some cases, "rarely arranged subterminally to a mucro, or variously awned" (Bentham, 1883). However, grasses with awned lemmas are also found in the Stipeae and Sporoboleae. The position of the awn on the lemma in the Euagrostaeae does not easily separate this subtribe, and the Stipeae and Euagrostaeae show no distinctive features to separate them clearly.

According to Bentham's description of *Muhlenbergia* (Stipeae), the major character to differentiate this genus from *Epicampes* (Euagrostaeae) was the relatively small size of the glumes as compared with the lemma and palea. Yet, even here species are included with the glumes subequal to the floret. The awn of the lemma in *Epicampes* was stated as minute and subterminal, although in *Muhlenbergia* the awn was described only as "rarely obsolete." There was no reference to its position on the lemma. Although Bentham gave these contrasting characters for the two genera, none was distinctive enough to separate all species of *Epicampes* from all species of *Muhlenbergia*.

<sup>2</sup> The treatment of Gramineae in *Genera Plantarum* (1883) was produced by Bentham whose "Notes on the Gramineae" (1881) was based on observations made during its preparation.

Following the lead of previous authors, Vasey (1885) placed *Epicampes* in the Agrostideae. Employing the system of Bentham and Hooker, he included *Muhlenbergia* in the subtribe Stipeae and *Epicampes* in the subtribe Euagrostae. According to Vasey's interpretation, the only essential character that differentiated the two subtribes was the position of the awn on the lemma. He said of the Stipeae, "beard of the flowering glume terminal," and of the Euagrostae, "flowering glume usually with a more or less twisted dorsal awn; rarely mucronate or awnless." Like Bentham and Hooker, he included the genera *Agrostis*, *Polypogon*, *Arctagrostis*, and *Cinna* in the same group of Euagrostae with *Epicampes*.

In his description of *Epicampes*, Vasey recognized three species: *E. distichophyllus* Vasey, *E. macroura* Benth., and *E. rigens* Benth. He stated that the spikelets of *Epicampes* are much like *Sporobolus* but contracted in a long, narrow, and dense panicle. He added,

. . . Outer glumes somewhat unequal, membranaceous, convex on the back, scarcely keeled, obtuse, three-nerved; flowering glume mostly equalling the outer ones, sometimes three to five nerved, entire or sometimes awned from the apex; palea hyaline, about equalling the flowering glume, two nerved or two-keeled.

Vasey seems to have considered long dense panicles and glumes a little longer than the lemma as the important features of *Epicampes*. He erred, however, in stating that the glumes are 3-nerved; previous agrostologists had emphasized the nerveless or 1-nerved condition of the glumes in species of this group. He also said that the lemmas ("flowering glumes") are entire or awned from the apex, but did not recognize the dorsal position of the awn as a diagnostic feature. Nevertheless, in *E. distichophyllus* Vasey (*M. emersleyi* Vasey) the awn is clearly dorsal, or subterminal, rather than terminal.

Hemsley received a copy of Fournier's manuscript of *Mexicanas Plantas* before its publication and drew upon it in *Biologia Centrali-Americana* (1885). In the introduction, Hemsley remarked, "with regard to many of the new species described by Fournier which we have had an opportunity of examining, we consider them as varieties undeserving of distinctive names even." Hemsley's treatment included many of Fournier's species, and he comments that of the 16 species proposed up to that time, several were not distinguishable as such. The genus *Epicampes* followed *Sporobolus* in his treatment, in accordance with contemporary taxonomic opinion. Both Hemsley's and Fournier's works merely contain listings of genera and species, with a brief description of each species but no descriptions of the genera. Fournier and Hemsley followed the treatment of Gramineae as proposed earlier by Bentham (1881).

Hackel (1890) in *The True Grasses* (a translation by F. Lamson Scribner and E. Southworth) also followed Bentham and placed *Epicampes* in the Euagrosteeae. Hackel mentioned 12 species in contrast to the 13 recognized by Fournier.

Vasey (1892) listed two species of *Epicampes*, *E. ligulatus*, described as new, and *E. rigens* Benth. (*Muhlenbergia rigens* [Benth.] Hitchc.). One species that Vasey included in the genus *Muhlenbergia*, *M. emersleyi* Vasey,<sup>3</sup> was later transferred to *Epicampes* by A. S. Hitchcock. Vasey's concept of the generic limits of *Epicampes* did not fully coincide with the general established concept, for he certainly would have included *M. emersleyi* within *Epicampes* if he had been familiar with the characters used to delimit the genus. Except for the glabrous lemmas of *E. ligulatus* and *E. rigens*, no characters would exclude them from his concept of *Muhlenbergia*—but, even then, under *Muhlenbergia* he remarked that the flowering glumes, or lemmas, are "frequently" pubescent below. Although Vasey recognized *Muhlenbergia* and *Epicampes*, he failed to select good characters to distinguish these two genera.

A key to nine species of *Epicampes* was given by Beal in 1896. In his discussion, Beal remarked that all species of *Epicampes* seemed near *Agrostis*, but some closest to *Cinna*, others to *Muhlenbergia*, and yet others to *Sporobolus*. He stated:

. . . the chief general feature is the long narrow dense panicle with very numerous rather small spikelets, the awn of the floral glume, when it exists, much smaller than in *Muhlenbergia* and often not quite terminal; the unawned species are distinguished from *Sporobolus* by the fruiting glume and grain which are nearly those of *Agrostis*.

The notes on *Epicampes* by Marcus Jones (1912) point up the confusion that had developed in establishing the boundaries for *Epicampes*. Jones' conclusions, based solely on morphological observations, are corroborated to a large extent by anatomical studies made by the present author. Jones considered as the most important character of *Epicampes* the specialized awn of the lemma that arises from just below the tip, that is, dorsally or from an emarginate tip.

Although Jones erred in associating *Bealia mexicana* Scribn. (*Muhlenbergia biloba* Hitchc.), *M. argentea* Vasey, and *M. clomena* Trin. with *Epicampes*, he did recognize that certain other species associated with *Epicampes* belong to a separate group. This group includes the species with spikelike panicles, coarse ribbed leaves, and firm ligules. Jones followed Fournier in assigning such species to the genus *Crypsinna*. He also included *Epicampes macroura* Benth.

<sup>3</sup> Vasey also listed another *Muhlenbergia*, *M. distichophylla* Kunth. The specimen referred to, however, was *M. emersleyi* and is not to be confused with *M. distichophylla* of Mexico and Guatemala.

in the genus, as Fournier had done, and further considered *E. rigens* Benth. to be a member.

Fournier originally established the genus *Crypsinna* based in part upon *Crypsis* H. B. K. and in part on *Cinna* Kunth (not L.), and included species with 1-flowered spikelets and dense spikelike panicles. Bentham chose to reduce *Crypsinna* to *Epicampes*, but Jones accepted Fournier's genus and did not recognize those species with spikelike panicles as belonging to *Epicampes*.

Hitchcock in 1914 and in earlier works recognized the genus *Epicampes*, although later he united it with *Muhlenbergia*. His description of *Muhlenbergia* indicated that "it grades on the one hand into *Sporobolus*, from which it differs in having an awned or mucronate lemma, and on the other into *Epicampes*, from which it differs in having a relatively firmer lemma." Bentham used the firm lemma in *Epicampes* as a character in contrast with the thinner lemmas of *Sporobolus*.

Hitchcock (1920) based his description of *Epicampes* on the characters of the equal glumes, the awn of the lemma which, when present, characteristically rises from just below the tip, the caespitose, perennial habit of the plants, and the open, narrow, or spikelike panicles. Hitchcock regarded *Crypsinna* as a synonym of *Epicampes*. He also transferred *Muhlenbergia emersleyi* Vasey and *M. vaseyana* Scribn. (*M. distichophylla* sensu Vasey) to *Epicampes*, bringing the number of species to 15.

Bews (1929) regarded the texture of the lemmas as a significant character in differentiating genera within the Agrostideae. Under the first category of the tribe, "lemma usually hyaline or membranaceous at maturity, at least as delicate as the glumes, or more so," he included *Sporobolus*, *Agrostis*, and *Epicampes*, in addition to many other genera. *Muhlenbergia* is found under the second category, "lemma indurated at maturity, or at least firmer than the glumes." Bews listed the same species of *Epicampes* that Hitchcock had listed in his 1920 publication.

A significant change was made in the disposition of *Epicampes* by Hitchcock in 1934. In transferring *Epicampes ligulatus* Scribn. to *Muhlenbergia* (*M. longiligula* Hitchc.), he commented:

. . . the character which I have used to differentiate the two, the awn from the back of the lemma, just below the apex in *Epicampes* and from the tip in *Muhlenbergia*, has several exceptions in the latter genus. Since it is impossible to find a clear line of division to separate the genera, I am uniting *Epicampes* with *Muhlenbergia*.

Hitchcock (1935) contributed a complete treatment of all North American species of *Muhlenbergia*, in which he transferred all species

of *Epicampes* to *Muhlenbergia*. His disposition of the group has been followed subsequently by most American taxonomists.

The inclusion of *Epicampes* within *Muhlenbergia*, however, has not been universally accepted. The most recent system of classification of the grasses treating all known genera was that of Robert Pilger in 1954, with a more complete form in 1956. Pilger placed *Epicampes* in the tribe Eragrosteae which he divided into six subtribes. Subtribe 5, Sporobolinae, included not only *Sporobolus*, but also *Epicampes*, *Crypsis*, *Heleochoa*, *Urochondra*, *Sphaerocaryum*, and *Blepharoneuron*. *Muhlenbergia*, excluding the *Epicampes* species, formed subtribe 6, the Muhlenbergiinae. A translation of the section of his key separating the Sporobolinae and Muhlenbergiinae follows:

- I. Spikelets often broad; glumes thin; lemmas awnless; caryopsis more or less wide . . . . . Subtribe 5. SPOROBOLINAE  
 II. Spikelets small; glumes firm; glumes often more or less shorter than the lemmas, these often more or less long-awned; caryopsis small, cylindrical. Subtribe 6. MUHLENBERGIINAE

Pilger did not enumerate the species he recognized under *Epicampes*, but most of the species traditionally regarded as members of this genus possess awned lemmas. The type specimen of the genus, *E. strictus* Presl, is figured with short-awned lemmas. Moreover, since Presl established *Epicampes* the position of the awn on the lemmas has been used as a generic character of great importance. It is therefore surprising that Pilger should have placed *Epicampes* in a tribe composed of members with awnless lemmas.

Hubbard, in his treatment of Gramineae (1959, rev.), recognized *Epicampes*. *Sporobolus*, often regarded as showing a relationship with *Epicampes*, was placed in the tribe Sporoboleae, along with *Blepharoneuron*. *Muhlenbergia* and *Epicampes*, in addition to *Agrostis*, *Calamagrostis*, *Lagurus*, *Gastridium*, *Triplachne*, *Echinopogon*, *Dichelachne*, *Polypogon*, *Phleum*, and *Alopecurus*, among others, constituted the tribe Agrostae.

It is apparent that *Epicampes* never has been clearly understood. Different characters have been used by botanists to delineate the genus and few of their descriptions fully agree. The American, A. S. Hitchcock, incorporated the species of *Epicampes* into the genus *Muhlenbergia*, and since then most American taxonomists have accepted his treatment.

#### Leaf Anatomy and Epidermis

The first suggestion that the anatomy of grass leaves might be useful in systematics was made by Duval-Jouve (1875) who found differences in the distribution of bulliform cells among species of different tribes. Additional anatomical differences were pointed out by Schwendener (1890). In 1898, Pée-Laby recognized five groups

based on characters of leaf anatomy, although these groups were based on poor characters (Brown, 1958). Avdulov's system (1931) incorporated the characters of leaf anatomy and chromosome size and number. Prat (1936) found that characters of the leaf epidermis are useful from a systematic standpoint and that the results based on these characters correlate well with those derived from a study of the internal anatomy. He referred to Avdulov's major groups as "panicoid" and "festucoid" and segregated the former into two subgroups, the "eupanicoid" and "chloridoid."

Brown (1958), in a study of the leaf anatomy of 101 species in 72 genera, found that six groups can be delimited by characters of the internal anatomy. Various combinations of these characters make it possible to differentiate the six basic groups that Brown designated bambusoid, festucoid, arundoid, panicoid, aristidoid, and chloridoid.

Tateoka et al. (1959) surveyed the leaf epidermis of 238 species of grasses and found that two groups, which differ in the type of microhairs present, correspond to the panicoid and chloridoid groups of Prat. They also reported that the bicellular microhairs of several genera have distinctive features which suggest that leaf epidermal characters may be useful at the generic level.

The most detailed survey of leaf anatomy and epidermis of grasses was made by Metcalfe (1960). He compiled the diagnostic features of the leaf epidermis and internal anatomy of 206 genera, representing 413 species. In addition, he included information on numerous other species, summarized from the literature. The survey by Decker (1964) of 135 genera traditionally placed in the tribe Festuceae demonstrates the value of leaf anatomy in reinterpreting a large, long-recognized tribe.

In the present study, the leaf anatomy and epidermis were studied by the author in about 50 species of *Muhlenbergia*, including those traditionally placed within *Epicampes*. About 50 additional species of *Muhlenbergia* were studied by Reeder at Yale University, and the author was fortunate to have the results of Reeder's unpublished studies for comparison with his own findings.

#### LEAF ANATOMY

Comparative studies of leaf anatomy were made from transverse sections of leaves of herbarium specimens. Mature blades were selected from about the middle of the culm and sections taken from a point in the blade approximately 1 cm. from the ligule (at this point the vascular bundles and associated structures are well developed; more distally the blades become narrower and certain features become altered). The dry blade was placed in boiling water for several minutes to soften and to bring it back as much as possible to the

pliable condition of a fresh leaf. In some cases the blades were soaked in a 0.3–0.4 percent solution of trisodium phosphate in a 60° paraffin oven for 1½–2 hours, although equally good results were obtainable without this additional treatment.

Freehand sections were made in all cases. The leaves were heavily sclerified and their rigidity permitted thin sections to be made by hand, thus obviating the use of a microtome. The blade was placed between halves of a block of celloidon and sections cut with a sharp single-edged razor blade. The sections were stained with Chlorazol Black E for ½ hour and then washed and brought through the alcohol series to absolute ethyl alcohol, and made permanent by mounting in diaphane.

*Muhlenbergia* species traditionally treated as *Epicampes* possess panicles that are either spikelike or open and pyramidal or columnar. The leaves in the former group become inrolled upon drying (*M. rigens*); in the latter group the leaves become folded upon drying (*M. gigantea*). Anatomical studies of the leaves of those two species reveal striking structural differences and the leaves of the other species of the *Epicampes* group are of one type or the other. For purposes of discussion, species with the leaf anatomy of *M. rigens* are referred to as having a "Rigens" type, and species with a leaf anatomy of *M. gigantea* are referred to as having a "Gigantea" type.

Plates 4–14 contain photomicrographs of leaf cross sections of a number of species of *Muhlenbergia*, including those of the *Epicampes* group. A partial leaf cross section of *M. rigens* appears in plate 5, figures 1 and 2, and of *M. gigantea* in plate 7, figure 2. The anatomical features of *Epicampes* leaves are illustrated on plate 4 in cross sections of *M. lindheimeri* and *M. palmeri* leaves. These two species have a leaf anatomy that corresponds, respectively, to that of *M. gigantea* and *M. rigens*.

#### Anatomical Structure of Leaves of the *Epicampes* Group<sup>4</sup>

UNITS: The leaf consists of a series of units of varying sizes, each unit representing a single rib of the leaf. The individual unit contains a vascular bundle and associated structures between and including the upper and lower epidermis.<sup>5</sup> On plate 4, figure 2 are

<sup>4</sup> The author is grateful to Dr. C. R. Metcalfe of the Royal Botanic Gardens, Kew, for his aid in interpreting the anatomical structures of the cross section of the leaf of *M. lindheimeri* from the photomicrograph sent to him.

<sup>5</sup> I am employing the term "unit" as used by Brown (1958, p. 176) to describe leaves of chloridoid grasses—"In these groups each bundle, sheath, and associated radial chlorenchyma constitute a discrete unit of structure separated from the similar adjacent units by large, empty, bulliform cells"—but I consider also the upper and lower epidermis and include sclerenchyma as part of this unit. The words "primary," "secondary," and "tertiary" to distinguish units are mine.

shown four units of a blade of *Muhlenbergia lindheimeri* and below, figure 3, seven units of a blade of *M. palmeri*.

Units are designated primary ( $1^\circ$ ), secondary ( $2^\circ$ ), and tertiary ( $3^\circ$ ), from largest to smallest. In the Gigantea type, only  $1^\circ$  and  $2^\circ$  units are found. The median unit is heavily sclerified at the base. This  $1^\circ$  unit and adjacent units are "embedded" in a mass of parenchyma, the whole arrangement constituting the "midvein area," or keel. The keel structure is shown on plate 4, figure 1. The  $1^\circ$  units alternate with one to three  $2^\circ$  units throughout the leaf. In the Rigens type,  $3^\circ$  units often are present, in addition to  $1^\circ$  and  $2^\circ$  units. As seen in *M. palmeri* one  $2^\circ$  and two  $3^\circ$  units occur between the two  $1^\circ$  units. Such an alternation of units occurs throughout the leaf and the central units are not specialized into a keel.

**VASCULAR BUNDLES:** The phloem of the  $1^\circ$  vascular bundles of *M. lindheimeri* and *M. palmeri* appears as darkly-stained groups of cells among nonstained thick-walled cells. All of the phloem is darkly stained in the  $2^\circ$  and  $3^\circ$  bundles of these species. The phloem of the  $1^\circ$  bundles is sclerosed, i.e., partly converted to lignified fibers. In cross section the active parts of the phloem (sieve tubes and parenchyma) appear as darkly-stained strands embedded in a fibrous ground tissue that is not stained. Sclerosis of the phloem is less pronounced, or lacking, in the  $2^\circ$  and  $3^\circ$  bundles.

The xylem of the  $1^\circ$  bundles is characterized by large metaxylem vessels on either side of the protoxylem. (The line marking the xylem in the photomicrograph of *M. palmeri*, plate 4, points to the metaxylem.) These large metaxylem vessels are lacking in the  $2^\circ$  and  $3^\circ$  bundles; in these bundles both the xylem and phloem stain black and are indistinguishable in the photomicrographs.

The  $1^\circ$  units are defined as those having metaxylem vessels, which are lacking in the  $2^\circ$  and  $3^\circ$  units. In cases where the  $1^\circ$  and  $2^\circ$  units are about equal in size, they are distinguished on the basis of whether or not they possess such metaxylem vessels.

**BUNDLE SHEATHS:** Two distinctive layers of cells, or "sheaths," surround the vascular bundle. The innermost, variously termed the "mestome sheath," "inner sheath," or "endodermis" is composed of thick-walled cells. The cells of the inner sheath adjacent to the xylem are larger; the cells adjacent to the phloem fibers are smaller and often indistinguishable from the latter.

The inner sheath is surrounded by a single layer of conspicuously larger, thin-walled cells, termed the "parenchyma sheath" or "outer sheath." The outer sheath may be continuous around the inner sheath, or interrupted below, above, or both. In the  $1^\circ$  units of *M. lindheimeri* the outer sheath is interrupted above and below, but only above in the  $2^\circ$  units. It is continuous in the  $2^\circ$  and  $3^\circ$  units

of *M. palmeri*. (The closed condition is typical of every unit of the leaf in some species of *Muhlenbergia*—cf. plate 12, figures 1, 2, and plate 13, figure 1.)

**CHLORENCHYMA:** The chlorenchyma lies adjacent to the outer sheath and both are stained black in the photomicrograph. Although not evident in the photomicrograph, the cells are radially arranged. The chlorenchyma assumes the same pattern as the outer sheath in the unit, being continuous around the inner sheath or interrupted. (Photosynthetic activity is confined to this narrow layer of chlorenchyma and, presumably, the outer sheath also; together, they constitute a relatively small part of the whole unit [Brown: 1958, p. 176]).

**SCLERENCHYMA:** The individual units, especially the 1° ones, possess caps of sclerenchyma cells subjacent to the upper and lower epidermis. The amount of sclerenchyma varies, but it is especially well developed at the base of the central unit where it reinforces the keel of the blade. In a species with the Rigens type of leaf anatomy the sclerenchyma often forms a continuous layer subjacent to the lower epidermis.

**THICK-WALLED PARENCHYMA:** Between the vascular bundle and subepidermal sclerenchyma is a mass of large parenchymatous cells. They are referred to here as "thick-walled" parenchyma,<sup>6</sup> as the walls of these cells appear to be thicker than in normal parenchymatous cells. These cells constitute a large part of the 1° units, a smaller part of the 2° units, and are lacking in the 3° units.

In some cases the thick-walled parenchyma of the units is confluent between them. Such a condition is found in the keel of leaves of the Gigantea type in which the vascular bundles and surrounding sheaths give the appearance of being embedded in a mass of parenchyma cells. In such cases there is no observable difference between parenchyma cells of the units and those that occur between them as they are confluent.

**COLORLESS CELLS:** Between the units are found one to several rows of cells that look similar to thick-walled parenchyma. Metcalfe refers to these as colorless cells. In some grasses bubble-like cells that are part of the epidermis are referred to as bulliform cells. Technically, the cells marked (bc) in the photograph of *M. lindheimeri* are bulliform cells. The cells subjacent to these bulliform cells are the colorless cells (cc). In species of the Epicampes group

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<sup>6</sup> According to Metcalfe (personal communication), "It is quite in order to refer to the cells as thick-walled parenchyma unless they can be shown in l.s. to be appreciably longer than wide. Even if they are somewhat elongated it is best to refer to them as 'elongated parenchymatous cells' as they are not fibrous or sclereids."

there is no obvious difference between the bulliform and colorless cells apart from the position they occupy.

### The Rigens and Gigantea Types of Leaf Anatomy

The leaf anatomy of the following species, traditionally placed in *Epicampes*, was examined: *Muhlenbergia distans*, *M. distichophylla*, *M. emersleyi*, *M. gigantea*, *M. grandis*, *M. lindheimeri*, *M. longiligula*, *M. macrotis*, *M. macroura*, *M. pubescens*, *M. rigens*, *M. robusta*, *M. speciosa*, and *M. virletii*.

All the above species possess the following anatomical features: (1) The phloem of the 1° vascular bundles is partly sclerosed. (2) The vascular bundle is surrounded by an inner sheath and an outer sheath. Adjacent to the outer sheath is the chlorenchyma, appearing under high power to consist of a layer of narrow cells, radially arranged. (3) A large amount of thick-walled parenchyma occurs adaxial, sometimes abaxial, to the vascular bundle. (4) A thick cap of sclerenchyma lies below the upper and lower epidermis of the 1° units. Apart from shape, the units of all species of *Epicampes* are of similar structure. The major differences are in the kinds of units present and in their arrangement.

The Rigens type of leaf anatomy is characterized by the following features: (1) A similar alternation of units occurs throughout the leaf. The 1° units alternate with one or two 2° units or three to five smaller units (consisting of two to four 3° units and a 2° unit). There is no differentiation of central units into a keel. (2) The lower surface of the blade is flat, or ribbed and furrowed; the upper surface is ribbed and furrowed. (3) The 1° units are rounded above in *M. macroura* (cf. *M. dubia*, pl. 5, fig. 3), obtriangular in *M. rigens* (pl. 5, figs. 1, 2), and in some species more or less rectangular (e.g., *M. elongata*, pl. 11, fig. 2).

The following species of the *Epicampes* group possess a Rigens type of leaf anatomy: *M. macroura* and *M. rigens*.

The Gigantea type of leaf anatomy is characterized by the following features: (1) Only 1° and 2° units are present. The central units of the blade are specialized into a keel. The thick-walled parenchyma of these units is confluent and a large cap of sclerenchyma is developed at the base of the central unit. (See *M. gigantea*, pl. 9, fig. 1, for illustrations of the central and adjacent units of the keel.) Beyond the midrib area is a regular alternation of 1° and 2° units. The 1° units are separated by one to three 2° units. (2) The upper and lower surfaces of the blade are ribbed and furrowed. Beyond the midrib area the units are separated by several layers of colorless

cells. The sclerenchyma subjacent to the lower epidermis is confined to the individual units and therefore does not form a continuous layer between them. (3) The 1° units are more or less rectangular. The central 1° unit of the keel is rounded or obtuse below.

The following species of the *Epicampes* group possess a Gigantea type of leaf anatomy: *M. distans*, *M. distichophylla*, *M. emersleyi*, *M. gigantea* (pl. 7, fig. 2, and pl. 9, fig. 1), *M. grandis*, *M. lindheimeri* (pl. 7, fig. 3, and pl. 8, fig. 3), *M. longiligula* (pl. 10, fig. 1), *M. macrotis* (pl. 7, fig. 1), *M. pubescens*, *M. robusta*, *M. speciosa*, *M. virletii*.

### The Rigens or Gigantea Type in Species of *Muhlenbergia*

Apart from the anatomical differences that separate the species of the *Epicampes* group into the Rigens and Gigantea types, the two groups have the same basic unit structure in the leaves and share the following gross morphological features: Plants perennial, caespitose (usually strongly so); culms erect, not branching at the nodes; and panicle usually densely flowered.

The species with a Rigens type of leaf anatomy have rounded basal sheaths, a firm ligule, and the leaves become inrolled upon drying. In contrast, most species with a Gigantea type of leaf anatomy have compressed-keeled basal sheaths, a membranous ligule, and the leaves become folded upon drying.

Many species of *Muhlenbergia* share the morphological features common to all of the species of the *Epicampes* group. These species may be grouped into those having compressed-keeled basal sheaths and a membranous ligule, and those with rounded basal sheaths in association with a firm ligule. Because of the close morphological similarities to the *Epicampes* group, a study of the leaf anatomy was made, with the following results:

#### *Muhlenbergia* species with the Rigens type of leaf anatomy:

<i>M. angustata</i>	<i>M. holwayorum</i>
<i>M. arenicola</i>	<i>M. jaliscana</i>
<i>M. articulata</i>	<i>M. lucida</i>
<i>M. capillaris</i> (pl. 10, fig. 2)	<i>M. metcalfei</i>
<i>M. dubia</i>	<i>M. nigra</i>
<i>M. dubioides</i>	<i>M. reverchonii</i> (pl. 11, fig. 1)
<i>M. elongata</i> (pl. 11, fig. 2)	<i>M. rigida</i>
<i>M. expansa</i> (pl. 6, fig. 2)	<i>M. setifolia</i>
<i>M. firma</i>	<i>M. subaristata</i>
<i>M. glabrata</i>	<i>M. xerophila</i>

All of the above species have rounded basal sheaths and a firm ligule. (The rather variable species *M. rigida* sometimes may have a long membranous ligule.)

Species that have the Gigantea type of leaf anatomy:

<i>M. aurea</i>	<i>M. longiglumis</i> (pl. 10, fig. 3)
<i>M. breviligula</i>	<i>M. mutica</i>
<i>M. gooddingii</i>	<i>M. pubigluma</i>
<i>M. inaequalis</i>	<i>M. reederorum</i>
<i>M. involuta</i>	<i>M. scoparia</i>
<i>M. iridifolia</i>	<i>M. versicolor</i>
<i>M. lehmanniana</i>	<i>M. xanthodas</i>

These species have compressed-keeled basal sheaths and membranous ligules with the exception of *M. involuta* and *M. reederorum* in which the sheaths are rounded (rarely compressed) and ligules firm below and membranous above.

Some species of *Muhlenbergia* exhibit certain anatomical features that require special mention:

*M. longiligula* (pl. 10, fig. 1). The several 1° units of the midrib area are of equal size. The central unit does not possess a larger basal cap of sclerenchyma than the adjacent units of the keel. The basal sheaths are either rounded or sometimes compressed, but never strongly keeled. However, the structure of the units, the sclerosed phloem of the 1° bundles, and the midrib area of thick-walled parenchyma are characteristic of the Gigantea group of species.

*M. longiglumis* (pl. 10, fig. 3). The central unit is a 1° bundle with sclerosed phloem and a large basal cap of sclerenchyma; both are characters of the Gigantea type of leaf anatomy. The central units, however, are not embedded in a mass of thick-walled parenchyma. On the basis of leaf anatomy, this species does not conform well to either anatomical type but shows more similarity to the Gigantea type.

*M. aff. montana* (pl. 11, fig. 3). The units have an arrangement similar to that of the Rigens type. However, the phloem of the 1° units is not sclerosed.

*M. involuta*. All of the units of the leaf are embedded in a continuous layer of thick-walled parenchyma, unlike the Gigantea species in which such a condition is confined to the keel. The phloem of the 1° bundles is sclerosed and the central units possess a large basal cap of sclerenchyma, as in the Gigantea type. The anatomy of the leaf most closely approaches the Gigantea type.

*M. stricta*. The units are all very large and are connected by a continuous layer of thick-walled parenchyma and the phloem of the 1° bundles is sclerosed. The central unit does not possess an additional amount of basal sclerenchyma. On the basis of leaf anatomy this species exhibits greater similarity to the Gigantea type, but its gross morphology is more like that of species in the Rigens group.

*M. torreyana* (pl. 9, fig. 3). The leaves of this species have a keel structurally like that of the Gigantea group, but the phloem of the 1° bundles is not sclerosed. Morphologically it is unlike species of the Gigantea group in having short, very scaly rhizomes and branching culms, and a minute, ciliate, firm ligule.

#### *Muhlenbergia* Species Unlike the Rigens and Gigantea Types

Most species of *Muhlenbergia* have a leaf anatomy quite different from the Gigantea and Rigens types. Although the anatomical structure of all cannot be discussed here, several points should be mentioned to illustrate how these species compare with the Epicampes group and allies.

Photomicrographs of 11 species of *Muhlenbergia* with a leaf anatomy distinct from the Rigens or Gigantea types are shown on plate 9, figure 3, plate 11, figure 3, and plates 12-14.

All 11 of these species of *Muhlenbergia* differ from species of the Rigens and Gigantea types in the condition of the phloem. The phloem of all the bundles, including the 1° ones, when these are differentiated, is darkly stained throughout, indicating it is completely functional and not sclerosed. Special reference is made to *M. aff. montana* (pl. 11, fig. 3) and *M. torreyana* (pl. 9, fig. 3). In these species the 1° units are similar to those of the Epicampes group but the phloem of the 1° units is not sclerosed.

The annual species are characterized by a relatively simple unit structure, with little additional sclerenchyma or thick-walled parenchyma. Note, for example, the annuals *M. confusa* (pl. 13, fig. 1), *M. crispiseta* (pl. 14, fig. 1), *M. peruviana* (pl. 12, fig. 1), and *M. pulcherrima* (pl. 12, fig. 2). In *M. peruviana* and *M. pulcherrima* the units are of equal size; the outer sheath and chlorenchyma are continuous above. Additional sclerenchyma and parenchyma are lacking in the units and the phloem is not sclerosed. *M. crispiseta* has sclerenchyma developed in the central unit and some in each of the other units. The outer sheath and chlorenchyma entirely circle the vascular bundle without interruption and the phloem in the bundles is not sclerosed.

Among perennial *Muhlenbergias*, plates 12-14, are *M. arizonica* (pl. 12, fig. 3), *M. asperifolia* (pl. 14, fig. 2), *M. plumbea* (pl. 13, fig. 3), and *M. richardsonis* (pl. 13, fig. 2). The structure of the individual units in *M. richardsonis* and *M. asperifolia* approaches that of the Epicampes group in its specialization. However, the phloem of the 1° bundles in these two rhizomatous perennials is not sclerosed. *Muhlenbergia plumbea*, another rhizomatous perennial, has units mostly equal in size, except for the central unit which has a basal

cap of sclerenchyma. Note that the outer sheath and chlorenchyma are continuous around the vascular bundles. The phloem of the bundles is not sclerosed. The leaf of *M. arizonica*, a perennial that branches at the nodes, is not too unlike that of *M. plumbea*. The units are mostly equal in size, and the median one is heavily sclerified. The outer sheath and chlorenchyma are continuous around the vascular bundles outside of the central unit. The phloem of the vascular bundles is not sclerosed.

Various anatomical configurations in the leaves of the remaining species of *Muhlenbergia* examined are not illustrated here.<sup>7</sup> In all of these species the phloem of the vascular bundles is not sclerosed.

### Conclusions

The leaves of species traditionally placed in *Epicampes* are characterized by an inner sheath (or endodermis), a parenchyma (outer) sheath, and chlorenchyma, consisting of cells radially arranged. All are features of the chloridoid type of leaf anatomy, as pointed out by Brown (1958). On the basis of leaf anatomy these species are allied to *Muhlenbergia*, *Sporobolus*, *Lycurus*, and other genera of the chloridoid alliance. In contrast, the leaves of *Agrostis* and *Cinna* are of the festucoid type, as Brown has shown, and therefore do not show a relationship to *Epicampes*. On the basis of leaf anatomy, *Epicampes* should be removed from the Agrostideae and placed with other members of the chloridoid alliance. The present investigations have shown that *Epicampes* is most closely related to species of *Muhlenbergia* which not only have similar gross morphological features, but leaf anatomical features; most noteworthy is the unique condition of sclerosed phloem in the 1° vascular bundles. These findings support those of Schwabe (1949) who in a study of the foliar anatomy of 22 species of *Muhlenbergia*, including two species of the *Epicampes* group, concluded that the latter should probably be included in the former.

### LEAF EPIDERMIS

Sections were taken from the upper and lower epidermis of the leaf. In all cases the preparations were made from leaves taken from herbarium specimens. Sections of the blade, 1-1½" long, were placed in boiling water until softened, just as in preparing

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<sup>7</sup> The reader is referred to the treatment of Schwabe (1949) in which features of the leaves of many additional species of *Muhlenbergia* are illustrated.

the whole leaf for cross sections. To remove the epidermis of the abaxial surface the blade was placed with the abaxial surface down on a clean glass slide. With the aid of the 10 × power of a binocular microscope, the tissue of the leaf was scraped away with a scalpel until only the epidermis remained. The same process was repeated for the adaxial surface with the adaxial surface down.<sup>8</sup> The epidermal scrapes were stained with methylene blue and counterstained with ruthenium red. They were then washed in water to remove the excess dye, brought through the alcohol and xylene series, and mounted in Permount.

### Constituents

The epidermis of the grass leaf contains a number of different cell types, among them microhairs, prickle-hairs, papillae, long cells, stomatal cells, interstomatal cells, and silica cells. The bicellular microhairs<sup>9</sup> and silica cells exhibit the greatest differences between the groups of species within *Epicampes*.

**MICROHAIRS:** All species studied of *Muhlenbergia* (including *Epicampes*) have bicellular microhairs. Differences are found in the shape and in the ratio of the length of the basal to the upper (distal) cell. In some species the microhairs are short and broad; the basal cell is equal to, or a little longer than, the distal cell. In other species the microhairs are longer and narrower, and the basal cell is much longer than the distal cell.

**SILICA CELLS:** Silicon-containing cells in the epidermis are referred to as "silica cells" or "siliceous cells." Characterized by a wall heavier than that of adjacent cells with small granules within the cell, they occur in rows and are a major constituent of the epidermis in species of the *Epicampes* group. In some species all of the silica cells are saddle-shaped and rather simple in outline; in others most of them are dumbbell- or cross-shaped; in still others the majority are saddle-shaped, with cross-shaped cells occurring infrequently among them.

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<sup>8</sup> In many species, e.g., *M. macroura*, the blade is characterized by a flat abaxial surface and an adaxial surface of ribs and furrows. In such cases the whole epidermis scrapes off easily from the abaxial surface but only strips of epidermis can be removed from the adaxial surface, representing the top surfaces of the ribs only.

<sup>9</sup> Metcalfe (1960, p. xliii) remarks, "Micro-hairs are not always easy to examine, but it is generally rewarding to persevere with them because they are valuable indicators of the affinities of the grasses in which they occur."

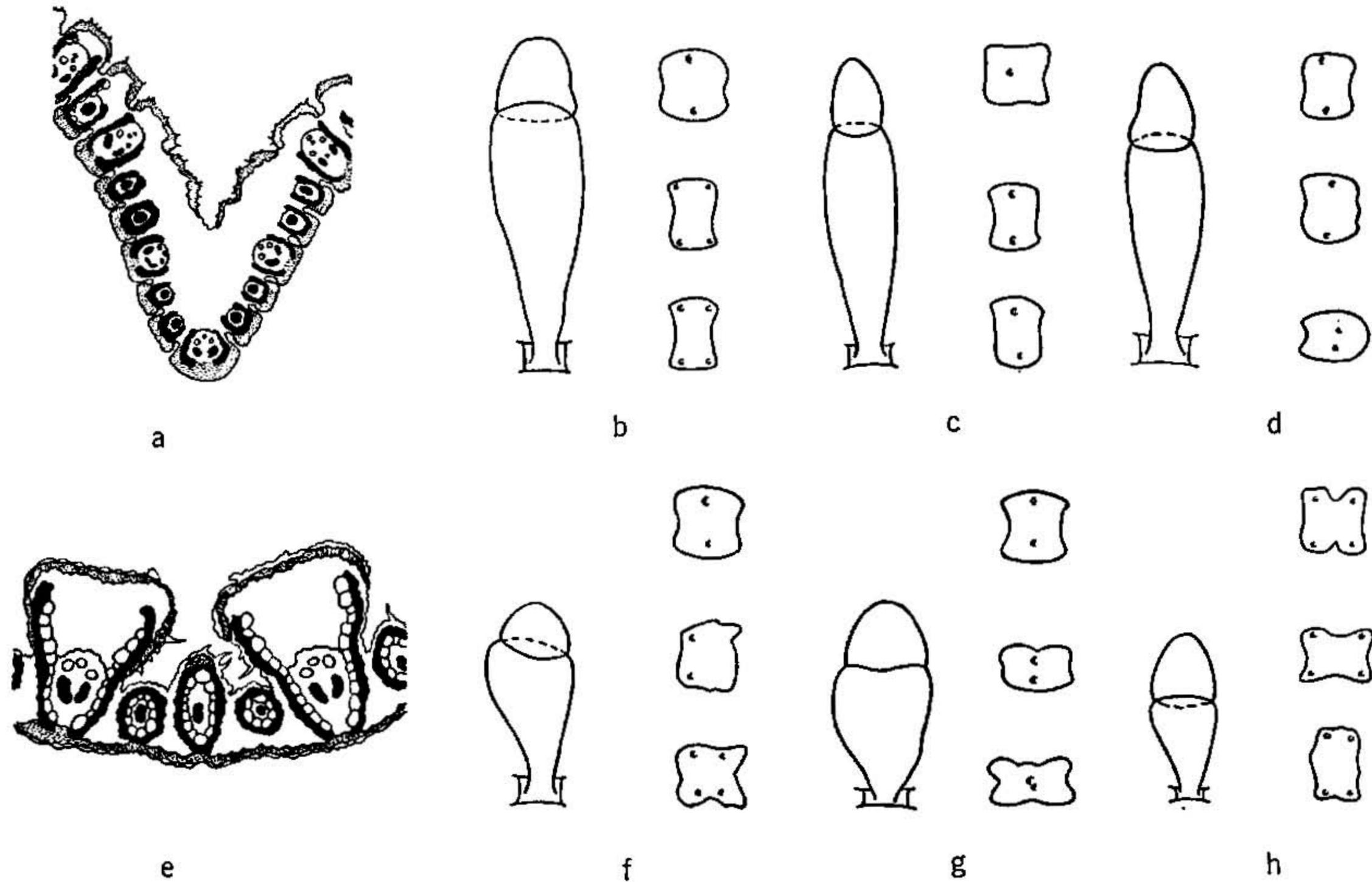


FIGURE 1.—Bicellular microhairs and silica cells. *a-d*, Species of section *Epicampes*: *a*, Diagrammatic cross section of the leaf of *Muhlenbergia lindheimeri*; *b*, *M. pubescens* (Soderstrom 692); *c*, *M. gigantea* (Reeder & Reeder 2488); *d*, *M. macrotis* (Mexia 9098). *e-h*, Species of section *Podosemum*: *e*, Diagrammatic cross section of the leaf of *M. rigens*; *f*, *M. rigens* (Reeder & Reeder 2662); *g*, *M. dubioides* (Soderstrom 931); *h*, *M. macroura* (Matuda 2829). These are all diagrammatic and are not drawn to scale.

Following is a summary from epidermal studies in *Epicampes* species:

<i>Species</i>	<i>Average ratio of basal to distal cell of microhair</i>	<i>Shape of silica cells:</i> s = saddle-shaped x = cross-shaped d = dumbbell-shaped
<i>M. distans</i>	6.6:1	s
<i>M. distichophylla</i>	5.1:1	s
<i>M. gigantea</i>	4.0:1	s
<i>M. grandis</i>	3.2:1	s
<i>M. lindheimeri</i>	-	s
<i>M. macrotis</i>	5.7:1	s
<i>M. macroura</i>	2.2:1	mostly x or d
<i>M. pubescens</i>	4.7:1	s
<i>M. rigens</i>	2.3:1	mixed, s and d
<i>M. robusta</i>	4.3:1	s
<i>M. speciosa</i>	-	s
<i>M. virletii</i>	4.0:1	s

Species of the *Epicampes* group with a Rigens type of leaf anatomy (*M. macroura* and *M. rigens*) exhibit certain characteristics in their epidermis different from the other species of *Epicampes*. The bicellular microhairs are short and broad in these species and silica cells are dumbbell-shaped, cross-shaped, or saddle-shaped. In the species that have a Gigantea type of leaf anatomy, the bicellular microhairs are generally long and narrow, and the upper cell is usually much shorter than the basal cell. In these species the silica cells are always saddle-shaped.

The epidermis of other species of *Muhlenbergia* with a Rigens or Gigantea type of leaf anatomy also was studied. In these, likewise, the epidermis of members with a Gigantea type is characterized by mostly long and narrow bicellular microhairs and rectangular or saddle-shaped silica cells. And in the epidermis of species with a Rigens type the silica cells are cross-shaped, saddle-shaped, or rectangular, and the bicellular microhairs relatively short and broad. In figure 1 are illustrated the major types of silica cells and bicellular microhairs encountered.

### Conclusions

Epidermal features of the species of *Muhlenbergia*, including *Epicampes*, are panicoid in nature; microhairs are present and the silica cells are rectangular, saddle-shaped, cross-shaped, or dumbbell-shaped. Relationship with the chloridoid group is apparent in the club-shaped or globose microhairs and membranes of equal thickness on the upper and lower cells (Prat, 1936; Tateoka, Inoue, and Kawano, 1959; Metcalfe, 1960).

### The Embryo

Until recently the structure of the grass embryo has been of passing interest to grass taxonomists. Bruns (1892), who dealt with about 60 species, was the first worker to publish on grass embryos. Later, Van Tieghem (1897) and Kennedy (1899) added to the understanding of the grass embryo, the work of the former being more significant from the standpoint of systematics. Not until Yakolev (1950) and Reeder (1953) was the value of the embryo in grass systematics again stressed. Reeder (1957) in a paper of great significance presented his findings based on a study of the caryopses of about 300 species of grasses. These included over 150 genera, representing all of the tribes in the traditional Hackelian system. Reeder showed that several embryo groups could be recognized, and the criteria he used to distinguish them are the relative size of the embryo to endosperm in the caryopsis, as well as the features observable in the transverse and median sagittal sections of the embryo. He listed six groups of grasses based on various combinations of four embryo characters: festucoid, panicoid, chloridoid-eragrostoid, bambusoid, arundinoid-danthonioid, and oryzoid-olyroid. Reeder later (1962) reinterpreted the oryzoid-olyroid genera as bambusoid but segregated a further group, the centothecoid.

In the present study, mature caryopses were selected from herbarium specimens, placed in boiling water for a few minutes, then soaked overnight in FAA. They were then transferred to a 3 percent solution of KOH for 1-2 hours to soften the endosperm. After removing the endosperm, the embryo was embedded in agar and the agar block, containing the embryo, run through the butyl alcohol series and embedded in paraffin. Serial sections  $10\mu$  in thickness were made, transversely and longitudinally, in the sagittal plane. Safranin and Fast Green were used in staining.

Embryos of 10 species of *Muhlenbergia* were sectioned, of which 9 species have been traditionally associated with *Epicampes*. Of these, 7 have a Gigantea type of leaf anatomy: *M. emersleyi*, *M. gigantea*, *M. grandis*, *M. longiligula*, *M. macrotis*, *M. pubescens*, and *M. robusta*. All are illustrated in figure 2 except *M. emersleyi*. Two have a Rigens type: *M. macroura* (fig. 3) and *M. rigens* (fig. 2). Additional species, represented in figure 3, are *M. nigra*, with a Rigens type, and *M. schreberi*, the type species of *Muhlenbergia*. For comparison, diagrams also of the embryos of five genera that have been suggested as bearing a relationship to *Epicampes* appear in figure 3: *Agrostis*, the type genus of the classical tribe Agrostideae, *Cinna*, *Polypogon*, *Sporobolus*, and *Stipa*.

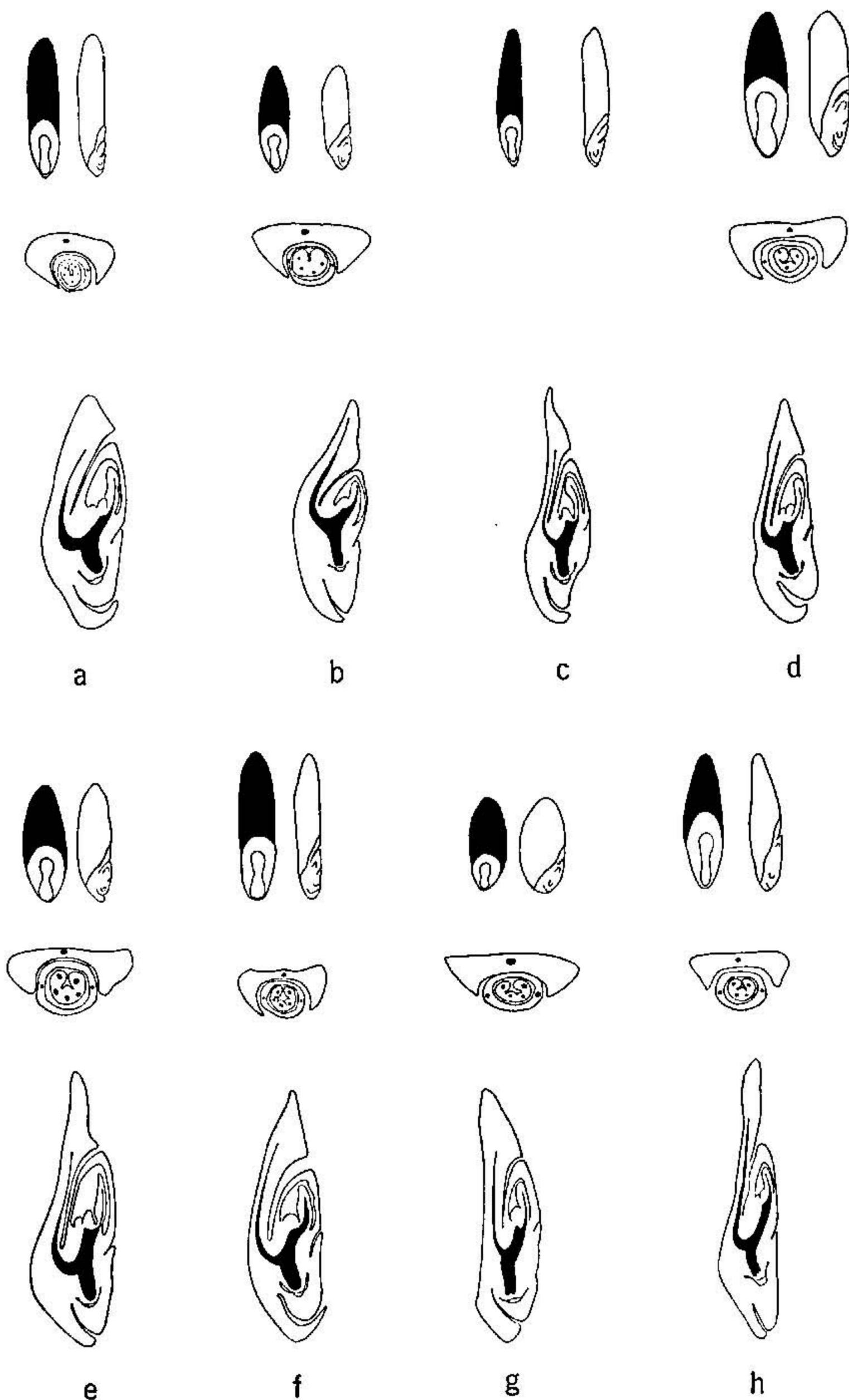


FIGURE 2.—Outline drawings of caryopses, median sagittal sections, and transverse sections through the coleoptile region of *Muhlenbergia* embryos: *a*, *M. macrotis* (Pringle 2360); *b*, *M. robusta* (Standley 59136); *c*, *M. robusta* (Pringle 2321); *d*, *M. grandis* (Pringle 2765); *e*, *M. gigantea* (Pringle 3335); *f*, *M. pubescens* (Arsène); *g*, *M. longiligula* (Reeder & Reeder 2699); *h*, *M. rigens* (Blumer 1491). Drawings are diagrammatic and not drawn to scale.

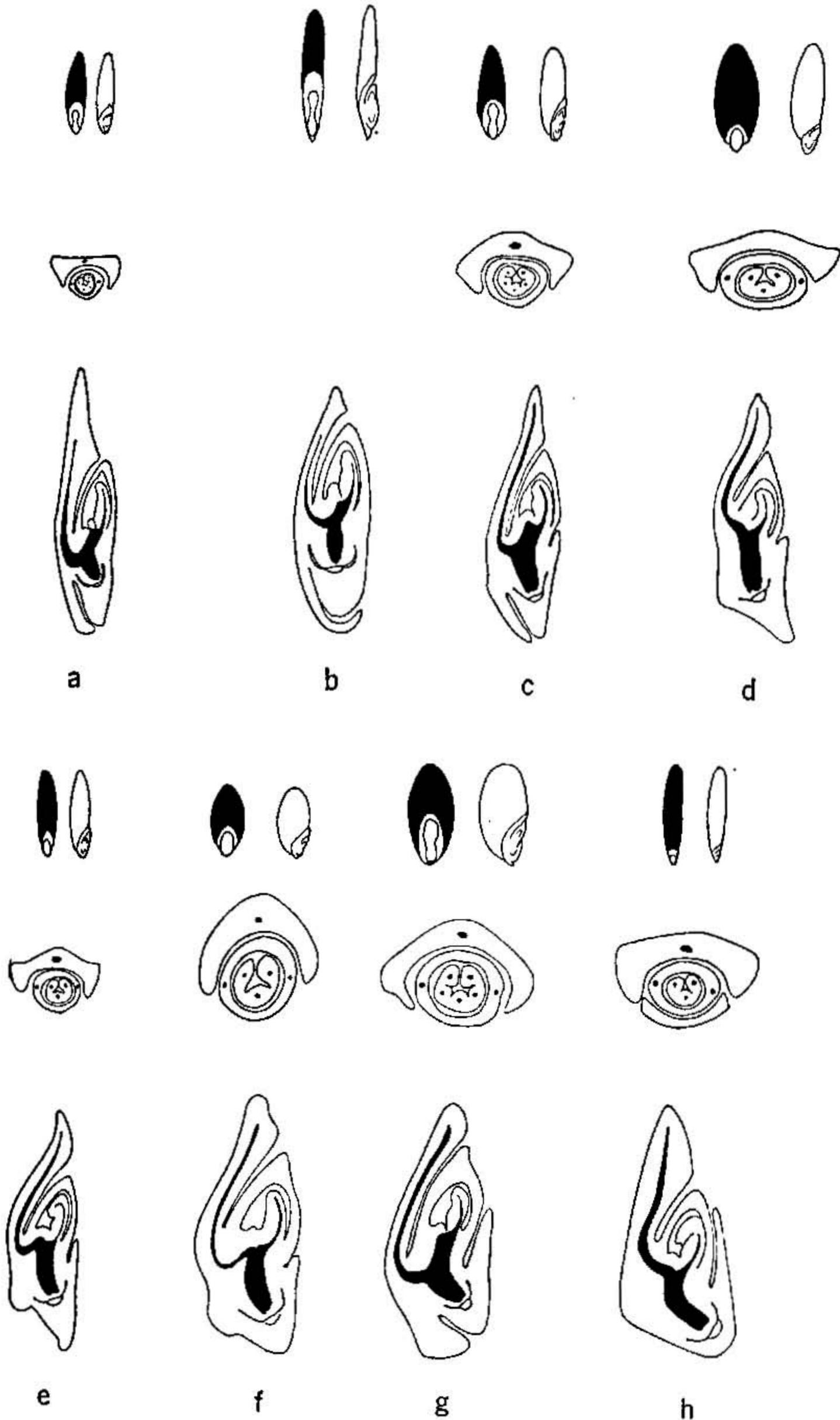


FIGURE 3.—Outline drawings of caryopses, median sagittal sections, and transverse sections through the coleoptile region of embryos of *Muhlenbergia* and other genera: *a*, *Muhlenbergia macroura* (Arsène); *b*, *M. nigra* (Cook); *c*, *M. schreberi* (no voucher); *d*, *Agrostis scabra* (Goodding); *e*, *Cinna arundinacea* (Tweedy); *f*, *Polypogon monspeliensis* (Hortus Botanicus Bruxellensis); *g*, *Sporobolus wrightii* (Goodding); *h*, *Stipa avenacea* (Reeder & Reeder 233). Drawings are diagrammatic and not drawn to scale.

The caryopses and embryos of *Muhlenbergia* species of the Epicampes group have the following features:

Caryopsis: The embryo is relatively large in comparison with the endosperm.

Embryo: Median sagittal section.

1. A distinct internode is present in the vascular system between the point of divergence of the trace to the scutellum and the trace to the embryonic leaves (P).
2. An epiblast is present (+).
3. A cleft is present between the lower part of the scutellum and the coleorhiza (P).

Embryo: Transverse section.

4. The margins of the embryonic leaf contain few bundles and the margins do not overlap (F).

The embryo formula (see Reeder, 1957) for these species is P+PF, the chloridoid-eragrostoid type: *Muhlenbergia* and *Sporobolus* also are chloridoid-eragrostoid, but *Agrostis*, *Cinna*, *Polypogon*, and *Stipa* are festucoid.

*Muhlenbergia macroura* and *M. nigra* differ from the other species in lacking an epiblast, unusual for chloridoid-eragrostoid species. On the basis of gross morphology and leaf anatomy, however, they are quite similar to *M. rigens* and an epiblast is present in that species as well as in *M. dubioides*.

Of 12 caryopses examined from a single specimen of *Muhlenbergia pubescens* (Soderstrom 693), 7 had double embryos. However, other specimens of *M. pubescens* from different localities and all other species examined had single embryos.

### Conclusions

The embryos of *Muhlenbergia* do not show basic differences characteristic of individual groups, except *M. macroura* and *M. nigra* which differ in the absence of an epiblast. As emphasized by Reeder, the embryo is most useful in indicating the placement of a grass within one of six natural groups of genera. The species of the Epicampes group are like other species of *Muhlenbergia* and *Sporobolus* and are related to grasses of the chloridoid-eragrostoid group. They do not show a relationship to *Agrostis* and other festucoid genera of the Agrostideae with which they have been traditionally associated. A summary of embryo characters follows (see also figs. 2 and 3):

Genus and/or species	Embryo/ endosperm large (P) small (F)	Internode in trace present (P) absent (F)	Epiblast present (+) absent (-)	Cleft in scutellum present (P) absent (F)	Embryonic leaf margins meet, bundles few (F) margins overlap, bundles many (P)	Formula
<i>Muhlenbergia</i>						
Gigantea type of leaf anatomy						
<i>M. emersleyi</i>	P	P	+	P	F	P+PF
<i>M. gigantea</i>	P	P	+	P	F	P+PF
<i>M. grandis</i>	P	P	+	P	F	P+PF
<i>M. longiligula</i>	P	P	+	P	F	P+PF
<i>M. macrotis</i>	P	P	+	P	F	P+PF
<i>M. pubescens</i>	P	P	+	P	F	P+PF
<i>M. robusta</i>	P	P	+	P	F	P+PF
Rigens type of leaf anatomy						
<i>M. macroura</i>	P	P	-	P	F	P-PF
<i>M. nigra</i>	P	P	-	P	(Not seen)	P-P
<i>M. rigens</i>	P	P	+	P	F	P+PF
Type species						
<i>M. schreberi</i>	P	P	+	P	F	P+PF
<i>Agrostis</i>	F	F	+	F	F	F+FF
<i>Cinna</i>	F	F	+	F	F	F+FF
<i>Polypogon</i>	F	F	+	F	F	F+FF
<i>Sporobolus</i>	P	P	+	P	F	P+PF
<i>Stipa</i>	F	F	+	F	F	F+FF

### Lodicules

Lodicules are small hyaline or fleshy scalelike structures sessile between the lemma and palea of a grass floret. At time of anthesis when they reach their maximum development they become swollen and force the lemma and palea apart, thereby allowing the stamens to become exerted from the spikelet. They are thought to represent a reduced inner whorl of perianth parts, the outer whorl having been lost completely through evolution. Although only two lodicules are found in most genera, three are present in the floret of *Stipa* and most bamboos; lodicules are lacking entirely in *Anthoxanthum*, *Cenchrus*, and *Pennisetum*. The lodicules are usually separate, but are fused in *Melica* and *Glyceria*. Not only are differences in lodicules among genera found with respect to the number present, but also in size and shape, manner of thickening, and vascularization.

Zuderell (1909) examined the lodicule anatomy of about 50 species of grasses and in the same year Krause mentioned that lodicules might be of systematic value. Apparently, not until recently has real emphasis been placed on these structures as indicators of natural

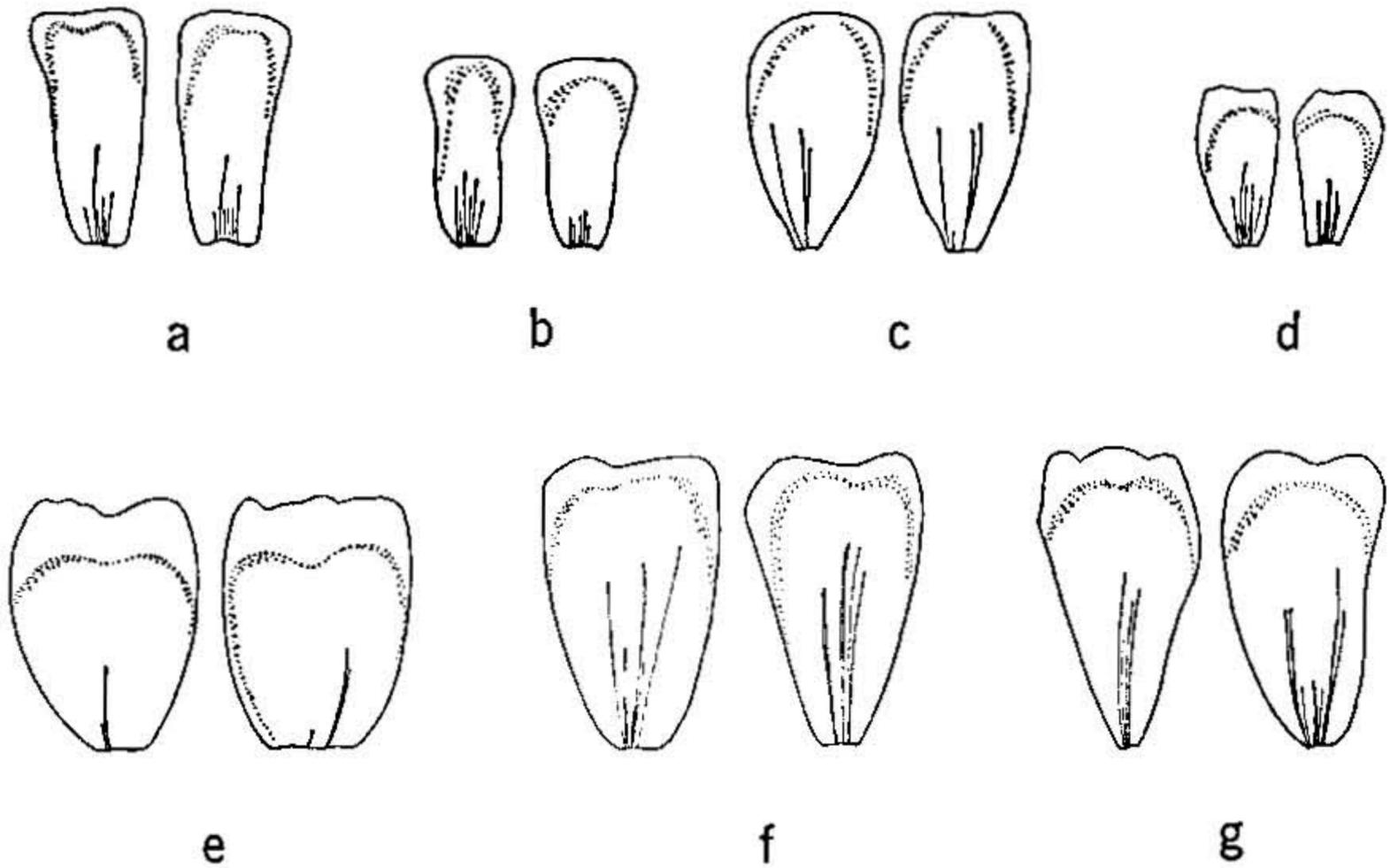


FIGURE 4.—Lodicules of Muhlenbergias in the *Podosemum* section, all times 46: *a*, *M. angustata* (Camp E-2519); *b*, *M. glabrata* (Amer. Gr. Nat. Herb. 1356); *c*, *M. dubia* (Soderstrom 509); *d*, *M. rigida* (Soderstrom 640); *e*, *M. macroura* (Soderstrom 551); *f*, *M. nigra* (Pringle 11739); *g*, *M. palmeri* (Pringle 1417).

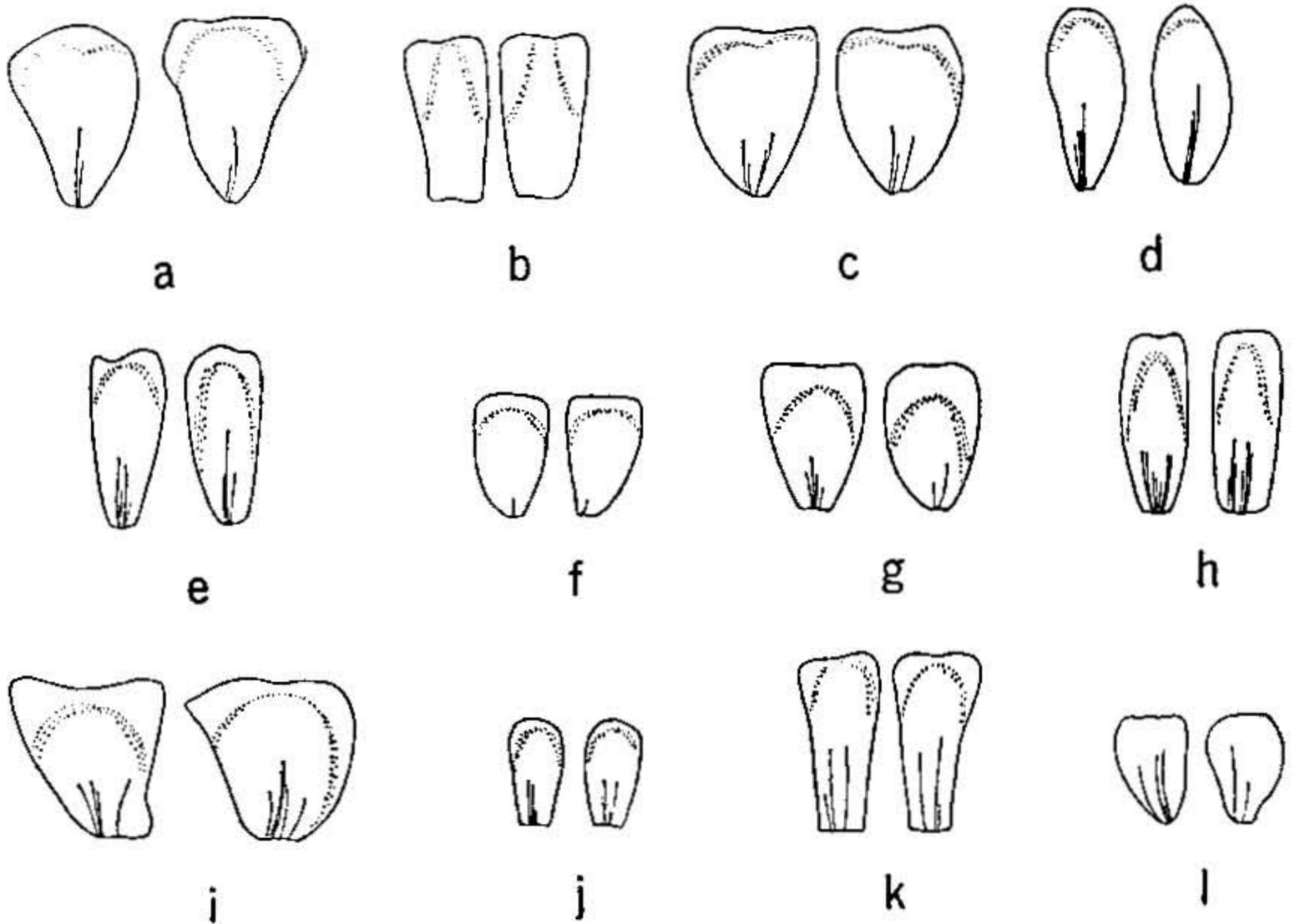


FIGURE 5.—Lodicules of Muhlenbergias in the *Podosemum* and *Epicampes* sections, all times 45: *a*, *M. firma* (Amer. Gr. Nat. Herb. 1351); *b*, *M. rigens* (Soderstrom 731); *c*, *M. capillaris* (Kral & Godfrey 54211); *d*, *M. xerophila* (Goodding A-9493); *e*, *M. expansa* (Godfrey 8151); *f*, *M. arenicola* (Pringle 479); *g*, *M. articulata* (Pringle 3913); *h*, *M. reverchonii* (Silveus 2478); *i*, *M. longiglumis* (Pringle 2365); *j*, *M. stricta* (Soderstrom 642); *k*, *M. involuta* (Silveus 780); *l*, *M. emersleyi* (Soderstrom 746).

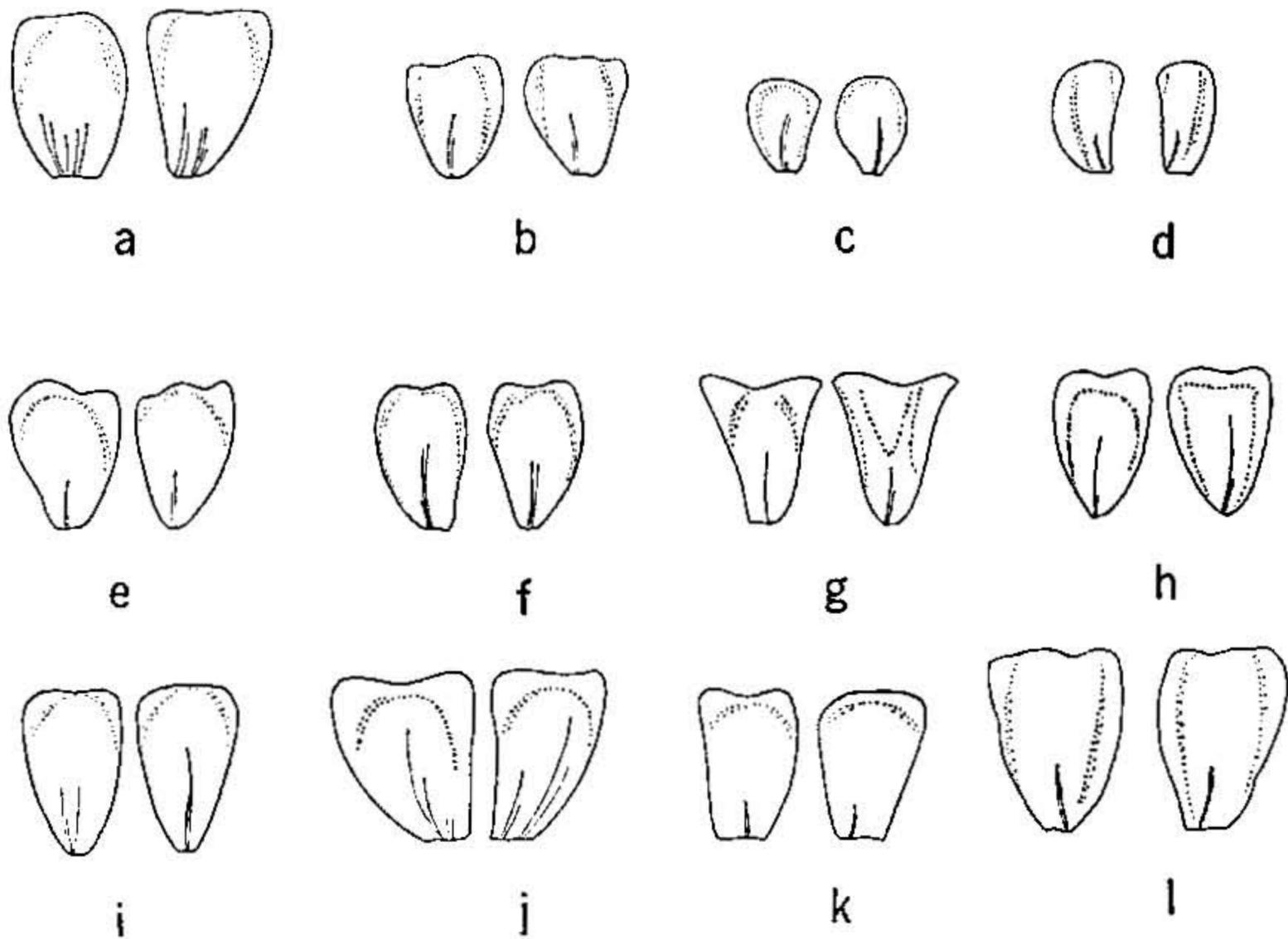


FIGURE 6.—Lodicules of Muhlenbergias in the *Epicampes* section, all times 46: a, *M. distans* (Pringle 5374); b, *M. speciosa* (Reeder & Reeder 2476); c, *M. grandis* (Pringle 2765); d, *M. distichophylla* (Pringle 2346); e, *M. robusta* (Arsène); f, *M. versicolor* (Smith 927); g, *M. macrotis* (Mexia 9098); h, *M. pubescens* (Soderstrom 483); i, *M. lindheimeri* (Burr 513); j, *M. robusta* (Soderstrom 382); k, *M. longiligula* (Reeder & Reeder 3222); l, *M. gigantea* (Reeder & Reeder 2488).

relationships. Stebbins (1956), in a study of intergeneric hybrids of *Lolium* and *Festuca*, pointed out that cytological findings agree with those based on studies of the grass flower and caryopsis. He illustrated four types of lodicules which he designated panicoid, chloridoid, festucoid, and bambusoid. In the panicoid and chloridoid types the lodicules are truncate at the apex, but pointed in the festucoid and bambusoid types. Church (1949) also mentioned the value of using characters of the grass flower, including lodicules, in systematics. Although Hubbard (1934, 1959 rev.) figured the lodicules of many species, he did not discuss them from a comparative viewpoint. Some understanding of the diversity of structure among genera can be gained from his sketches of the lodicules of nearly every species of grass from the British Isles (1954). Bor (1960) likewise included sketches of the lodicules of many grasses.

Reeder and Ellington (1960) demonstrated that the genus *Calamovilfa* is chloridoid and should be removed from the Agrostideae. Their conclusions were based on lodicule anatomy along with embryo structure, leaf anatomy and epidermis, and chromosome size and number. Tateoka (1960a) also used lodicules, among other floral

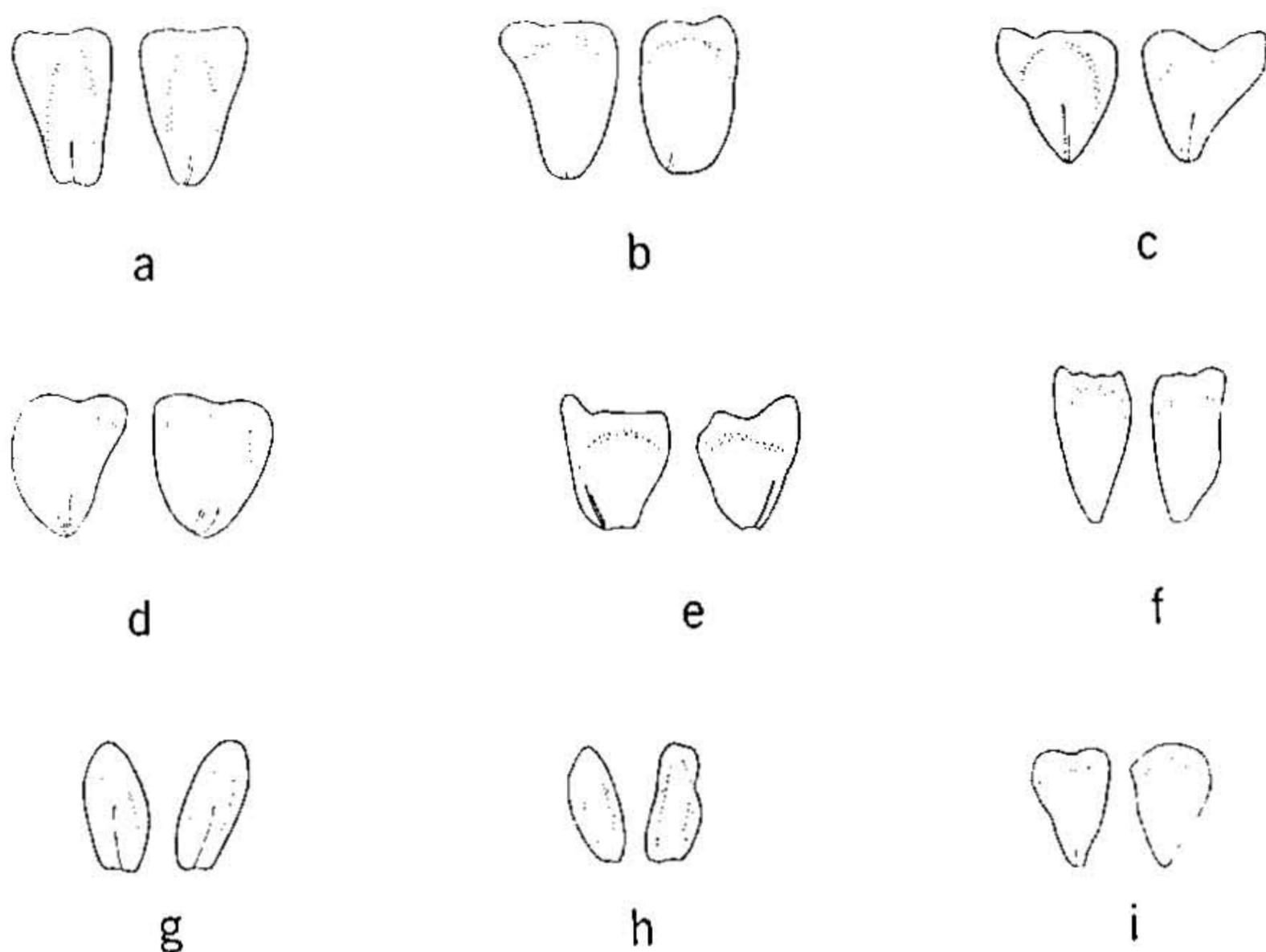


FIGURE 7.—Lodicules of Muhlenbergias other than the *Podosemum* or *Epicampes* sections, all times 50: a, *M. quadridentata* (Hinton 4389); b, *M. montana* (Arsène 5811); c, *M. schreberi* (no voucher); d, *M. wrightii* (Goodding & Hardies A-8498); e, *M. uniflora* (Miller 130); f, *M. biloba* (Pringle 819); g, *M. depauperata* (Reeder & Reeder 2279); h, *M. brevis* (Reeder & Reeder 2620); i, *M. torreyi* (Goodding M-189).

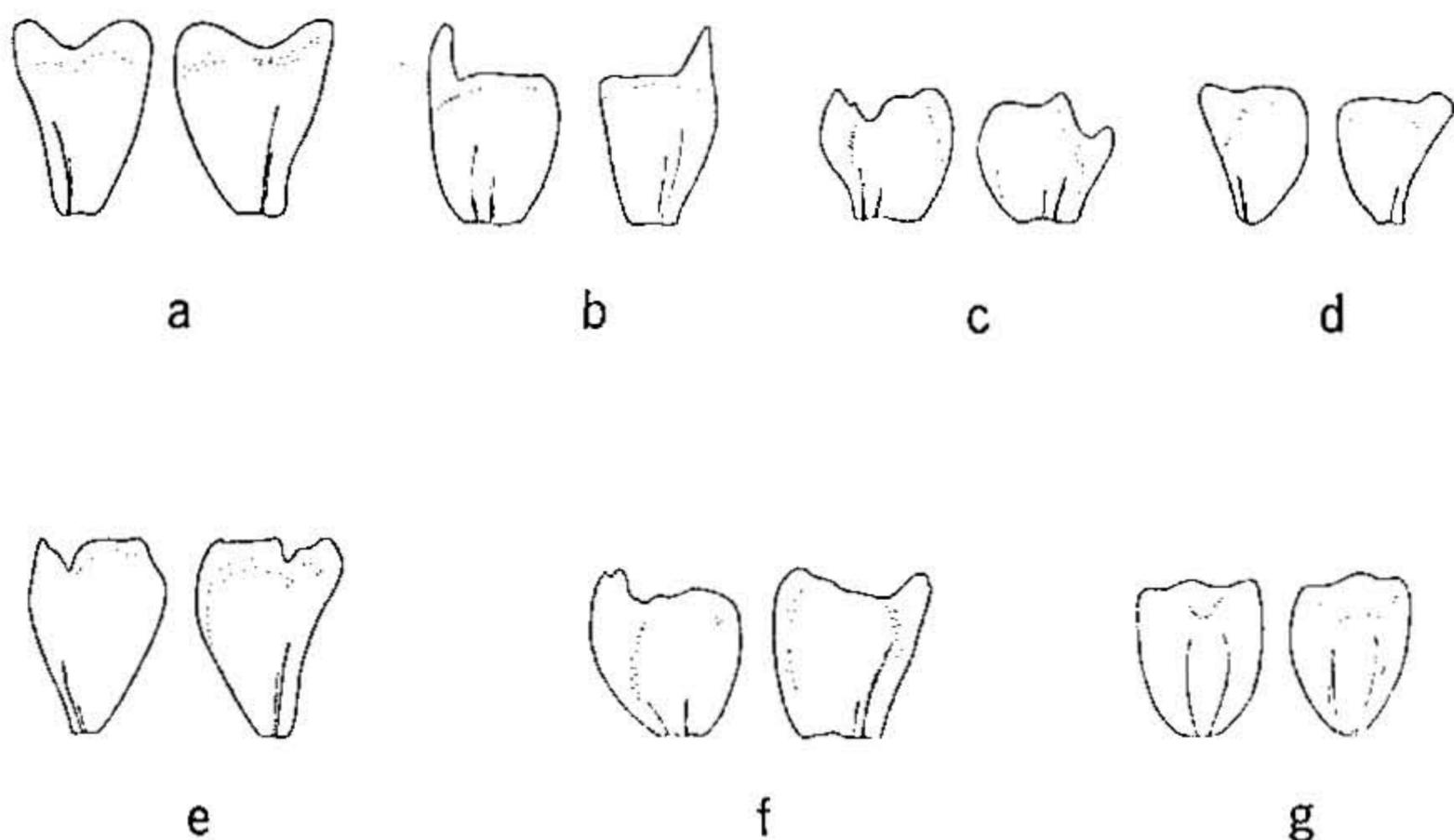


FIGURE 8.—Lodicules of Muhlenbergias other than the *Podosemum* or *Epicampes* sections, all times 45: a, *M. sylvatica* (no voucher); b, *M. racemosa* (Cornman); c, *M. frondosa* (no voucher); d, *M. andina* (Reeder & Reeder 1808); e, *M. glomerata* (Reeder & Reeder 944); f, *M. mexicana* forma *ambigua* (no voucher); g, *M. torreyana* (Bissell).

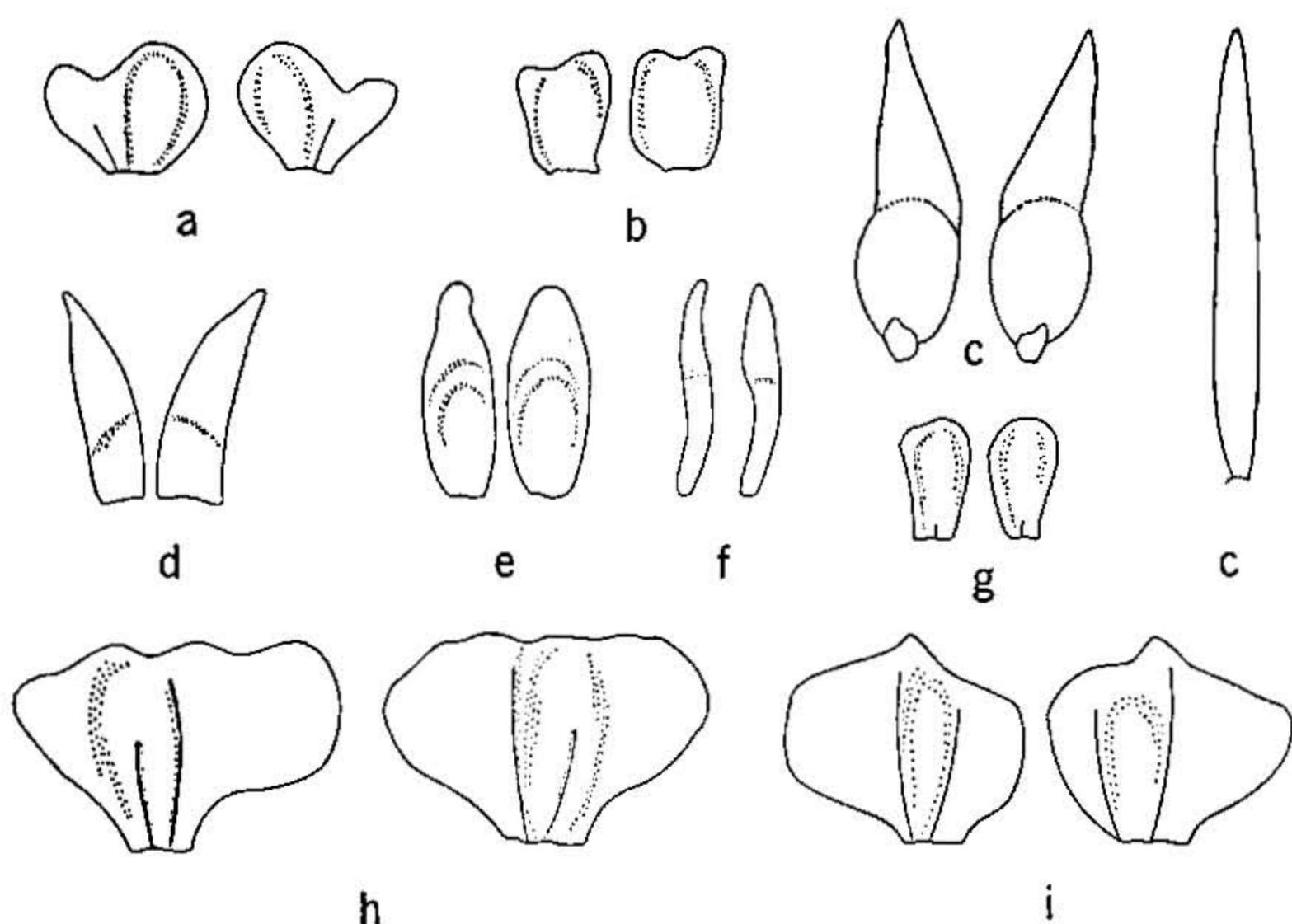


FIGURE 9.—Lodicules of genera that have been associated with *Epicampes*, all times 44: a, *Sporobolus wrightii* (Toumey); b, *Blepharoneuron tricholepis* (Reeder & Reeder 1807); c, *Stipa avenacea* (Reeder & Reeder 233); d, *Agrostis alba* (Dudley); e, *Cinna arundinacea* (no voucher); f, *Polypogon monspeliensis* (Swan); g, *Lycurus phleoides* (Reeder & Reeder 2352); h, *Sporobolus asper* (Nichols); i, *Sporobolus heterolepis* (Nichols).

features, to show the relationships of several genera of the Festuceae. Reeder<sup>10</sup> reported on the preliminary results of his study of the lodicules of over 300 species, representing 230 genera. Decker (1964), in a study of 135 genera, utilized information from the lodicules, along with other microcharacters, to determine the naturalness of the classical tribe Festuceae. Hsu's (1963) study is an example of lodicules figured for several species in a single genus.

In the present study the lodicules of 47 species of *Muhlenbergia* (including *Epicampes*) have been examined. Included are 13 species with a Gigantea type of leaf anatomy, 15 with a Rigens type, 3 intermediate between the two, the type species of *Muhlenbergia*, and 15 additional species. Line drawings of the lodicules of each of these species, in addition to those of several other genera with which *Epicampes* has been associated, appear in figures 4–9. The vascular tissue of the lodicules and manner of thickening are indicated in these drawings.

All lodicules were selected from spikelets of herbarium specimens in which the anthers were fully developed but not yet exerted.

<sup>10</sup> Paper read at meetings of the American Institute of Biological Sciences, Stillwater, Oklahoma, 1960.

The spikelets were boiled in water for several minutes, transferred to a watch glass, and the lodicules dissected out under the low power of a binocular microscope. The shape of the lodicules was drawn at this time and the areas of thickening noted, then the lodicules were mounted in glycerine jelly without staining. From 2 to 3 weeks later the excess glycerine jelly was removed and the slides ringed with diaphane. The vascularization was drawn later from the slides under the high power of a compound microscope.

Most of the species of *Muhlenbergia* examined possess lodicules more or less rectangular in outline. The thickened portion of the lodicules extends from the base to near the apex; the upper margins are of a thinner texture. One to many vascular traces usually are present in the form of annular tracheids—rarely are they lacking entirely. According to Stebbins (1956) and Reeder and Ellington (1960), these lodicules are of the chloridoid type.

The lodicules of species with a *Gigantea* type of leaf anatomy (figs. 5*l* and 6*a-j, l*) possess one to four or five vascular traces. Apart from small differences in size and amount of vascularization, the lodicules appear to be rather similar. Lodicules of the species with a *Rigens* type of anatomy (figs. 4*a-g* and 5*a-h*) usually possess two to many traces. The lodicules of *M. rigens* (fig. 5*b*) are atypical in having no vascular traces; in *M. arenicola* (fig. 5*f*) the one or two traces present are almost negligible. The considerable difference in lodicule size is attributable to the difference in the size of the spikelets. The large lodicules of *M. macroura* (fig. 4*e*), *M. nigra* (fig. 4*f*), and *M. palmeri* (fig. 4*g*) reflect the large spikelet size in these species. Lodicule shape, degree of thickening, and vascularization, with little exception, are similar in all species with a *Rigens* type of leaf anatomy.

Species of *Muhlenbergia* not of the *Rigens* or *Gigantea* groups exhibit the same kind of thickening in the lodicules and in degrees of vascularization. The lodicules of many of them are like the species with a *Rigens* or *Gigantea* type of anatomy—*M. torreyana* (fig. 8*g*), *M. quadridentata* (fig. 7*a*), *M. montana* (fig. 7*b*), and *M. wrightii* (fig. 7*d*).

In the type species of *Muhlenbergia*, *M. schreberi* (fig. 7*c*), the upper margin of the lodicule is extended on one side into a small "wing." A similar lodicule is found in *M. uniflora* (fig. 7*e*). In *M. racemosa* (fig. 8*b*), a species with scaly rhizomes, the upper corners of the lodicules are prominently projected. Other species with scaly rhizomes also have winglike extensions, to a lesser or greater degree—*M. sylvatica* (fig. 8*a*), *M. frondosa* (fig. 8*c*), *M. andina* (fig. 8*d*), *M. glomerata* (fig. 8*e*), and *M. mexicana* forma *ambigua* (fig. 8*f*).

Interesting differences are found among lodicules of various genera that, in one system of classification or another, have been considered

as closely related to the Epicampes group. Of the festucoid type *Agrostis* (fig. 9d), *Cinna* (fig. 9e), *Polypogon* (fig. 9f), and *Stipa* (fig. 9c) have long narrow lodicules with only the lower part thickened. *Stipa* further differs in having three, rather than two, lodicules. *Blepharoneuron* (fig. 9b) possesses truncate lodicules in which the thickening extends from the base to the apex, and is thus of the chloridoid type, as are the lodicules of *Lycurus* (fig. 9g) and *Sporobolus* (figs. 9a,h,i). *Blepharoneuron* and *Lycurus* show no fundamental differences from *Muhlenbergia*. However, the lateral unthickened margins in *Sporobolus* are considerably wider than in any of the species of *Muhlenbergia* examined.

### Conclusions

On the basis of lodicules, the species of *Muhlenbergia*, including *Epicampes*, are of the chloridoid type, along with such genera as *Blepharoneuron*, *Lycurus*, and *Sporobolus*. They are unlike the festucoid genera *Agrostis*, *Cinna*, *Polypogon*, and *Stipa*.

Differences of lodicules among the species of *Muhlenbergia* are of comparatively little value in recognizing groups of related species. However, the type species of *Muhlenbergia* and similar species with scaly rhizomes do exhibit a difference in the shape of the lodicules, and further studies on the remaining species of this genus may reveal that other species have distinctive lodicules.

A summary of the lodicule characters for each of the genera discussed follows (see also figs. 4-9):

Genus	Lod- cules per floret	Shape	Thickening	Vascular- ization	Lodicule group
<i>Muhlenbergia</i> Gigantea type of leaf anatomy	2	truncate	thickened from base to near apex; lateral margins thin	1-many traces	C *
Rigens type of leaf anatomy	2	truncate	thickened from base to near apex; lateral margins thin	1-many traces	C
Type species, <i>M. schreberi</i> and allies	2	truncate, with pro- jections	thickened from base to near apex, lateral margins thin	2-4 traces	C

\*See footnote at end of table.

<i>Genus</i>	<i>Lodicles per floret</i>	<i>Shape</i>	<i>Thickening</i>	<i>Vascularization</i>	<i>Lodicle group</i>
<i>Agrostis</i>	2	narrow, pointed	thickened below; thin above	lacking	F
<i>Blepharoneuron</i>	2	truncate	thickened from base to apex, lateral margins thin	lacking	C
<i>Cinna</i>	2	narrow, rounded	lower $\frac{3}{4}$ thickened, upper $\frac{1}{4}$ thin	lacking	F
<i>Lycurus</i>	2	truncate	thickened from base to near apex; lateral margins thin	1 short trace	C
<i>Polypogon</i>	2	narrow, pointed	lower $\frac{1}{2}$ thickened, upper $\frac{1}{2}$ thin	lacking	F
<i>Sporobolus</i>	2	very wide, more or less truncate	thickened from base to near apex; lateral margins thin	1-several traces	C
<i>Stipa</i>	3	narrow, pointed	thickened below, thin above	lacking	F

C=chloroid. F=festucoid.

### Chromosomes

Avdulov (1931) was the first worker to utilize cytological information as a basis for a new system of classification of the Gramineae. Subsequent workers, Prat (1936), Pilger (1954), and Stebbins (1956), have also employed cytological in addition to other data in their proposed systems. The role of cytology in grass systematics has been thoroughly reviewed by Tateoka (1960b).

Although cytological studies were not undertaken in the present investigation, several workers have published results of studies on many species of *Muhlenbergia* (including *Epicampes*) and putative allied genera, from which the following summary was made.

According to Darlington and Wylie (1956)  $x=7$  is the basic chromosome number for *Agrostis*, *Cinna*, and *Polypogon*. These genera traditionally have been placed with *Epicampes* in the tribe Agrostideae, along with *Stipa*, *Sporobolus*, and *Muhlenbergia*. On the basis of cytology, *Agrostis*, *Cinna*, and *Polypogon* are festucoid, in corrobo-

ration with the conclusions based on other studies. The basic numbers Darlington and Wylie listed for *Stipa* are  $x=9, 10, 11, 12, 14, 16,$  or  $17$ ; for *Sporobolus*,  $x=9, 10,$  or  $12$ ; and for *Muhlenbergia*,  $x=9, 10,$  or  $21$ . A survey of the chromosome numbers published for *Sporobolus* indicates that most of the species have a basic number of 9 chromosomes, whereas most of the species of *Muhlenbergia* (including *Epicampes*) have a basic number of  $x=10$ . *Stipa*, in which a high degree of aneuploidy occurs (Stebbins & Love, 1941, p. 379), does not appear to have a consistent basic number. Stebbins (1956) considers this genus to be a member of a specialized line, the Stipeae, the members being neither completely festucoid nor panicoid. He lists  $x=11$  or  $12$  as the basic number for this group.

Chromosome counts of seven species of the Epicampes group of *Muhlenbergia* are listed below: *M. emersleyi* ( $2n=40$  &  $60$ ); *M. gigantea* ( $2n=20$ ); *M. lindheimeri* ( $2n=20$ ); *M. macroura* ( $2n=40$ ); *M. pubescens* ( $2n=40$ ); *M. rigens* ( $2n=40$ ); and *M. reederorum* ( $2n=68$ ). Following is a list of American species of *Muhlenbergia* for which chromosome numbers have been determined:

Species of <i>Muhlenbergia</i>	$2n$	Authority
Gigantea type of leaf anatomy		
<i>M. emersleyi</i>	40	Brown (1950)
	60	Reeder (1961, unpublished)
<i>M. gigantea</i>	20	Tateoka (1962)
<i>M. lindheimeri</i>	20	Brown (1950)
	20	Reeder (1965, unpublished)
<i>M. pubescens</i>	40	Reeder (1961, unpublished)
<i>M. reederorum</i>	68	Reeder (1965, unpublished)
Rigens type of leaf anatomy		
<i>M. macroura</i>	40	Tateoka (1962)
<i>M. reverchonii</i> Vasey & Scribn.	40	Brown (1951)
<i>M. rigens</i>	40	Stebbins & Love (1941)
	40	Reeder (1961, unpublished)
<i>M. rigida</i> (H.B.K.) Trin.	40	Gould (1958)
Other species		
<i>M. andina</i> (Nutt.) Hitchc.	20	Myers (1947; counted by Stebbins)
<i>M. asperifolia</i> (Nees & Mey.) Parodi	20	Myers (1947; counted by Stebbins)
<i>M. brachyphylla</i> Bush	40	Brown (1950)
<i>M. filiformis</i> (Thurb.) Rydb.	18	Myers (1947; counted by Stebbins)
<i>M. mexicana</i> Trin.	40	Avdulov (1931)
<i>M. monticola</i> Buckl.	40	Brown (1951)
<i>M. polycaulis</i> Scribn.	20	Brown (1951)
<i>M. porteri</i> Scribn.	20	Brown (1951)
	40	Gould (1960)
<i>M. pungens</i> Thurb. in A. Gray	42	Nielsen & Humphrey (1937)
	60	Nielsen (1939)

<i>Species of Muhlenbergia</i>	<i>2n</i>	<i>Authority</i>
<i>M. racemosa</i> (Michx.) B.S.P.	40	Avdulov (1931)
<i>M. repens</i> (Presl) Hitchc.	60	Brown (1951)
<i>M. richardsonis</i> (Trin.) Rydb.	40	Stebbins & Love (1941)
<i>M. schreberi</i> Gmel.	40	Gould (1958)
<i>M. squarrosa</i> (Trin.) Rydb.	40	Bowden (1960)
	40	Stebbins & Love (1941)
<i>M. sylvatica</i> (Torr.) Torr. ex Gray	40	Avdulov (1931)
<i>M. tenuifolia</i> (H.B.K.) Kunth	40	Tateoka (1962)
<i>M. uniflora</i> (Muhl.) Fern.	ca. 42	Bowden (1960)

On the basis of cytology, *Muhlenbergia* (including the *Epicampes* group) is panicoid (or chloridoid) rather than festucoid, as the chromosomes are small and in multiples of 10. The chloridoid genus *Sporobolus* has a basic number of 9 and thus is distinct from *Muhlenbergia*. Of the few species known cytologically, the diploid species of the *Epicampes* group, *M. lindheimeri* and *M. gigantea*, are quite uniform morphologically as would be expected. Two counts are available for the *M. emersleyi* complex, one a tetraploid and the other a hexaploid; further counts will probably reveal a range of numbers among the various forms assigned to the species. The most interesting count is of *M. reederorum*, evidently an aneuploid. From the gross morphology *M. reederorum* appears to have been derived in part from *M. longiligula*, but we have no count for that species.

In regard to the disposition of *Epicampes* itself, Stebbins & Love (1941, p. 379) said:

The chromosome number and size obtained for *Muhlenbergia richardsonis* (Trin.) Rydb. and *M. rigens* (Benth.) Hitchc. ( $2n=40$ , fig. 22) agrees with that reported by Avdulov (1931) for other species of *Muhlenbergia*. Since the chromosomes of *M. rigens* are closely similar to those of the other species of the genus, the union by Hitchcock of the genera *Epicampes* and *Muhlenbergia* is well supported by the cytological evidence.

### The Disposition of *Epicampes*

The results of studies of the leaf anatomy and epidermis, embryos, lodicules, and chromosomes agree that the species traditionally regarded as *Epicampes* are of the chloridoid alliance. Several genera of the tribe Agrostideae, *Agrostis*, *Cinna*, and *Polypogon*, are of the festucoid alliance and are not closely related to *Epicampes* as has often been suggested.

Features of the embryos have been useful only in demonstrating that the species of the *Epicampes* group are chloridoid but did not serve to differentiate genera within this alliance. The lodicules of the *Epicampes* group are also of the chloridoid type as are those of *Muhlenbergia* but no fundamental differences were found among

them. The lodicules of *Sporobolus* were found to be somewhat distinctive in being larger and wider than those of *Muhlenbergia* (including *Epicampes*). In the few species of the *Epicampes* group with a known chromosome number, the basic number is the same as that of other species of *Muhlenbergia*, but differs from that of *Sporobolus*. This cytological information should indicate that species of the *Epicampes* group are more closely related to *Muhlenbergia* than to *Sporobolus*.

The studies most useful in clarifying the relationships of the *Epicampes* group have been those of leaf anatomy and, to a more limited extent, the leaf epidermis. They have shown that the *Epicampes* group is chloridoid and have pointed to the most closely related species within *Muhlenbergia*.

The species of *Muhlenbergia*, including the *Epicampes* group, possessing a *Rigens* or *Gigantea* type of leaf anatomy have the following morphological features in common (all species examined with other types of leaf anatomy also differ morphologically in one or more respects from these):

1. Plants perennial, strongly caespitose (rhizomes never produced).
2. Culms stout, robust, erect, not branching or rooting at the nodes.
3. First and second glumes nerveless or 1-nerved.

This group is well defined not only on the basis of gross morphology but also in characters of leaf anatomy and epidermis; on this evidence I feel this group of species should be treated as a subgenus of *Muhlenbergia* comprising two sections. The section *Epicampes*, characterized by a *Gigantea* type of leaf anatomy, includes among others *M. robusta* (including *E. strictus*, the type of the genus *Epicampes*). The section *Podosemum*, characterized by a *Rigens* type of leaf anatomy, includes among others *M. rigens*, *M. macroura*, and *M. capillaris* (based on *P. capillare*, the type species of the genus *Podosemum*).

## Systematic Treatment

### Muhlenbergia

*Muhlenbergia* Schreb. in L. Gen. Pl., ed. 8, 55. 1789.

Type species: *Muhlenbergia schreberi* Gmel. in L., Syst. Nat., ed. 13, 2:171. 1791.

Subgenus 1. *Muhlenbergia*.

Subgenus 2. *Podosemum* (Desv.) Soderstrom, stat. nov.

*Podosemum* Desv., Nouv. Bull. Soc. Philom. Paris 2:188. 1810.

Type species: *Podosemum capillare* (Lam.) Desv. = *Muhlenbergia capillaris* (Lam.) Trin. Originally described as *Stipa capillaris* Lam. Tabl. Encycl. 1:158. 1791.

**MORPHOLOGICAL FEATURES:** Plants perennial, caespitose, rhizomes not produced; culms rather stout to robust, erect, not branching or rooting at the nodes; glumes nerveless or 1-nerved (rarely an additional faint nerve or nerves present).

**ANATOMICAL FEATURES OF THE LEAF:** Phloem of the 1° vascular bundles sclerosed; large caps of sclerenchyma present in the 1° units.

### Section 1. *Podosemum*<sup>11</sup>

**MORPHOLOGICAL FEATURES:** Basal sheaths rounded; ligule firm; glumes equal or unequal, shorter to longer than the floret, membranous to firm; awn of lemma (when present) arising terminally or dorsally, from just below the tip.

**ANATOMICAL FEATURES OF THE LEAF:** Central 1° unit not differentiated from other 1° units; no keel present; 3° units often present in addition to 1° and 2° units, the units alternating in a like fashion throughout the leaf.

**SPECIES INCLUDED** (asterisked species originally described as *Epicampes*): *M. angustata*, *M. arenicola*, *M. articulata*, *M. capillaris*, *M. dubia*, *M. dubioides*, *M. elongata*, *M. expansa*, *M. firma*, *M. glabrata*, *M. holwayorum*, *M. lucida*, *M. macroura*, *M. nigra*, *M. palmeri*, *M. reverchonii*, \**M. rigens*, *M. rigida*, *M. xerophila*.

### Section 2. *Epicampes* (J. S. Presl) Soderstrom, stat. nov.

**Basionym:** *Epicampes* J. S. Presl in K. B. Presl, Rel. Haenk. 1:235. t. 39. 1830. Type species: *Epicampes strictus* Presl, loc. cit. = *M. robusta* (Fourn.) Hitchc.

**MORPHOLOGICAL FEATURES:** Basal sheaths compressed-keeled; ligule membranous throughout (firmer below, membranous above in a few); glumes about equal, generally longer than the floret, membranous, nerveless or indistinctly 1-nerved; awn of lemma (when present) arising from a mucronate tip or dorsally, from just below the tip.

**ANATOMICAL FEATURES OF THE LEAF:** Central 1° unit with a large basal cap of sclerenchyma—this and adjacent units sunken in a confluent mass of thick-walled parenchyma, forming a keel; only 1° and 2° units present, these alternating in a like pattern on either side of the keel.

<sup>11</sup> Since this section includes the type species of the next higher rank, the subgenus *Podosemum*, it appears without author citation. It does, however, coincide with Section 7 *Podosemum* (Desv.) Pilger in Die Natürlichen Pflanzenfamilien, 2nd ed., 14d:71. 1956, except for *Muhlenbergia distichophylla* (Presl) Kunth which, under the present treatment, belongs in section 2, *Epicampes*. Section 4 *Cinnastrum*, of Pilger's work (p. 69), also belongs in section *Podosemum* of my treatment.

SPECIES INCLUDED (asterisked species originally described as *Epicampes*): *M. aurea*, *M. breviligula*, *M. distans*, *M. distichophylla*, \**M. emersleyi*, \**M. gigantea*, *M. gooddingii*, \**M. grandis*, *M. inaequalis*, *M. iridifolia*, *M. lehmanniana*, \**M. lindheimeri*, *M. longiglumis*, \**M. macrotis*, \**M. mutica*, *M. pubescens*, *M. pubigluma*, \**M. robusta*, *M. scoparia*, *M. speciosa*, *M. versicolor*, \**M. virletii*, *M. xanthodas*.

### Species Intermediate Between *Epicampes* and *Podosemum*

*M. involuta*, \**M. longiligula*, *M. reederorum*, *M. stricta*.

### Key to the major groups of *Muhlenbergia*

- Phloem of the primary vascular bundles partially sclerosed; strongly caespitose perennials; culms erect, simple, usually stout and robust; glumes nerveless or 1-nerved . . . . . Subgenus **Podosemum**
- Basal sheaths rounded; ligule firm (coriaceous); glumes equal or unequal, shorter to longer than the floret . . . . . Section 1. **Podosemum**
- Basal sheaths compressed-keeled; ligule membranous (sometimes firm below); glumes about equal, generally longer than the floret . Section 2. **Epicampes**
- Phloem of the primary vascular bundles not sclerosed; morphologically different in one or more of the above characters. . . . . Subgenus **Muhlenbergia**

### Key to the species of Section *Epicampes*

(Including species intermediate between sections *Epicampes* and *Podosemum*)

- Ligule broadly decurrent, firm and brown below, often membranous above; basal sheaths rounded, compressed, or compressed-keeled; old blades involute and somewhat arcuate.
- Basal sheaths rounded or compressed, but not strongly keeled.
- Lemmas long-awned, slightly pubescent on the margins toward the base (Arizona and Sonora, Mexico) . . . . . 1. ***M. gooddingii***
- Lemmas awnless or with an awn no longer than 2 mm., glabrous.
- Spikelets mostly 2.5-3 mm. long; blades 3-5.5 mm. wide, flat or inrolled; basal sheaths rounded (southwestern United States and northern Mexico) . . . . . 2. ***M. longiligula***
- Spikelets mostly 3-4 mm. long; blades 1-2 mm. wide, involute; basal sheaths compressed and somewhat keeled.
- Glumes equal to or longer than the floret; lemmas cuspidate or with an awn to 1 mm. long; spikelets averaging 4 mm. long (Mexico: Durango) . . . . . 3. ***M. reederorum***
- Glumes shorter than the floret; lemmas with an awn 1-2 mm. long; spikelets averaging 3.5 mm. long (Texas) . . . . . 4. ***M. involuta***
- Basal sheaths strongly compressed-keeled.
- Glumes and lemmas glabrous to scaberulous; culms glabrous to scaberulous below the nodes (Texas and Coahuila, Mexico) . . . . . 5. ***M. lindheimeri***
- Glumes and lemmas pubescent to lightly villous; culms pubescent below the nodes (Mexico: Coahuila and Nuevo León) . . . . . 6. ***M. pubigluma***

Ligule not broadly decurrent, membranous (rarely somewhat firm below); basal sheaths strongly compressed-keeled; old blades flat or folded, not arcuate.

Sheath auricles present, long and pointed, often more than 1 cm. long.

Lemmas mostly glabrous.

Lemmas awnless or cuspidate, glabrous; spikelets mostly 2.5–3 mm. long; sheath auricles usually 1 cm. or more long (Mexico [Sinaloa to Oaxaca] and Guatemala) . . . . . **7. *M. macrotis***

Lemmas long-awned, glabrous except for short hairs on the margins toward the base; spikelets mostly 2–2.5 mm. long; sheath auricles usually less than 1 cm. long (Mexico [Jalisco south] and Guatemala).

**8. *M. distichophylla***

Lemmas villous (Michoacán, Mexico, south to Honduras). **9. *M. versicolor***  
Sheath auricles lacking, or, if present, broad and rudimentary, not long and pointed.

Branches of the very large panicles widely spreading (tending to open after seed-set), long-naked below; lemmas completely glabrous; ligule usually about 1 cm. or more long.

Glumes equaling the floret, rounded or acutish; spikelets generally 1.5–2.2 mm. long (Mexico: Durango to Chiapas) . . . . . **10. *M. gigantea***

Glumes several mm. longer than the floret, acute; spikelets generally 2.5–3 mm. long (Mexico: Veracruz and Chiapas) . . . . . **11. *M. mutica***

Branches of the panicle ascending or appressed (usually opening outward at anthesis, tending to become appressed at seed-set), long-naked below or floriferous to base; lemmas with some pubescence (except usually *M. robusta*, this species with a short ligule unlike that of *M. gigantea* and *M. mutica*).

Glumes awn-tipped.

Lemma short-pilose over the lower half (Colombia and Venezuela).

**12. *M. inaequalis***

Lemma glabrous except for a tuft of short hairs at the base.

Spikelets 1–2 mm. long; glumes unequal; blades narrow, 2–3 mm.; ligule 8–16 mm. long, hyaline (Mexico: Chihuahua to Michoacán).

**13. *M. scoparia***

Spikelets about 4 mm. long; glumes about equal; blades wider, 4–7 mm.; ligule 5–7 mm. long, firm (Mexico: Jalisco).

**14. *M. iridifolia***

Glumes muticous, not awn-tipped.

Basal sheaths, blades, and culms moderately to densely villous.

Ligule about 1 mm. or less long; spikelets averaging 2 mm. long; awns of lemma 1 cm. or more long (Mexico: Chihuahua to Jalisco).

**15. *M. speciosa***

Ligule 1.5–6 (usually 2–4) mm. long; spikelets mostly 2–3 mm. long; awn of lemma lacking or, when present, up to 7 mm. long (Mexico: Chihuahua to Puebla) . . . . . **16. *M. pubescens***

Basal sheaths, blades, and culms glabrous to scabrous, but never villous.

Lemma all or mostly glabrous (the hairs confined to the base of the margins or rarely present on the midnerve at the base), awnless or rarely short-awned; plants robust.

Sheath auricles present, about 3 mm. long; ligule mostly 2–3.5 mm. long; spikelets 2–3 mm. long, ashy gray or purple; lemma glabrous, the margins rarely pubescent at the base (Mexico [Nayarit south], Guatemala, and Nicaragua). . **17. *M. robusta***

Sheath auricles lacking; ligule 4–12 (usually 4–8) mm. long; spikelets 3–3.6 mm. or more long, dark green; margins of lemma generally short-pilose at the base (Mexico: San Luis Potosíto Puebla) . . . . . 18. *M. virletii*

Lemma pubescent on the midnerve or lower part to densely villous throughout, if glabrous, then long-awned.

Ligule a short rim, generally not over 5 mm. long.

Blade much narrower than the sheath at their juncture; old basal sheaths conspicuously brown, curled and fibrillose (Guatemala and Honduras).

19. *M. breviligula*

Blade not much narrower than the sheath at their juncture, old basal sheaths not conspicuously brown, curled, and fibrillose.

Lemmas moderately pubescent or villous on and between the nerves (Mexico: Chihuahua to Puebla) . . . . . 16. *M. pubescens*

Lemmas glabrous above, the pubescence confined to the very base of the margins and midnerve.

Culms glabrous below the nodes; ligule 0.3–1.5 mm. long; spikelets 2–2.2 mm. long; glumes slightly awn-tipped (Guatemala: Quezaltenango) . . . . . 20. *M. aurea*

Culms pubescent below the nodes; ligule 1.5–6 mm. long; spikelets usually 1.5–2 mm. long; glumes acute or slightly erose (Mexico: Sinaloa to Jalisco) . . . . . 21. *M. grandis*

Ligule often 1 cm. or more long, at least more than 5 mm. long.

Lemmas pubescent or villous on and between the nerves; spikelets usually 3 mm. or more long, green or greenish brown.

Lemmas densely villous throughout, with awns over 1 cm. long; panicles lead-green or purplish green (Mexico [Michoacán south] and Honduras).

9. *M. versicolor*

Lemmas sparsely villous, awnless or short-awned (awns much less than 1 cm. long when present); panicles greenish brown or tan (Mexico [Durango south] and Guatemala). . . . . 22. *M. distans*

Lemmas glabrous or pubescent on the midnerve and/or margins, but not (or hardly) pubescent between the nerves.

Spikelets 5–7 mm. long; glumes sparsely pubescent, awn-tipped (Mexico: Jalisco and Aguascalientes) . . . . . 23. *M. longiglumis*

Spikelets 2–3 mm. long (rarely longer); glumes glabrous, muticous.

Palea pubescent between the keels; callus of floret truncate (southwestern United States to Oaxaca, Mexico) . . . . . 24. *M. emersleyi*

Palea glabrous between the keels; callus of floret truncate or acute.

Glumes glabrous, shining, almost translucent, nerveless or indistinctly 1-nerved; panicle branches short, appressed; callus of floret truncate (Mexico: Chiapas) . . . . . 25. *M. xanthodas*

Glumes scabrous, distinctly 1-nerved; panicle branches long, ascending or spreading; callus of floret acute (Costa Rica to Colombia).

26. *M. lehmanniana*

#### 1. *Muhlenbergia gooddingii* Soderstrom, sp. nov.

Perennis caespitosa, culmis erectis glabris, ca. 60–110 cm. altis, nodis 4, vaginis inferioribus teretibus compressis vel paullo carinatis glabris; ligula utrinque decurrente, basin versus firma fuscaque, alibi membranacea, margine versus apicem lacerata, ca. 15 mm. longa, laminis arcuatis ad apicem attenuatis, involutis, 50 cm. longis vel

longioribus, ca. 2 mm. latis, panícula densa nutante straminea vel purpureo-viridi, axe scaberulo, ramis primariis 3–9.5 (plerumque 3–5) cm. longis, secundariis plerumque 1–2 cm. longis, tertiariis ad 1 cm. longis, pedicellis scaberulis, 1–1.5 mm. longis, spiculis acutis 2–3 mm. longis, glumis acutis, nonnullis minute aristatis, plerumque aequalibus, quam flosculo longioribus, glabris vel scaberulis, nervis 0 vel 1 indistinctis, lemmatibus acutis glabris basin versus margine (et plerumque in nervo centrali) puberulis, palea glabra.

A *M. emersleyi* Vasey vaginis magis teretibus, ligula utrinque decurrente, laminis involutis arcuatisque, lemmatibus minus pubescentibus, et palea glabra differt.

Caespitose perennial; culms 60–110 cm. tall; nodes 4, glabrous below; basal sheaths rounded to strongly compressed, rarely slightly keeled, glabrous, stramineous, inflated when old; ligule firm, brown, and broadly decurrent at the base, becoming more membranous and lacerate above, the firm lower part 4–7 mm. long, the upper membranous part 1 cm. or longer; sheath auricles lacking; blades of the culm long and narrow, becoming filiform, conduplicate or somewhat involute when dry, 50 cm. or longer, about 2 mm. wide when unfolded, upper surface of blade scaberulous or scabrous, the lower surface scabrous, the blades when old firm, brown, and strongly arcuate at the base; upper throat glabrous to scaberulous; collar glabrous.

Panicle narrow, nodding, the branches appressed or ascending, dense, stramineous or light purplish green, 22–45 cm. long, 2–4 cm. wide; axis scaberulous; primary branches mostly 3–5 (rarely as much as 9.5) cm. long, floriferous to near the base, the secondary branches mostly 1–2 cm. long, tertiary branches lacking or, when present, 1 cm. or less long; pedicels 1–1.5 mm. long, scaberulous; spikelets 2–3 mm. long (averaging 2 mm. in the holotype); glumes equal or the second a little longer than the first, acute, dentate, many bearing a tiny awn, glabrous or punctate-scaberulous, nerveless or indistinctly 1-nerved; lemma a little shorter than the glumes, acute, mostly glabrous except for sparse hairs toward the base of the lateral margins and/or midnerve, 3-nerved, excurrent from below the tip as a flexuous yellow or purple awn 1 cm. or longer; palea about equal to the lemma, glabrous or rarely with sparse short hairs between the keels toward the base.

Holotype in the herbarium of Yale University; collected in canyon north of Moristo Canyon, Baboquivari Mountains, altitude 4,000 ft., November 19, 1945, by Leslie N. Goodding (No. 462–45). Isotypes at ARIZ and NY.

DISTRIBUTION: Restricted in range—collected in mountains near the Mexican border in the southernmost Arizona counties of Cochise, Pima, and Santa Cruz, at elevations of 3,000–7,000 ft. Of the two

additional collections from Sonora, Mexico, one is questionably *M. gooddingii*.

UNITED STATES: ARIZONA: COCHISE COUNTY: West slope of Mule Mountains, *Goodding* M-345 (ARIZ), M-346 (ARIZ); Garden Canyon, Huachuca Game Reserve, *Goodding* 586-49 (ARIZ); Dragoon Mountains, *Goodding* 50-56 (ARIZ); Mule Mountains, *Goodding* 307-61 (ARIZ), 451-61 (ARIZ); Fort Huachuca Military Reservation, *Goodding* 271-62 (ARIZ). PIMA COUNTY: Quinlin Mountains, *Goodding* 179-45 (ARIZ); Baboquivari Peak, *Goodding* 281-45 (ARIZ, NY, YU); Moristo Canyon, Baboquivari Mountains, *Goodding* 408-45 (ARIZ, NY, YU), 457-45 (ARIZ, NY, YU), 460-45 (ARIZ, YU), 468-45 (ARIZ, NY, YU); Canyon N. of Moristo Canyon, Baboquivari Mountains, *Goodding* 462-45 (YU holotype, ARIZ, NY, isotypes); Coyote Mountains, *Goodding & Hevly* 53-57; (ARIZ); Quinlin Mountains, *Goodding & Lusher* 179-45 (NY, YU). SANTA CRUZ COUNTY: Sycamore Canyon, *Goodding* CG-18 (US, YU), 2996 (UNM), M-394 (ARIZ, YU), G14-40 (YU).

MEXICO: SONORA: El Cañon de la Bellota, Sierra de la Cabellera, *Santos* 2110 (SMU, TEX, US); (?) N. of Babiadora on road to Cumpas, *Wiggins* 7393 (ARIZ, DS, MICH, UC, US).

This species superficially resembles some forms of *M. emersleyi*, as most of the collections have been named. It differs in the rounded or compressed, but rarely keeled, basal sheaths, firm ligules brown below and membranous above, and long-attenuate blades becoming threadlike or filiform. The old blades are usually arcuate at the base. Of the spikelet features to distinguish the species, the lemma and palea are significant; in *M. gooddingii* the hairs on the midnerve and margins are sparse and confined to the lower part and the palea is glabrous between the keels. The panicles of *M. gooddingii* are narrow and densely flowered and the lemmas are always awned. Such plumelike panicles among the filiform foliage probably create a distinctive look to this species in the field.

*Muhlenbergia gooddingii* cannot be called a typical member of section *Epicampes* because its features of the firm ligule, brown below, and the more or less rounded basal sheaths are characteristic of the *Podosemum* section.

Because of its combination of characters a possible ancestry is suspected in *M. emersleyi* and *M. longiligula*, for the new species occurs in the overlap of range of the other two species and *M. gooddingii* has features of both. A comparison of many characters from descriptions in this paper illustrates the intermediate position of *M. gooddingii*, as shown below:

	<i>M. emersleyi</i>	<i>M. longiligula</i>	<i>M. gooddingii</i>
culms	1-1.5 (occasionally to 2) meters	60-130 (100) cm.	60-110 cm.
nodes	3-4, glabrous or somewhat puberulent below	1 or 2 on lower part, glabrous	4, glabrous below

	<i>M. emersleyi</i>	<i>M. longiligula</i>	<i>M. gooddingii</i>
basal sheaths	compressed, keeled, glabrous	rounded, rarely compressed, but never keeled; scaberulous; old sheaths expanded	rounded to strongly compressed, rarely slightly keeled; glabrous; old sheaths expanded
ligule	membranous, usually a little firmer at base than above where thin and usually lacerated into narrow strands	firm, brown, decurrent, sometimes becoming membranous at tip	firm, brown, broadly decurrent at base, becoming membranous and lacerate above
blades	2-6 mm. wide, flat or folded, 23-47 (mostly 20-40) cm. long	long-attenuate to a brown, pointed tip, flat or inrolled at edges; to 65 (20-40) cm. long, 3-5.5 (usually about 4 mm.) wide	long, narrow, becoming filiform; conduplicate or somewhat involute when dry; 50 cm. long, about 2 mm. wide
blade surface	upper: glabrous to scaberulous lower: scabrous	upper: glabrous to scaberulous (mostly scaberulous) lower: mostly scabrous	upper: scaberulous or scabrous lower: scabrous
old blades	brown, not especially firm, not arcuate	brown, firm, folded and somewhat arcuate	firm, brown, strongly arcuate at base
panicle	typically lax above, branches loosely ascending or spreading; light purple to purplish tan	erect, narrow greenish to purple	nodding, the branches appressed or ascending, dense, stramineous or light purplish green
panicle dimensions	20-40 (mostly 30-40) cm. long, 4-7 cm. wide (more in field)	15-55 (30-45) cm. long, 1-5 (generally 1.5-2) cm. wide	22-45 cm. long, 2-4 cm. wide
1° branches	9-17 (9-12) cm. long	to 13 (generally 3-5) cm. long	3-5 (to 9.5) cm. long
2° branches	3-9 (3-5) cm. long	to 5 (generally 1-2) cm. long	1-2 cm. long
3° branches	0.5-4.5 (0.5-1.5) cm. long	lacking	lacking or to 1 cm. long
spikelets	2.2-3.2 (2.5-2.7) mm. long	2-3.5 (usually 2.5-3) mm. long	2-3 (2) mm. long

	<i>M. emersleyi</i>	<i>M. longiligula</i>	<i>M. gooddingii</i>
glumes	broadly acute	acutish, sometimes midnerve extending into a minute awn	acute, dentate, many bearing a tiny awn
lemma	acutish; pubescent on midnerve and margins $\frac{1}{2}$ – $\frac{3}{4}$ their length	glabrous (rarely scaberulous)	mostly glabrous except for sparse hairs toward base of margins and/or midnerve
awn of lemma	0 to 1.5 cm. long	rarely a minute awn present	1 cm. or more long
palea	pubescent between the keels $\frac{1}{2}$ – $\frac{3}{4}$ their length	glabrous	glabrous or rarely with sparse short hairs between the keels toward the base

This species, with a few exceptions, has been collected by Mr. Leslie N. Goodding, a long-time resident of Arizona, staunch conservationist, and botanist keenly interested in the Arizona flora. It is a pleasure to recognize Mr. Goodding's interest in grasses and contributions to Arizona botany by naming for him this predominantly Arizona species.

**2. *Muhlenbergia longiligula* Hitchc. Amer. Journ. Bot. 21:136. 1934.**

*Epicampes ligulata* Scribn. in Vasey, Contr. U.S. Nat. Herb. 3(1):58. 1892. Basis of *Muhlenbergia longiligula* Hitchc., not *M. ligulata* Scribn. and Merr. (Pringle, Santa Rita Mts., Arizona, July 26, 1884, selected by A. S. Hitchcock as lectotype).

*Epicampes anomala* Scribn. in Beal, Grasses N. Amer. 2:311. 1896. (Pringle 1423, Arroyo Ancho, Sierra Madre, Chihuahua, Mexico). Not *Muhlenbergia anomalis* Fourn. 1896.

*Epicampes distichophylla* var. *mutica* Scribn. in Beal, Grasses N. Amer. 2:308. 1896 (Toumey 740, July 23, 1892, Arizona).

*Epicampes stricta* var. *mutica* Jones. Contr. West. Bot. 14:6. 1912. Based on *E. distichophylla* var. *mutica* Scribn.

Strongly caespitose perennial; culms glabrous, becoming scaberulous toward the panicle, 60–130 cm. (usually about 1 meter) tall; nodes 1 or 2, on the lower part, glabrous; basal sheaths rounded, rarely compressed, but never keeled, glabrous to scaberulous, loosely imbricate, the old sheaths expanded, yellowish brown, persistent; ligule firm, brown, decurrent, sometimes becoming membranous at the tip, especially in the uppermost blades of the culm, 1–3 (usually 1–1.5) cm. long, distinctly 2-keeled when large and broad; sheath auricles lacking; blades of the culm to 65 (usually 20–40) cm. long, long-attenuate to a brown, pointed tip, flat or inrolled at the edges, 3–5.5 (usually about 4) mm. wide when flat, the uppermost blade of the culm beneath the panicle short, the upper surface of the blade glabrous to scabrous

(mostly scaberulous), the lower surface mostly scabrous, the old blades brown, firm, folded, and somewhat arcuate at the point of attachment to the sheath; upper throat glabrous; collar glabrous (rarely scaberulous).

Panicle erect, narrow, the panicle branches borne in bunches along the axis, branches of the lowest cluster shorter than the clusters above, an interruption usually present between the basal and remaining clusters, greenish to purple, 15–55 (usually 30–45) cm. long, 1–5 (usually 1.5–2) cm. wide; axis glabrous to scabrous (mostly scabrous), the primary branches to 13 (usually 3–5) cm. long, the secondary branches to 5 (usually 1–2) cm. long, bearing spikelets almost to the point of attachment of the secondary with the primary branches, tertiary branches lacking; pedicels very short, glabrous to scaberulous (rarely scabrous); spikelets 2–3.5 (mostly 2.5–3) mm. long; glumes usually longer than the floret, but often shorter, especially in the longer spikelets, usually equal or the second a little longer than the first, glabrous to scaberulous, acutish at the tip, sometimes extending into a minute awn, nerveless or 1-nerved; lemmas 2.5–2.9 mm. long, glabrous (rarely scaberulous), indistinctly 3-nerved, rarely with a minute awn; palea equal to or often a bit longer than the lemma, glabrous.

Lectotype in the U.S. National Herbarium, no. 746686, collected in the Santa Rita Mountains, Arizona, elev. 4,000 ft., July 26, 1884, by C. G. Pringle (without number). Hitchcock has written on the type sheet, "Selected as probable type. The Texas specimens are different and do not agree with the description. Note long firm ligule." Isolectotypes at F, GH.

**DISTRIBUTION:** Rocky mountain slopes and canyons, at elevations of 5,000–9,000 feet, most frequently found in exposed areas of the pine-oak zone at 6,000–8,000 feet, occasionally in lightly frosted areas where more shaded. Rather common from New Mexico to Arizona into northern Mexico, occurring in Sonora, Chihuahua, and Durango. Also reported from western Texas and southern Nevada.

**UNITED STATES:** NEW MEXICO: Mountains W. of Gray, *Goodding* M-252 (ARIZ, US), M-254 (ARIZ). CATRON COUNTY: Apache National Forest, *Laney* 16 (UNM); *Solheim & Solheim* 2343 (GH). Mangas, *Metcalf*, Sept. 14, 1897 (GH, NY, US). GRANT COUNTY: Black Range, *Goodding & Goodding* 367 (ARIZ). Santa Rita del Calve, *Wright* 1973 (CAS, GH, MO, NY, UC, US). GREENLEE COUNTY: Castle Creek, Apache, *Utzat* 14 (UNM). SOCORRO COUNTY: Mogollon Mountains, *Metcalf* 556 (ARIZ, GH, MO, NY, POM, US). ARIZONA: *Emersley* 47 (US). Upper Oak Creek, *Fulton* 7345 (ARIZ). Peña Blanca Mountains, *Goodding*, Sept. 20, 1935 (ARIZ); *Jones*, Sept. 20, 1884 (US). Rocky Canyon, *Rothrock*, in 1874 (F, GH, NY). Oak Creek Canyon, *Weatherwax* 2782 (TAES). APACHE COUNTY: Diamond Creek, *Gould & Robinson* 5030 (ARIZ, NY, TAES). Reservation Ranch, *Wasser*, Aug. 1936 (ARIZ). COCHISE COUNTY: Chiricahua Mountains, *Blumer* 189 (ARIZ). Barfoot Park, *Blumer*

1424 (ARIZ, DS, F, GH, MO, NY, US). Herb Martyr Dam Area, "Chiricahua Vegetation Team" 59-803 (ARIZ). Carr Canyon, Darrow, Gould, Phillips, & Pultz 1437 (MO). Rock Canyon, Huachuca Game Reserve, Goodding 884-49 (ARIZ). Fort Huachuca Military Reservation, Goodding 568-58 (ARIZ, YU), 720-58 (YU). Pinery Pass, Goodding & Goodding 463 (ARIZ, UC). Carr Canyon, Gould, Darrow, Pultz & Phillips 2461 (CAS, UC, US). Divide between Carr and Ramsey Canyons, Gould & Haskell 3363 (ARIZ, NY, UC, US). Rucker Canyon, Gould & Haskell 4585 (ARIZ, GH). Bowie, Jones 4290 (ARIZ, POM, SMU, US). Huachuca Mountains, Jones, Sept. 3, 1903 (POM); Lemmon & Lemmon 2921 (GH), Sept. 1882 (US). Pine Canyon, Toumey, Sept. 10, 1896 (US). COCONINO COUNTY: Long Valley Ranger Station, Coconino National Forest, Darrow 3262 (ARIZ, CAS, US). Pine Flat Camp, Oak Creek Canyon, Darrow, Sept. 16, 1943 (ARIZ). GILA COUNTY: Mt. Ord, Goodding 123-47 (ARIZ). Young, Goodding & Goodding 341 (ARIZ). Long Valley, Pine-Winslow Road, Goodding & Goodding 354 (ARIZ). 5 mi. N. of McFadden Peak on Young Road, Gould 3915 (ARIZ, US). Workman Creek Canyon, Gould & Hudson 3793 (ARIZ, MO, UC, US). Cassadore Range, Gould & Robinson 4896 (ARIZ, UC). White Mountains, Griffiths 5367 (US), 5409 (GH, US), 5434 (US). GRAHAM COUNTY: 3 mi. SW. of Point of Pines, 70 miles E. of San Carlos, Bohrer 421 (ARIZ, CAS). Bluejay Ridge, Gandy 8 (UNM). Mt. Graham, Hope 9999 (ARIZ, MICH, US). GREENLEE COUNTY: Red Bluffs road above Blue, Goodding & Goodding 349 (ARIZ, US). Big Lue Range, Gould & Haskell 4064 (ARIZ, UC). 15 mi. N. of Blue, Gould & Robinson 5143 (ARIZ, TAES, UC). MARICOPA COUNTY: Sugar Loaf Mt. Wonderland of Rocks, Darrow, July 8, 1937 (ARIZ). NAVAJO COUNTY: Fort Apache, Mayerhoff 89 (F); Schroeder, in 1937 (ARIZ). PIMA COUNTY: Mt. Lemmon Road, Benson 9106 (ARIZ, DS, POM). Manning Camp, Blumer 3412 (ARIZ, DS, GH, MO, UC). Santa Catalina Mountains, Brown 135 (ARIZ), Darrow, Oct. 3, 1937 (GH). Prison Road, Ginter, Oct. 6, 1941 (UC). Moristo Canyon, Goodding 451-45 (ARIZ, NY). Santa Rita Mountains, Griffiths & Thornber 122 (US). Mt. Lemmon, Bear Canyon, Hevly 1028 (ARIZ). Santa Rita Mountains, Kearney & Peebles 10543 (ARIZ, MICH, US). Bigelow Tower, Leader & Leader 276 (ARIZ). San Luis Mountains, Mearns 373 (US). Rincon Mountains, Nealley 65 (NY, US), Aug. 1881 (GH, MO). Upper Bear Canyon, Santa Catalina Mountains, Parker 7099 (ARIZ). Mt. Lemmon, Peebles & Harrison 2294 (US); Peebles, Harrison & Kearney 2539 (ARIZ, US). Santa Rita Mountains, Pringle, July 26, 1884 (US lectotype, F, GH, isolectotypes). Madera Canyon, Silveus 3468 (TAES, TEX, US). Marshall Gulch, Thornber 2767 (ARIZ). Box Springs, Thornber, Aug. 10, 1906 (ARIZ). Tucson, Toumey 740 (DS, NY, US, isotypes of *E. distichophylla* var. *mutica*). SANTA CRUZ COUNTY: White House (Madera) Canyon, Benson 9780 (POM); Gould 2597 (ARIZ, UC, US); Leader & Leader 198 (ARIZ). Sycamore Canyon, Goodding M-111 (ARIZ), M-259 (ARIZ, US). Santa Rita Mountains, Griffiths 6074 (MO, US). Santa Catalina Mountains, Thornber 7689 (ARIZ). YAVAPAI COUNTY: Jerome, Benham M-34 (ARIZ), M-105 (ARIZ); Goodding 75-46 (ARIZ). Mingus Mountain, Benham 43-B (ARIZ, MICH). Prescott, Purchase 513 (ARIZ).

MEXICO: SONORA: San José Mountains, Marshall 173 (ARIZ); Mearns 996 (US), 1649 (US). El Tigre, Río de Bavispe, Santos 1963 (ARIZ, GH, MO, NY, SMU, TEX, US). El Picacho del Pilar, Río de Bavispe, Santos 2164 (GH, SMU). CHIHUAHUA: Between Río Chico and Río Caballo, Barlow, Sept. 30, 1911 (F, UC, US). Sánchez, Hitchcock 7667 (NY, US). Marsh Lake, Jones, Sept. 19, 1903 (POM). N. de Cd. Madera, Martínez F-2477 (CHAP, US). 35 km. SW. of Miñaca, Pennell 18928 (MEXU). NE. of Colonia Pacheco,

*Pennell* 19194 (US). Arroyo Ancho, *Pringle* 1423 (GH, US, isotypes of *E. anomala*) Sierra Madre, *Pringle* 1427 (F, GH, NY, US), 1703 (UC). 27 mi. NW. of Cd. Madera, *Reeder & Reeder* 2663 (YU). Ca. 43 mi. SW. of Casas Grandes, *Reeder & Reeder* 2692 (YU). 38 mi. S. of Casas Grandes, *Reeder & Reeder* 2699 (YU). 31 mi. W. of Colonia Juárez, *Reeder & Reeder* 3222 (YU). Palimos Cañon ca. 13 mi. E. of Chuhuichupa, *Reeder, Reeder, & Goodding* 1222 (YU). S. of Hernández, *Reeder, Reeder, & Soderstrom* 3505 (US, YU), 3509 (US, YU), 3531 (US, YU). DURANGO: 6.5 mi. W. of El Salto, *Reeder & Reeder* 2639 (YU). 25 mi. W. of Durango, *Reeder, Reeder, & Soderstrom* 3439 (US, YU).

*Muhlenbergia longiligula* is distinguished by its long, firm, decurrent ligule and rounded basal sheaths. On the basis of leaf anatomy, the long glumes, the dorsal awn (when present), and the general habit in the field, it seems to belong with the *Epicampes* section of *Muhlenbergia*. The firm ligule and rounded basal sheaths are also characteristics of species in the *Podosemum* section. Thus, *M. longiligula* possesses characters of both sections, and it appears to be more of a link between them than a distinct member of either. The closely allied species of the subgenus *Podosemum*, *M. lindheimeri*, *M. involuta*, *M. pubigluma*, and *M. reederorum*, all possess the decurrent ligule. Of these *M. involuta* and *M. reederorum*, like *M. longiligula*, lack strongly compressed-keeled sheaths. All occur within the same general range, *M. longiligula* ranging from southwestern United States into northern Mexico, *M. lindheimeri* in south-central Texas and Coahuila, *M. involuta* in Texas, *M. pubigluma* in Coahuila and Nuevo León, and *M. reederorum* in Durango, Mexico.

### 3. *Muhlenbergia reederorum* Soderstrom, sp. nov.

Perennis caespitosa, culmis angustis scabris, ca. 1 m. altis, basin versus nodis 3, puberulentis, vaginis inferioribus compressis et paullo carinatis glabris; collis scaberulis; ligula utrinque decurrente, basin versus firma et fusca, alibi membranacea et margine versus apicem lacerata, ca. 10–15 mm. longa; laminis culmi usque ad 65 cm. longis laete viridibus involutis, attenuatis et ad apicem filiformibus, laminis vetustis fuscis firmis arcuatis, ca. 1.5 mm. latis, utrinque scabris; panícula erecta, cetera laxa, laete viridi 30–47 cm. longa, quando appressa 2–3 cm. lata, axe scabro, ramis primariis 4–6 cm. longis, secundariis ca. 2 cm. longis, tertiariis ca. 5 mm. longis, pedicellis scaberulis, lateralibus 1.5–2.5 mm. longis, terminalibus 2–3 mm. usque ad 6 mm. longis; spiculis lanceolatis 3.5–4.6 (plerumque 4) mm. longis, glumis acutis fere aequalibus, quam flosculo longioribus, scaberulis, nervis 0 vel 1, indistinctis, lemmatibus scaberulis, infra apicem minute aristatis, quam glumis paullo brevioribus.

A *M. involuta* Swallen vaginis magis carinatis, glumis quam lemmatibus paullo longioribus, spiculis longioribus, paniculis longioribus, et aristis quam lemmatibus brevioribus differt.

Caespitose perennial; culms rather slender, scabrous, erect, about 1 m. tall; nodes 3, puberulent below; basal sheaths compressed and somewhat keeled or compressed only, glabrous, purplish toward the base when young; collar scaberulous; ligule decurrent, the lower  $\frac{1}{2}$ – $\frac{3}{4}$  firm and brown, the upper half membranous and lacerate, about 10–15 mm. long; sheath auricles lacking; blades of the culm up to 65 cm. long, light green, tightly folded, long-attenuate becoming filiform, the old blades brown, firm and arcuate, about 1.5 mm. wide when flat, the upper and lower surfaces scabrous; upper throat scabrous.

Panicle erect, grayish green, 30–47 cm. long, 2–3 cm. wide when appressed, more open at anthesis; axis scabrous; branches of the panicle narrow, the primary branches 4–6 cm. long, secondary branches 1–2 cm. long, tertiary branches lacking or about 5 mm. long; pedicels evenly scaberulous, those of the lateral spikelets 1.5–2.5 mm. long, of the terminal spikelets 2–3 (to 6) mm. long; spikelets lanceolate, 3.5–4.6 (averaging 4) mm. long; glumes acute, about equal, scaberulous, nerveless or indistinctly 1-nerved; lemmas a little shorter than the glumes, scaberulous, 3-nerved, bearing a rudimentary awn 0.2–2.5 mm. long from just below the tip; palea glabrous.

Holotype in the Yale University Herbarium, collected in the Sierra Madre Occidental (W. of Ciudad Durango), 7 miles E. of Navíos, Durango, Mexico, elevation 7,700 ft., Sept. 26, 1963, by *J. R. & C. G. Reeder* (no. 3834). Isotypes at F, K, MEXU, MICH, NY, P, UC, and US.

DISTRIBUTION: Known from Durango and possibly Jalisco, Mexico. The type specimen was collected in the Sierra Madre Occidental west of the city of Durango, where the large caespitose clumps are found on rocky canyon walls in the pine-oak zone at elevations of 7,700–8,800 ft.

MEXICO: DURANGO: 4 mi. W. of Navíos, *Reeder & Reeder* 4230 (US, YU); 7 mi. E. of Navíos, *Reeder, Reeder, & Soderstrom* 3436 (US, YU). 2 mi. SW. of Buenos Aires, *Reeder, Reeder, & Soderstrom* 3347 (YU). (?) JALISCO: Mountains N. of Autlán, 3–5 mi. above Mina San Francisco, *McVaugh* 19669 (MICH, US).

*Muhlenbergia reederorum* exhibits greatest similarity to *M. involuta*, known only in Texas. In *M. involuta* the basal sheaths are compressed, but not keeled; in *M. reederorum* they are usually more keeled, but the keel is not strong. In *M. reederorum* the glumes are a little longer than the floret, but much shorter in *M. involuta*, the spikelets are longer, averaging 4 mm., the panicle is longer, up to 47 cm., and the glumes are acute and entire at the apex. *Muhlenbergia longiligula* is also similar in many respects but its unawned lemmas and flat, wider (3–5.5 mm.) blades separate it from the new species. The many long, narrow blades of *M. reederorum* produce softer and more delicate

clumps in the field than the typical coarser clumps of other species of the *Epicampes* section. A unicate specimen (*Reeder, Reeder, & Soderstrom* 3347) collected near Buenos Aires, Durango, differs from the material of the type locality in the more membranous ligule, the longer awn of the lemma (up to 2 mm.), and the wider blades (up to 2.5 mm. wide).

This previously undescribed species is named in honor of Professor John R. Reeder of Yale University and his wife, Charlotte Goodding Reeder. Because of their interest in the Gramineae, especially of Mexico, and the genus *Muhlenbergia* it is appropriate that a *Muhlenbergia* from that country bear their name.

4. *Muhlenbergia involuta* Swallen. Amer. Journ. Bot. 19: 436. f. 2. 1932.

Caespitose perennial; culms glabrous or scaberulous at the base, to 135 (usually 70–100) cm. tall; nodes 4 or more, mostly glabrous or puberulent beneath; basal sheaths compressed, but not strongly keeled, tightly imbricate, yellowish brown, not becoming fibrillose when old; ligule decurrent, firm and brown at the base, becoming acute and membranous only toward the tip, often firm about three-quarters of its length, membranous one-quarter of the length, to 1.2 cm. long; sheath auricles lacking; blades of the culm to 45 cm. long, pale green, often arcuate, long-attenuate to a firm point, tightly folded, 1–2 mm. wide when unfolded, the upper surface of the blade scabrous, bearing a mat of numerous tightly appressed white hairs (spicules), the lower surface of the blade scabrous; upper throat scabrous; collar scaberulous.

Panicle erect, greenish to tan, to 40 (usually 20–30) cm. long, 1.5–7 cm. wide, branches of the panicle long; axis scabrous, the primary branches 6–9 (usually 6–8) cm. long, the secondary branches 1–4 (usually 2–3.5) cm. long, the tertiary branches to about 2 (usually 1 or less) cm. long; pedicels of the terminal spikelets very long, equaling the spikelet or, more often, much longer, pedicels of the lateral spikelets usually shorter than the spikelet; spikelets 3–4 (averaging 3.5) mm. long; glumes equal or the second 1 mm. or more longer than the first, slightly toothed at apex, occasionally bearing a rudimentary awn, usually glabrous but sometimes scaberulous, 1-nerved; lemmas 3.2–4.2 (usually 3.5) mm. long, usually much longer than the glumes, rarely about equal, glabrous or with a few hairs at the base of the lateral margins, rather strongly 3-nerved, awned, the awns 1–2.4 (usually 1–2) mm. long; palea about equal to lemma, glabrous.

Type in the U.S. National Herbarium, no. 1501594, collected on draws in hills, 20 miles NE. of San Antonio, Texas, Oct. 10–31 (year not cited), by W. A. Silveus (no. 358).

**DISTRIBUTION:** Rocky banks and draws of hills, usually on limestone soil. Of very limited distribution, in south-central Texas.

**UNITED STATES: TEXAS: BANDERA COUNTY:** Bandera, *Silveus* 7393 (TEX). **BEXAR COUNTY:** Hills NE. of San Antonio, *Silveus* 314 (TEX, US). 20 mi. NE. of San Antonio, *Silveus* 358, = *Amer. Gr. Nat. Herb.* 1324 (US Holotype, CAS, GH, LL, MO, SMU, UC, isotypes). **BOERNE COUNTY:** Open calcareous hillsides, *Palmer* 10829, in 1916 (US). **BURNET COUNTY:** S. of Burnet, *Silveus* 7676 (ARIZ, CAS, DS, SMU, TAES, TEX). **HAYS COUNTY:** W. of Cedar Valley, Edwards Plateau, *Gould* 5336 (TAES). **KENDALL COUNTY:** Spanish Pass, *Cory* 26212 (TAES, US). SW. of Boerne on the Boerne-Bandera road, *Silveus* 780 (TEX, US). Comfort, *Silveus* 2335 (CAS, TAES, TEX), 7339 (CAS, TAES, TEX). **KERR COUNTY:** NW. of Kerrville, *Reed*, Sept. 28, 1937 (US). **TRAVIS COUNTY:** W. of Trading Post on cut off road to Pedernales Bridge, *Brown* 50-323 (SMU, TAES, TEX). Glen Rose, W. of Austin, *Moon* 167 (TEX). Austin, *Tharp* 3968 (TEX), 5198 (TEX). Pedernales road, 8 mi. W. of Bee Cave, *Tharp* 53-250 (TEX). W. of Austin, *Warnock* 45-27 (TEX, US). Hamilton Pool, *Webster* 1961 (TEX).

*Muhlenbergia involuta* is distinguished by its firm, decurrent ligule, in combination with the compressed but not keeled basal sheaths, the tightly folded arcuate blades, and glabrous lemmas that usually exceed the glumes in length. Swallen, in describing this species, remarked, "*Muhlenbergia involuta* is related to *M. distichophylla* (Presl) Kunth but in that species the spikelets are only 1.5-2 mm. long, the awns are 10-15 mm. long, the blades are flat, as much as 5 mm. wide, and the sheaths bear auricles 2-3 cm. long. In both species the glumes are shorter than the floret." However, *M. involuta*, is by no means closely related to *M. distichophylla*. The latter is allied to *M. macrotis* and *M. robusta* in which the sheaths bear rudimentary to very long auricles, the lemmas are glabrous, and the ligule membranaceous throughout. In *M. involuta* the ligule is decurrent, very firm and brown at the base, becoming membranaceous only at the tip. This character, in addition to the pale green, firm, tightly folded arcuate blades, indicates that it is closer to *M. lindheimeri*, *M. pubigluma*, and *M. reederorum*. *Muhlenbergia involuta* is endemic to Texas, *M. lindheimeri* to Texas and Coahuila, *M. pubigluma* is known only from Coahuila and Nuevo León in northern Mexico, and *M. reederorum* only from Durango (and possibly Jalisco), Mexico. The distribution of these species in Texas, Coahuila, and Durango separates them from *M. distichophylla* from farther south, Jalisco, Mexico, into Guatemala.

5. *Muhlenbergia lindheimeri* Hitchc. *Journ. Washington Acad. Sci.* 24(7):291. 1934.

*Epicampes gracilis* Trin. *Mem. Acad. St. Petersb. VI. Sci. Nat.* 4:271. 1841. Fragments of panicle of this specimen ex Trinius herbarium (LE), in type collection at the U.S. National Herbarium marked "*Epicampes gracilis* in 'Mexico de Karwinsky.' *Hb. Reg. Monac* (Munich) no. 595." The published locality of this specimen is Mexico, but the species is known only

from south-central Texas. This reference is doubtless made to territory now Texas but which was still part of Mexico in 1841. Not *Muhlenbergia gracilis* (H. B. K.) Kunth. 1829.

Strongly caespitose perennial; culms stout, robust, glabrous, 0.5–1.5 (mostly more than 1) meters tall; nodes 4, glabrous beneath the nodes; basal sheaths compressed-keeled, glabrous, tightly imbricate and usually yellowish or purplish brown; ligule decurrent, firm and brown at the base, becoming membranous above, usually enclosed within the tightly folded blade, up to 3.5 (mostly 1–1.5) cm. long; sheath auricles lacking; blades of the culm 25–55 (usually 30–45) cm. long, narrow, pale green, very firm and conduplicate, 2–4 (usually 2–3) mm. wide when flat, the upper surface of the blade scabrous, bearing a tight mat of dense short white hairs, the lower surface scaberulous to scabrous; upper throat scabrous, bearing a dense mat of short white hairs; collar glabrous to scaberulous.

Panicle erect, narrow, pale green or tan, the panicle branches floriferous almost to the base, occurring in bunches at intervals along the axis, the naked portion of the axis sometimes obvious, sometimes obscured by the overlapping appressed panicle branches, to 50 (mostly 20–30) cm. long, 1–3 (mostly 1.5–2) cm. wide; axis scabrous, the primary branches to 5 (mostly 2–4) cm. long, the secondary branches to 1.5 (mostly 0.5–1.5) cm. long, tertiary branches lacking; pedicels of the lateral spikelets to 0.5–1.2 (usually 0.5–0.8) mm. long, those of the terminal spikelets to 3 mm. long, scabrous; spikelets 2–3.5 (usually 2.5–3) mm. long; glumes about equal to (sometimes shorter than) the floret, the second a little longer than the first, glabrous to scabrous (mostly scabrous), rounded at the tip or blunt, rarely acute except in the longer spikelets, awnless, strongly 1-nerved; lemmas to 3 (mostly 2.4–2.6) mm. long, glabrous or rarely puberulent at the base, mostly rounded at the tip, 3-nerved (the nerves purple), awnless or rarely with awns as much as 4 mm. in length; palea a little shorter than the lemma, glabrous or occasionally with a few minute hairs at the base between the purplish keels.

Holotype in the U.S. National Herbarium, no. 998949, collected in 1847 by Ferdinand Lindheimer in Texas. Only the number 725 is given, this being the number of the "Plantae Lindheimerianae" series. According to Blankinship (1907) this represents Lindheimer's own collecting number of 465 (fasc. IV) and was collected in Friedrichsburg (now Fredericksburg), Gillespie County, Texas, in September 1847. Isotypes at F, GH, MO, and UC.

**DISTRIBUTION:** Dry sandy or limestone soil, in draws of hills and open areas. Of limited distribution in south-central Texas and Coahuila, Mexico.

UNITED STATES: TEXAS: Southern Texas, *Lindheimer*, in 1849-51 (NY); *Nealley*, in 1889 (GH). Foothills, upper Seco, *Reverchon* 1610 (F, MO, NY, TEX, US). Glen Rose Hills, *Tharp* 46293 (TAES, UC), *Tharp*, Dec. 7, 1928 (MO, NY, SMU). BANDERA COUNTY: N. of Medina, *Parks & Cory* 24422 (TAES). W.-NW. of Bandera, *Shinners* 16880 (SMU). BELL COUNTY: Maxdale, *Wolff* 2632 (TAES, US). BEXAR COUNTY: Onion Creek, near San Antonio, *Brown* 3487 (TEX). Pleasonton Road 15 mi. S. of San Antonio, *Burr* 513 (NY). Cibolo Creek, *Liles* 17 (TAES). North Loop, *Silveus* 11 (TEX, US), 355 (TEX, US). 20 mi. NE. of San Antonio, *Silveus* 354 (MICH, TEX, US). BURNET COUNTY: NE. of Lake Buchanan toward Lampasas, *Whitehurst*, Nov. 21, 1956 (LL). COMAL COUNTY: Comanche Spring, New Braunfels, etc., *Lindheimer* 1255 (ARIZ, F, GH, NY, TEX, UC, US). COMANCHE COUNTY: Comanche Spring, *Lindheimer* 176 (CAS, ILL, MO, TAES). EDWARDS COUNTY: Barksdale, *Palmer* 11004, in 1916 (MO, US); *Parks & Cory* 26893 (TAES). GILLESPIE COUNTY: Fredericksburg, *Thurber* 68 (NY). *Lindheimer* 465, = *Plantae Lindheimerianae* 725 (US holotype, F, GH, MO, UC, isotypes). HAYS COUNTY: Reagan Houston Ranch, *Johnson* 360 (TEX). KENDALL COUNTY: N. of Comfort, *Cory* 20732 (GH, UC); *Parks & Cory* 20729 (TAES), 20730 (TAES), 20731 (TAES). Spanish Pass, *Palmer* 10859, in 1916 (US). Comfort, *Silveus* 7334 (CAS, DS, SMU, TAES, TEX). KERR COUNTY: Kerrville State Park, *Cory* 50506 (DS, GH, NY, SMU, TAES, TEX, UC, US). 25 mi. NW. of Kerrville, *Gould* 8468 (SMU, TAES, UC). SW. of Kerrville, *Parks & Cory* 24840 (TAES). KIMBLE COUNTY: NE. of junction on Mason Highway, *Landers* 5223 (TAES). KINNEY COUNTY: W. of Bracketville, *Correll & Correll* 24740 (LL). MASON COUNTY: N. of Mason, *Reardon* 23 (TAES). REAL COUNTY: W. Fork of West Frio River, *Cory* 43240 (SMU, TEX). N. of Leakey, *Parks & Cory* 27385 (TAES). TRAVIS COUNTY: Austin, *Bodin*, Oct. 20, 1891 (DS). Oak Hill, *Rogers* 6520 (TEX). Barton Creek, Austin, *Tharp* 70 (TEX, US). Edwards Plateau, *Tharp* 3076 (US). Watkins Ranch, *Tharp* 49009 (US); *Tharp, Rogers, Wilkins, Cowan, Clark & Jeffrey* 49004 (TEX, US); *Tharp et al.* 51-516 (TEX). Austin, *Warnock* W1065 (TEX, US). WILLIAMSON COUNTY: Georgetown, *Bodin* 287 (NY).

MEXICO: COAHUILA: About 24.5 mi. SW. of Piedras Negras, *Reeder & Reeder* 3921 (US, YU). 8 mi. W. of Cuatro Cienegas, *Reeder & Reeder* 3945 (US, YU).

*Muhlenbergia lindheimeri* is distinguished by the decurrent ligule, long spikelets with glabrous lemmas, the glumes equal the floret, and the long-attenuate firm blades somewhat arcuate when old. It appears to be most closely related to *M. involuta* and *M. pubigluma*. The former differs in having basal sheaths somewhat compressed but not keeled and glumes shorter than the floret, the latter in having puberulent glumes and lightly villous lemmas.

6. *Muhlenbergia pubigluma* Swallen. Proc. Biol. Soc. Wash. 56:78. 1943.

Strongly caespitose perennial; culms stout, glabrous, about 75-125 cm. tall; nodes 3, pubescent below; basal sheaths compressed-keeled, glabrous, tightly imbricate, the old basal sheaths firm, dark brown, not becoming fibrillose; ligule decurrent, firm and brown at the base, becoming membranous for the greater part of its length, 5-13 mm. long, longer on the innovations; sheath auricles lacking;

blades of the culm to 35 cm. long, narrow, pale green, firm and conduplicate, long-attenuate to a firm brown point, 1-2 mm. wide when flat, the upper surface of the blade scabrous, bearing a tight dense mat of tiny white hairs, the lower surface scabrous; upper throat bearing a dense mat of short appressed hairs; collar scaberulous.

Panicle erect, narrow, the branches appressed, interrupted below, olive to grayish green, 20-34 cm. long, 1-2 cm. wide; axis scabrous; lower primary branches 4-5 cm. long, the secondary branches to 1.5 cm. long, tertiary branches lacking; pedicels much shorter than the spikelets, scabrous; spikelets 2.5-3.5 (averaging 3) mm. long; glumes rounded at the tips, mostly longer than the floret, the second a little longer than the first, hyaline, nerveless or indistinctly 1-nerved, lightly pubescent, awnless; lemmas 2.9-3.1 mm. long, acute at the tip, indistinctly 3-nerved, awns 0.5-3.5 mm. long, the lower two-thirds lightly villous, the upper one-third scabrous, the basal margins more densely villous; palea a little shorter than the lemma, pubescent on the lower two-thirds between the keels.

Holotype in the U.S. National Herbarium, no. 2209360, collected in shrub zones of lower canyon where common, Sierra de la Madera, Cañon del Agua, Municipio de Cuatro Ciénegas, Sept. 10, 1939, by C. H. Muller (no. 3264).

DISTRIBUTION: Known only from five collections made in canyons of Coahuila and Nuevo León, northern Mexico.

MEXICO: COAHUILA: La Cueva, Corte Blanco fork of Charretera Canyon, Johnston 9072 (GH, MEXU, MO). Cañon del Agua, Municipio de Cuatro Ciénegas, Muller 3264 (US holotype, GH, UC, isotypes). San Lorenzo Canyon, 6 mi. SE. of Saltillo, Palmer 401, in 1904 (F, GH, MO, NY, UC, US). NUEVO LEÓN: Between La Soledad and Escondida, Beetle M-406 (UC). 14 mi. W. of Doctor Arroyo, Shreve & Tinkham 9651 (GH).

*Muhlenbergia pubigluma* is distinguished by the broadly decurrent ligule, puberulent glumes and lightly villous lemmas. In the original description, the author related this species to *M. pubescens* (H.B.K.) Hitchc. (= *M. distans* Swallen, according to the present treatment). That species, however, does not have the narrow, firm, pale green, somewhat arcuate blades or broadly decurrent, firm at the base, ligules, characters that indicate a closer relationship to *M. lindheimeri* and *M. involuta*.

**7. *Muhlenbergia macrotis* (Piper) Hitchc. N. Amer. Fl. 17(6):463. 1935.**

*Muehlenbergia distichophylla* var. *mutica* Scribn. ex Urbina. Cat. Pl. Mex. 393. 1897. Nomen nudum. Of the two collections listed, Pringle 2360 = *M. macrotis*, and Pringle 5577 = *M. versicolor*.

*Epicampes macrotis* Piper. Proc. Biol. Soc. Washington 18:144. 1905. Basis of *Muhlenbergia macrotis* (Piper) Hitchc. (Rose 3528, Zacatecas, Mexico.)

*Epicampes minutiflora* Mez. Repert. Sp. Nov. Fedde 17:212. 1921. Basis of *Muhlenbergia meziana* Hitchc. 1935, not of *M. minutiflora* (Michx.) Hitchc. 1896. (Langlassé 750, El Canizal, "Michoacán et Guerrero," Mexico.)

*Muhlenbergia meziana* Hitchc. N. Amer. Fl. 17(6):461. 1935. Based on *Epicampes minutiflora* Mez.

Strongly caespitose perennial; culms narrow to very thick, glabrous to scaberulous,  $1\frac{1}{4}$ – $2\frac{1}{4}$  meters tall; nodes 3–5, glabrous, or sometimes pubescent below the nodes; basal sheaths compressed-keeled, glabrous, the old basal sheaths brown, persistent, becoming frayed; ligule membranous throughout, lacerate from the base or near the base, 3–15 (usually 5–8) mm. long; sheath auricles 1–10 (usually about 3) cm. long, the auricles of the sheaths higher on the culm often longer than those of the lower ones, straight or strongly twisted; blades of the culm very long, as much as 95 cm., becoming fine and threadlike at the tip, mostly folded, 2–6 mm. wide when flat, the blades at the base narrower than the sheaths, edges of the blades saw-toothed, the upper surface scaberulous to scabrous (mostly scabrous), the lower surface scabrous; upper throat scabrous; collar glabrous.

Panicle erect, columnar, the branches numerous, appressed, generally interrupted below, light green to whitish green, 25–65 cm. long, 1.5–6 cm. wide; axis scaberulous to scabrous (mostly scabrous), the primary branches 5–12 cm. long, the secondary branches to 4.5 cm. long and spikelet-bearing to the base, the tertiary branches to 1 cm. in length; pedicels 0.3–1 mm. long, shorter than the spikelets, scabrous; spikelets 2–3 mm. long, rarely as short as 1.5 mm. or longer than 3 mm.; glumes equal, usually longer than the floret, glabrous to scaberulous (mostly scaberulous), rounded at the tips, awnless, hyaline, white or whitish green, nerveless or obscurely 1-nerved; lemmas 1.8–2.5 mm. long, acutish, indistinctly 3-nerved, awnless or rarely cuspidate, completely glabrous, even on the lower margins, at most the surface punctate; palea equaling the lemma or rarely a little longer, glabrous.

Holotype in the U.S. National Herbarium, no. 302505, collected in the Sierra Madre, Zacatecas, Mexico, Aug. 17, 1897, by J. N. Rose (no. 3528).

DISTRIBUTION: Moist shaded canyon slopes, ravines, banks above streambeds, moist ditches, and wooded hillsides, at elevations of 6,000–7,000 feet. Common from Sinaloa and Durango, south to Guerrero and Oaxaca, Mexico. A single specimen has been collected in Guatemala.

MEXICO: SINALOA: Mazatlán, Ortega 5075 (US). DURANGO: Sierra Tres Picos, Gentry 5312 (ARIZ, DS, MO, NY); Harvey 5312 (GH). 23 mi. SW. of

Buenos Aires, *Reeder & Reeder* 4218 (US, YU). ZACATECAS: Sierra Madre, *Rose* 3528 (US holotype). NAYARIT: La Barranca, *Jones* 23445 (CAS, MO, NY, POM). SINALOA-NAYARIT: San Ignacio, San Javier, *Ortega* 1204 (MEXU). JALISCO: Tepatitlán-Guadalajara, *Hernández, Ruppert, & Guevara* X-2669 (US). SW. Autlán, *Hernández* X. 4641 (CHAP). La Barranca, Guadalajara, *Jones* 27656 (POM), 27677 (DS, MO, NY). Orendain, *Jones* 2767 (UC). Nevado de Colima, *McVaugh* 10170 (MICH). Sierra del Tigre, 3 mi. S. of Mazamitla, *McVaugh* 13085 (SMU, US). 1-2 mi. E. of Tapalpa, *McVaugh* 20519 (MICH, US). Real Alto, Trail to Tranquillas, *Mexia* 1713 (CAS, DS, F, GH, MICH, MO, NY, UC, US). Guadalajara, *Pringle* 2360 (ARIZ, CAS, F, GH, MICH, NY, TAES, UC, US), 2356 (F, GH, MO, NY, UC, US); *Soderstrom* 613 (US), 614 (US). GUANAJUATO: *Duges*, in 1897 (F). Ca. 8 mi. W. of San Felipe, Cerro del Fraile, *Sohns* 452 (MICH, MO, US). PUEBLA: Mexique-Acatzingo, District de Tepeaca, *Nicolas*, July 7, 1909 (F). DISTRITO FEDERAL: C. de Progreso, *Matuda* 19676 (MICH). MICHOACÁN: Quinceo, *Arsène* 3218 (GH, ILL, MO, NY, US). Loma Santa María, *Arsène* 8581 (MO, US). Cerro San Miguel, *Arsène* 9937 (MO, US). Atzimba National Park, *Beetle* M-128 (US). Zacapu, *Hernández, Ruppert, & Guevara* X-2822 (US). 18 mi. E. of Morelia, *King & Soderstrom* 5011 (MEXU, MICH, SMU, TEX, US). 8-10 mi. NW. of C. Hidalgo, *McVaugh* 9925 (MICH, US). Pátzcuaro, *Seler* 1227 (GH, US). Quiroga, *Soderstrom* 552 (US), 555 (US); *Sohns* 806 (US). GUERRERO: Petlaacala, *Mexia* 9098 (CAS, F, GH, MO, NY, UC, US). Between Ayusinapa and Petatlán, *Nelson* 2122 (US). "MICHOACÁN ET GUERRERO": El Canizal, *Langlassé* 750 (GH, US, isotypes of *M. meiziana*). OAXACA: Río Grande (N. of Niltepec) to Finca "La Gloria," *Hernández & Sharp* X-1257 (US).

GUATEMALA: HUEHUETENANGO: 10 km. W. of Aguacatán, *Williams, Molina, & Williams* 21844 (US).

*Muhlenbergia macrotis* is distinguished by the prominent sheath auricles that attain a length of 1 cm. or more (as much as 10 cm. in *Hernández* X-4641!) and in the mostly glabrous and awnless or cuspidate lemmas. It is closely allied to *M. distichophylla* which has long auricles, but the lemmas bear a tiny tuft of hairs toward the base of the margins and are usually long-awned. The culms and panicles of *M. macrotis* are usually thicker and more robust than in *M. distichophylla*. Comparison may also be made with *M. robusta*, but that species has only rudimentary sheath auricles and the lemmas, although mostly glabrous, sometimes have sparse short hairs at the base.

*Muhlenbergia macrotis* was originally described by Piper in 1905 as an *Epicampes* from a specimen collected by Rose in Zacatecas, Mexico, in 1897. It was known only from the type collection. Hitchcock transferred *E. macrotis* to *Muhlenbergia* in 1935, at the same time he transferred *E. minutiflorus* to the genus naming the latter *M. meiziana*.

*Muhlenbergia meiziana* Hitchc. is considered as synonymous with *M. macrotis* in the present treatment. The original description of the former characterizes a specimen with very long auricles (to 45 mm.

in length), flat blades to 4 mm. in width, a dense panicle, and spikelets 2.5–2.75 mm. long.

The collection listed by Mez in his description of *Epicampes minutiflorus* is "E. Langlassé, bei El Canizal, Michoacán (Mexico)," without collection number. The specimen in the U.S. National Herbarium marked as the type is E. Langlassé, no. 750, El Canizal, Michoacán. This specimen, however, does not agree in all respects with the original description, for the auricles are less than 1 cm. long and the spikelets are 2–2.5 (averaging 2) mm. long. This leaves some doubt as to the collection Mez had in mind when he described *E. minutiflorus*. Nevertheless, the completely glabrous lemmas, the white, almost translucent glumes, and relatively long auricles place it with other specimens of *M. meiziana*. The type appears, therefore, to be an aberrant representative of the species.

The holotype of *M. macrotis* agrees with *M. meiziana*, with the exceptions that the spikelets are often a little longer and the florets exceed the glumes in length. The glumes, however, are 2–2.5 mm. long, rounded, almost translucent, and nerveless, like those of *M. meiziana* specimens. Many of the spikelets in the panicle of the holotype of *M. macrotis* are diseased. I have noticed that in diseased panicles of other *Muhlenbergia* species the florets often become longer than normal, exceeding the glumes where the florets were normally contained within them. This perhaps explains why many of the florets are so long in the spikelets of the type specimen of *M. macrotis* which, in other respects, is similar to specimens of *M. meiziana*. Specimens similar in general to the type collection of *Muhlenbergia meiziana* occur in the same geographic region where the type of *M. macrotis* was found, and therefore it seems likely that the holotype of *M. macrotis* was only a diseased specimen of the species later described as *M. meiziana*. The following list, a comparison of the major characters of specimens of *M. meiziana* and the holotype of *M. macrotis*, illustrates the similarity.

	<i>M. meiziana</i>	<i>M. macrotis</i>
height	125–230 cm.	134 cm.
culm surface	mostly glabrous	glabrous
node surface	glabrous to slightly pubescent	glabrous
sheath surface	glabrous	glabrous
upper throat	scabrous	scabrous
collar	glabrous to scaberulous	glabrous
blade width	2–6 (mostly 3–4) mm.	4–5 mm.
upper surface of blade	scaberulous to scabrous (mostly scabrous)	scaberulous
lower surface of blade	scabrous	scabrous
ligule length	3–13.5 (usually 5–8) mm.	11 mm.

	<i>M. meztana</i>	<i>M. macrotis</i>
auricle length	1-7 (usually about 3) cm.	to 3.5 and 4 cm.
panicle length	26-65 cm.	38 cm.
panicle width	1.5-6 cm.	1.5 cm.
panicle color	light green or whitish green	greenish tan (old panicle only)
axis surface	scaberulous to scabrous	scabrous
length of panicle branches:		
primary	5-11.8 cm.	7 cm.
secondary	1-4.5 cm.	2 cm.
tertiary	to ca. 1 cm.	lacking
spikelet length	2-3 mm.	2.5-3.6 mm.
glumes	equal, sometimes less than floret	equal, usually less than floret
glume length	2-3 mm.	2-2.5 mm.
glume surface	glabrous, nerveless or rarely obscurely 1-nerved	glabrous, nerveless
lemma length	1.8-2.3 mm.	ca. 3.2 mm.
lemma surface	glabrous	glabrous
awn length	usually lacking, lemma rarely cuspidate	lacking

8. *Muhlenbergia distichophylla* (J. S. Presl) Kunth. Rev. Gram. Supp. xvi. 1830.

*Podosaemum distichophyllum* J. S. Presl. Rel. Haenk. I: 231. 1830. (Mexico: without precise locality, *Haenke* 173).

*Epicampes stricta* var. *distichophylla* (J. S. Presl) Jones, Contr. West. Bot. 14:6. 1912. Based on *Podosaemum distichophyllum* J. S. Presl.

*Muhlenbergia angustifolia* Swallen. N. Amer. Fl. 17(6): 457. 1935. (Mexico: Jalisco, *Pringle* 2346).

Caespitose perennial; culms stout, glabrous, 1-1.75 m. tall; nodes 4, glabrous or somewhat puberulent beneath; basal sheaths compressed-keeled, mostly glabrous, sometimes scaberulous; ligule membranous throughout, entire at the base and lacerate above, or finely lacerate throughout, 4-8 mm. long, longer on the innovations; sheath auricles 4-8 (usually 6-8) mm. long, the auricles of the upper culm sheaths longer than those of the lower; blades of the culm to 90 cm. long, long-attenuate, becoming threadlike at the tip, flat or folded, 1.5-4.5 (mostly 2-2.5) mm. wide when unfolded, narrow in comparison with the sheaths from which they depart, the upper surface of the blade scaberulous to scabrous, lower surface scabrous, the edges of the blades minutely saw-toothed; upper throat scabrous; collar glabrous to scabrous (mostly scaberulous).

Panicle erect, somewhat lax at the tip, light green to tan (rarely purplish), the branches spreading widely, 35-60 cm. long, to 5 cm. or more in width; axis scaberulous to scabrous (mostly scabrous), the lower primary branches 6-13 cm. long, the secondary branches 1-6 cm. long, the tertiary branches 0.5-2 cm. long; pedicles of the lateral

spikelets 0.2–0.8 mm. long, those of the terminal spikelets to 2 mm., glabrous to scaberulous (usually scaberulous); spikelets 1.5–2.5 (usually 1.7–2) mm. long; glumes longer than the floret, the first glume often a little longer than the second, glabrous to scaberulous, broadly acute, awnless, hyaline, nerveless; lemma 1.4–2.5 (usually 1.7–2) mm. long, glabrous throughout except for a tuft of short hairs at the base of the margins, rounded at the tip, 3-nerved, the middle nerve becoming purplish and thickened toward the tip, excurrent as an awn 4–16 mm. (usually 1 cm. or more) in length; palea equal to or slightly shorter than the lemma, glabrous.

Fragment of type in the U.S. National Herbarium, collected in Mexico, without precise locality, by Haenke (no. 173).

DISTRIBUTION: Rocky hills and exposed areas of oak woods, at elevations of 1,500–7,500 ft., from Jalisco, Mexico, southeastward into Guatemala. Apparently infrequent.

MEXICO: *Haenke* 173 (US fragment of type of *Podosaemum distichophyllum*, ex W). JALISCO: Barranca de Oblatos, *Hitchcock* 7335 (NY, US). SW. of La Resolana, road to La Huerta, *McVaugh* 21106 (MICH, US). Above (N. of) La Cuesta, road to Talpa de Allende, *McVaugh* 21224 (MICH, US), 21225 (MICH, US). Guadalajara, *Pringle* 2346 (GH, NY, UC, US, isotypes of *M. angustifolia*). MEXICO: Tejupilco, Temascaltepec, *Hinton* 2719 (GH, LL, NY, US). Luvianos, Temascaltepec, *Hinton* 5302 (ARIZ, NY, US). Amatepec, *Matuda* 29874 (US), 29875 (US). "MICHOCAN ET GUERRERO": Sierra Madre, *Langlassé* 607 (GH, US). Cerro Mamegal, *Langlassé* 674 (GH, US). GUERRERO: Carboneras-Filo Mayor, *Hinton* 9910 (MICH, US). Vallecitos, *Hinton* 11635 (ARIZ, LL, MO, NY, US). 15 mi. N. of Tierra Colorada, *Reeder & Reeder* 4159 (US, YU). CHIAPAS: Escuintla, *Matuda* 319 (MICH, US). Mt. Ovando, *Matuda* 322 (MICH, MO, US).

GUATEMALA: HUEHUETENANGO: E. of San Sebastián, *Standley* 81480 (US). Near crossing of Río San Juan Ixtán, E. of San Rafael Pétzal, *Standley* 83016 (US). W. of Huehuetenango, *Williams, Molina, & Williams* 22309 (US).

*Muhlenbergia distichophylla* is distinguished by long sheath auricles and awned lemmas that are glabrous except for a small tuft of hairs on the margins toward the base. It is apparently most closely allied to *M. macrotis*, also possessing long sheath auricles, but lemmas that are awnless and entirely glabrous. Moreover, it has a denser panicle than *M. distichophylla* and a more robust habit. Label data for *M. distichophylla* indicates flowering from the end of November through May; *M. macrotis* blooms earlier.

Although *M. angustifolia* Swallen was recognized in North American Flora (1935) and has been maintained as distinct in the U.S. National Herbarium, it is represented only by specimens of the original collection of 1889. Additional collections of *M. distichophylla* have been made since the description of *M. angustifolia*, and a critical comparison of all specimens with the holotype of the latter revealed that the characters that distinguish it are not of sufficient importance for specific

recognition. The following comparison of the two illustrates this point.

	<i>M. distichophylla</i> specimens	<i>M. angustifolia</i> holotype
height	135-173 cm.	111-139 cm.
culm surface	glabrous	glabrous
node surface	glabrous or puberulent below	glabrous to puberulent below
sheath surface	usually glabrous	glabrous
upper throat	scabrous	scaberulous or scabrous
collar	scaberulous to scabrous (rarely glabrous)	glabrous
blade width	1.5-4.5 mm.	1.5-2 mm.
blade length	37-91 cm.	48 cm.
upper surface of blade	scaberulous to scabrous	glabrous or scaberulous
lower surface of blade	scabrous	scaberulous to scabrous
ligule texture	membranous, lacerate	membranous, lacerate
ligule length	4-8 mm., sometimes more	6-14 mm.
auricle length	0.2-4.5 cm.	1.7-3 cm.
panicle length	30-58 cm.	30-48 cm.
panicle width	usually 3.5-5 cm.	2-2.5 cm.
axis surface	scaberulous to scabrous (mostly scabrous)	scabrous
panicle color	greenish tan	light green
panicle branches:		
primary, length	6-12 cm.	4-6.5 cm.
secondary, length	1.6 cm.	1.5 cm.
tertiary, length	0.2 cm.	lacking
spikelet length	1.5-2.5 mm.	2.2-2.5 mm.
glume surface	glabrous	glabrous
lemma length	1.4-2 mm.	2.1-2.3 mm.
lemma surface	glabrous except for hairs toward the base of the margins (in both)	
awn of lemma, length	4.5-16 mm.	8-9 mm.

**9. *Muhlenbergia versicolor* Swallen.** Contr. U.S. Nat. Herb. 29: 412. 1950.

*Muehlenbergia distichophylla* var. *mutica* Scribn. ex Urbina. Cat. Pl. Mex. 393. 1897. Nomen nudum. Of the two collections listed, *Pringle*, 2360 = *M. macrotis*, and *Pringle* 5577 = *M. versicolor*.

Caespitose perennial; culms glabrous or somewhat puberulent, 82-199 (mostly 100-150) cm. tall; nodes 3 or 4, glabrous or pubescent below; basal sheaths compressed, but not strongly keeled, the old sheaths brown and somewhat fibrillose; ligule membranous throughout, 5-22 (usually more than 10) mm. long, usually flanked on either side by auricles that become membranous and twisted above, the firm, brown base of such auricles usually 4-8 mm. long; blades of the middle of the culm shorter than those of the lower part, 12-27 cm. long, usually folded, 2-5 mm. wide when flat; upper surface of the blade scaberulous to scabrous, the lower surface scabrous (lower surface usually scabrous and the upper surface scaberulous); upper throat scaberulous to scabrous; collar glabrous to puberulent.

Panicle erect, narrow, the branches ascending, lead green to purplish green, 17–60 (usually 20–40) cm. long, 1.5–6 cm. wide; axis scaberulous to scabrous; primary branches 4–11.5 cm., secondary branches 1.5–3.5 cm. long, tertiary branches lacking or to 0.5 cm. long, when present; pedicels of the lateral spikelets 1–2.5 mm. long, those of the terminal spikelets relatively long, to 3–5 mm., the pedicels glabrous on the lower part, becoming scaberulous on the thickened part below the spikelet; spikelets 2.5–3.5 (usually 3 or more, rarely to 4) mm. long; glumes usually a little shorter than the floret, the second glume longer than the first, the tips erose (under high power) or awn-tipped, the awns to 1.2 mm. long, frequently only the second glume awned and the first acute, usually scaberulous (rarely glabrous), hyaline, nerveless or faintly 1-nerved; lemmas acute, 2.5–3.5 (mostly about 3) mm. long, 3-nerved, villous over the lower half or two-thirds of the back on and between the nerves, and more densely so on the margins, awn 17–30 mm. long, flexuous; callus of lemma long-pilose; palea equaling or a little longer than the lemma, moderately to densely villous between and, sometimes, on the keels.

Holotype in the U.S. National Herbarium, no. 1961991, collected about 170 kilometers north of Oaxaca City, Oaxaca, Mexico, December 13, 1945, by Efraím Hernández Xolocotzi and J. A. Jenkins (no. X-810).

**DISTRIBUTION:** Rocky mountainsides and ledges, and slopes of barrancas. Rather uncommon, ranging in Mexico from Michoacán and the state of Mexico southeastward to Honduras.

**MEXICO:** GUANAJUATO: NE. of Cd. Guanajuato, *Reeder & Reeder* 3095 (YU. PUEBLA: Zapotitlán de las Salinas, SE. of Tehuacán, *Hernández*, Oct. 27, 1960 (CHAP, US). Zapotitlán, near Tehuacán, *Ross*, Oct. 1906 (US). Between Apala and the top of Cerro Chichiltepec, *Smith, Peterson, & Tejeda* 3879 (US). MORELOS: Sierra de Ocuila rumbo Mexicapa, *Lyonnet* 2873 (US). Valle de Tepcite, *Lyonnet & Elcoro* 1838 (US). VERACRUZ: Maltrata, *Kerber* 226 (US). MEXICO: Rincón, Temascaltepec, *Hinton* 2081 (MO, NY, US). Socabón, Temascaltepec, *Hinton* 2324 (GH, LL, MICH, NY, US). Tejupilco, Temascaltepec, *Hinton* 2719 (GH). Sultepec, *Matuda* 26615 (US). Ixtaccihuatl, *Purpus* 1611 (ILL, MO, US). Salto de Agua, *Purpus* 1629 (US). 4 mi. S. of Tenancingo, *Reeder & Reeder* 4168 (US, YU). DISTRITO FEDERAL: Lomas de Tacubaya, *Gándara*, in 1938 (US). Villa Guerrero, *Tateoka* 1119 (US). MICHOACÁN: Lomas de la Huerta, *Arsène* 2465 (ILL, MO), 2465½ (F, US), 2825 (MO, NY, US), 5438 (NY, US), 5446 (ILL, MO, NY, UC, US), 5851 (MO, US), May 30, 1909 (US). Punguato, *Arsène* 2674 (US). Cerros de San Miguel, *Arsène* 5304 (NY, US), 6803 (US). Loma Santa Maria, *Arsène* 8585 (MO, US). Along road from Taitzio-Tiquicheo-Huetamo-Altamira, *Sohns* 880 (US). GUERRERO: Teotepec, Mina, *Hinton* 14803 (ARIZ, ILL, LL, NY, TEX, US). OAXACA: Ca. 170 km. N. of Oaxaca City, *Hernández & Jenkins* X-810 (US holotype). Ixtlan de Juárez, *Krueger & Gillespie* 25 (CAS, LL, MO). Mina de Dolores, near Talea, *Liebmann* 673 (US fragment), 984, in 1841–43 (US). Mecatlán, S. Andrés, *Liebmann* 736 (US fragment). Dolores, *Liebmann* 737 (MO, US). Reyes, *Nelson* 1780 (US).

(?)Sierra de San Felipe, *Pringle* 5576 (GH, MEXU, US), 5577 (US); (?)*Smith* 927 (in part) (MO, NY, US). Temascalapa to San Ildefonso de Villa Alta proper, *Santos* 3530 (NY, US). 45 mi. N. of Oaxaca, *Soderstrom* 417 (US). CHIAPAS: Between San Cristóbal Las Casas and San Gregorio, *Hernández & Sharp* 534 (US). Barranca Honda, Siltepec, *Matuda* 4124 (GH, LL, MICH, NY).

GUATEMALA: HUEHUETENANGO: Aguacatán road, 10 km. E. of Huehuetenango, *Standley* 82073 (F, US). Between San Sebastián H. and large peñasco above town, *Steyermark* 50504 (F, US). Barranco "Palo Negro" about 10 km. W. of Aguacatán, *Williams, Molina, & Williams* 21850 (US). SAN MARCOS: San Marcos, *Lehmann* 1578 (US fragment, ex G). SOLOLÁ: Lago Atitlán, *de Koninck* 146 (US).

HONDURAS: MORAZÁN: Suyapa, *Swallen* 11277 (US).

*Muhlenbergia versicolor* is distinguished by the long ligule and usually short sheath auricles, the narrow, densely flowered dark green or purplish-green panicles, the spikelets over 3 mm. long, the lemmas long-awned and villous over most of the surface on and between the nerves. It appears to be most closely related to *M. emersleyi*, and most herbarium specimens have been determined as that species. Although the two are similar in having long ligules and pubescence on the long-awned lemmas, they are easily separated. In *M. versicolor* almost the whole lemma is sparsely to densely villous on and between the nerves; in *M. emersleyi* the pubescence is confined to the midnerve and margins. The sheaths in *M. versicolor* are characterized usually by short auricles but these are lacking in *M. emersleyi*. The spikelet is dark green or purplish green in *M. versicolor*, but lighter and most often purplish or tan in *M. emersleyi*.

Specimens of *Epicampes* (*Smith* 927; *Pringle* 5576, 5577) collected on the summit ledges of Cerro de San Felipe (above the city of Oaxaca, at an elevation of about 10,000 ft.) are without doubt allied to *M. versicolor*. The base of the plant, the lead-green panicles, long spikelets, and villous lemmas are characteristics of *M. versicolor*. These specimens, however, exhibit some fundamental differences from the typical plants: The glumes are blunt rather than acute or dentate and awn-tipped as in *M. versicolor*; the auricles of the sheaths are very long, 1-3.5 cm., those of *M. versicolor* being less than 1 cm. long; the panicles are narrower, shorter, and the branches more appressed. In one specimen the lemmas are awnless, but long-awned in others, as in typical *M. versicolor*. When more information becomes available from additional field studies on Cerro de San Felipe, this curious group of specimens may prove to represent a distinct species.

**10. *Muhlenbergia gigantea*** (Fourn.) Hitchc. N. Amer. Fl. 17(6):461. 1935.

*Epicampes expansa* Fourn. Mex. Pl. 2:88. 1886. (*Botteri* 104 in part [*Botteri & Sumichrast* 104], Orizaba [Veracruz], Mexico. *Botteri* 104 in part is also cited by Fournier under *Epicampes mutica* Rupr. ex Fourn.)

- Epicampes bourgaei* Fourn. Mex. Pl. 2:88. 1886. (*Bourgeau* 2973, Escamela pr. Orizaba [Veracruz], Mexico.)
- Epicampes bourgaei* var. *mutica* Fourn. Mex. Pl. 2:88. 1886. (*Liebmann* 676, 678 Mirador [Veracruz], Mexico, and *Liebmann* 677, Tlaltengo [Veracruz], cited.)
- Epicampes laxiuscula* Fourn. Mex. Pl. 2:88. 1886. (*Botteri* 155, Orizaba [Veracruz], Mexico.)
- Epicampes gigantea* Fourn. Mex. Pl. 2:88. 1886. Basis of *Muhlenbergia gigantea* (Fourn.) Hitchc. (*Bourgeau* 3137, Río Blanco near Orizaba [Veracruz], Mexico.)
- Epicampes ehrenbergii* Mez. Repert. Sp. Nov. Fedde 17:212. 1921. (Type from Cuesta de Pinolco [Hidalgo?], Mexico.) This species was questionably referred to *Muhlenbergia robusta* (Fourn.) Hitchc. in N. Amer. Fl. 17(6):462. Although the type has not been seen, the description is that of *M. gigantea* for it states, in part: "ligulis magnis . . ." (the ligule of *M. robusta* is very short) and "Inflorescentia myriantha, bene thyrsoides, 3 pinnatim paniculata [sic] . . ." (which must refer to the typically large and widely spreading panicle of *M. gigantea*).
- Muhlenbergia alta* Hitchc. N. Amer. Fl. 17(6):461. 1935. (*Hitchcock* 7180, Jalisco, Mexico.)
- Muhlenbergia magna* Hitchc. N. Amer. Fl. 17(6):460. 1935. (*Pringle* 3335, Jalisco, Mexico.)

Strongly caespitose perennial; culms stout and thick, robust, glabrous or somewhat scaberulous, 130–300 cm. (mostly 1.5–2.5 m.) tall; nodes 3, glabrous below; basal sheaths strongly compressed-keeled, glabrous or somewhat scaberulous; ligule membranous throughout, generally undivided at the base, becoming lacerate above, 1–3.5 (usually 1–1.5) cm. long; sheath auricles lacking, rarely rudimentary ones present; blades of the culm 35–115 (usually more than 65) cm. long, flat, the edges saw-toothed, 2.5–12 (usually 5–8) mm. wide, upper surface of the blade usually scaberulous, the lower surface scaberulous to scabrous, scabrous-ciliate on the margins near the ligule; upper throat scaberulous to scabrous; collar glabrous (sometimes scaberulous).

Panicle very large and open, the branches weak and lax and somewhat drooping or more rigidly flexuous, purplish or purplish brown, 45–110 (usually 50–100) cm. long, 20–30 cm. or wider, the branches opening wide, long-naked below, the aggregates of spikelets borne on the tertiary and quaternary branches, the groups of branches borne distant from each other on the axis; primary branches 11–27 (usually 15–20) cm. long, the secondary branches 1.5–12 (usually 4–10) cm. long, the tertiary branches 0.5–5.5 (usually 1–4) cm. long, quaternary branches, when present, to 2.5 cm. long; pedicels shorter than the spikelets, usually glabrous (sometimes scaberulous); spikelets 1.4–2.5 (mostly 1.5–2.2) mm. long; glumes rounded or acutish at the tip, about equal, a little longer than the floret, glabrous or scaberulous, awnless, 1-nerved; lemmas rounded or acutish at the tip, 1.3–2.2 (mostly 1.6–2)

mm. long, glabrous, 3-nerved, awnless (the midnerve sometimes becoming darker and thickened toward the tip and extending beyond it as a tiny point); palea equaling the lemma, glabrous.

Fragment of type in the U.S. National Herbarium, collected in region d'Orizaba, Río Blanco, Veracruz, Mexico, Sept. 30, 1866, by Bourgeau (no. 3137).

DISTRIBUTION: Open rocky slopes and barrancas, at elevations of 2,000–7,500 ft., most commonly found at ca. 3,500–5,000 ft. Known only from Mexico, ranging from Sinaloa and Durango southeastward to Chiapas. Apparently infrequent.

MEXICO: SINALOA: E. of Santa Lucía, *Reeder & Reeder* 2488 (YU). DURANGO: W. of La Ciudad (Mazatlán-Durango road), *Reeder & Reeder* 2522 (YU). JALISCO: SW. Autlán, *Hernández* 4643 (CHAP). Zapotlán, *Hitchcock* 7180 (US, holotype of *M. alta*), 7247 (ILL, US). Puente San Pedro, SW. of Tecalitlán *McVaugh* 18096 (MICH). Guadalajara, *Pringle* 3335 (F, GH, NY, UC, US, isotypes of *M. magna*), 11738 (CAS, F, GH, MO, US). Sierra Madre, W. of Bolaños, *Rose* 3002 (US). Guadalajara, *Soderstrom* 607 (US, YU). VERACRUZ: Orizaba, *Botteri* 103 (US fragment, ex CGE), 104 (US fragment of type of *E. expansa*, ex CGE), 159 (US fragment, ex CGE). Escamela, region d'Orizaba, *Bourgeau* 2973 (US fragment of type of *E. bourgaei*, ex P). Orizaba, Río Blanco, *Bourgeau* 3137 (US fragment of type of *E. gigantea*, ex LE, P). Orizaba, Cerro del Borrego, "Curso de ecología vegetal," Dec. 14, 1959 (CHAP). Mango de Dn. Bartolo carretera-Veracruz-Córdoba, *Hernández, Tapia, & Malthus* SE-1482 (CHAP). Mirador, *Liebmann* 676 (US), 678 (US). Orizaba, "C. Mohr herbarium" (US). Orizaba, *Müller*, in 1850 (NY). Veracruz a 22 km. de Catemaco sobre la carretera Acayucan, *Tapia & Martínez* SE-644 (CHAP). Loc.? von *Rozynski*, in 1932 (1933?) (F, NY, YU). MEXICO: Cajones, Temascaltepec, *Hinton* 2386 (MO, NY, US). Vigas, Temascaltepec, *Hinton* 2626 (MO, NY, US). MICHOACÁN: Pto. Cruces, Coalcoman, *Hinton* 12471 (ARIZ, GH, LL, MO, NY, TEX, US). 22 km. S. of Uruapan, *King & Soderstrom* 4860 (MEXU, MICH, SMU, TEX, US). Between Charapengo and El Guaco on road from Uruapan to Apatzingán, *Moore, Hernández & Porras* 5750 (UC, US). GUERRERO: Machón, Mina, *Hinton* 9635 (MO, NY, US). 13 mi. N. of Tierra Colorada, *Reeder & Reeder* 4157 (US, YU). OAXACA: Cerro de San Felipe, *Conzatti* 710 (GH), *Conzatti* 2534 (US). Tepenixtlahuaca, distrito de Tuquila, *Conzatti* 4376 (GH, US). Reyes, *Nelson* 1779 (GH, US). Temascalapa to San Ildefonso de Villa Alta, district of Villa Alta, *Santos* 3531 (US). CHIAPAS: between San Geronimo and El Pozo via Abasolo and El Retiro, *Hernández & Sharp* X-597 (US). Tuxtla Gutiérrez, *Tateoka* 1103 (US).

*Muhlenbergia gigantea* is distinguished by its large size, robust culms, long ligule, large, wide-spreading panicles, and relatively small glabrous spikelets. It is most closely related to *M. mutica* and the type specimens of both are from Orizaba, Veracruz, Mexico. The spikelets differ in the ratio of glume length to floret length: In *M. gigantea* the glumes are about equal to the floret; in *M. mutica* the glumes exceed the floret by several millimeters. In the latter species

the glumes are very acute, but more rounded or acutish in the former. This is possibly a variation within the same species, for the terminal spikelets of *M. gigantea* rarely have elongated glumes extending beyond the floret for several millimeters. An example is found in the type material of *M. gigantea* (Bourgeau 3137). The spikelets average 2 mm. in length, but in one case the terminal spikelet is 2.5 mm., enclosing a 1.5 mm. floret. As relatively few collections of *M. mutica* have been made, I do not feel safe in generalizing on the variability of the species at this time, and for this reason am not combining them. Additional field work, particularly in the region of Orizaba, Veracruz, will be necessary before this problem can be solved.

Herbarium specimens of *M. robusta* are often confused with *M. gigantea*. When only a panicle is present, the wide-spreading habit is often not obvious in dried condition. If vegetative parts are present, the short ligule and rudimentary sheath auricles of *M. robusta* readily separate it from *M. gigantea*.

Hitchcock (1935) described two new species from Jalisco, Mexico: *Muhlenbergia magna* (Pringle 3335) and *M. alta* (Hitchcock 7180). These specimens, like *M. gigantea*, are large robust plants with long lacerate ligules, wide-spreading panicles, and glabrous spikelets. *Muhlenbergia alta* is described as differing from *M. gigantea* in its smaller spikelets, 1.5 mm., as opposed to 2–2.5 mm. A study of the holotype of *M. alta* reveals that the spikelets actually range from 1.5–2 mm. in length but such variability also occurs in specimens referred to *M. gigantea*! The holotype of *M. magna* exhibits no basic differences from *M. gigantea* except for the more rigid and erect panicle branches. Color of the panicle is the only character used in the key to separate the two species (purplish in *M. gigantea*, brownish in *M. magna*). Many of the specimens available for study could not be placed satisfactorily on the basis of erectness versus laxness of panicle branches or on the color of the inflorescence. A striking example of color difference was found in specimens collected in Durango, Mexico (*J. & C. Reeder* 2522, yellowish brown) and Sinaloa, Mexico (*J. & C. Reeder* 2488, dark purple). Both plants are similar except for color. The label of the former reads: "On a steep rocky slope. Both yellow and purple forms here."

Within limits, characters such as spikelet size and panicle color and habit are variable in species of *Epicampes* and are not of specific magnitude. As *M. magna* and *M. alta* appear to represent nothing more than normal variation within *M. gigantea*, they are here combined. The following comparison of characters of these three supposed species illustrates their similarity:

	<i>M. gigantea</i> specimens	<i>M. alta</i> holotype	<i>M. magna</i> holotype
height	160-300 cm.	193 cm.	172 cm.
culm surface	glabrous	glabrous	glabrous
node surface	glabrous	glabrous	glabrous
basal sheaths	glabrous, compressed-keeled	glabrous compressed-keeled	glabrous compressed-keeled
upper throat	scaberulous to scabrous	scaberulous	scaberulous
collar	mostly glabrous (sometimes scaberulous)	glabrous	glabrous
blade width	4-12 (usually 7-9) mm.	6-9 mm.	3.5 (in other specimens 2.5-7) mm.
upper surface of blade	glabrous to scaberulous (mostly scaberulous)	scaberulous	glabrous to scaberulous
ligule texture	membranous, becoming lacerate	membranous, becoming lacerate	membranous, lacerate
ligule length	5-35 mm. (usually 1 cm. or more)	6 mm.	ca. 10 mm.
sheath auricles	lacking	lacking	lacking
panicle length	45-110 cm.	100 cm.	46 cm.
panicle width	20-35 cm. or more, widely spreading	over 30 cm.	25 cm.
axis surface	scaberulous	scaberulous	glabrous to scaberulous
pedicel length	0.2-0.8 mm., less than spikelet	less than spikelet	0.4-0.7 mm., less than spikelet
pedicel surface	glabrous to scaberulous	glabrous	scaberulous
panicle color	purplish (sometimes brownish)	dark purple	brownish
panicle branches:			
primary	12-27 cm.	25 cm.	14 cm.
secondary	4-12 cm.	11 cm.	5.5 cm.
tertiary	1-5.5 cm.	2 cm.	1.5 cm.
quaternary	to 2.5 cm.	—	—
glume 1st/2nd	about equal	equal	equal
glume surface	glabrous to scaberulous	scaberulous	glabrous
spikelet length	1.4-2.5 mm.	1.5-2 mm.	1.7-2 mm.
lemma length	1.3-2.2 mm.	1.3 mm.	1.6 mm.
lemma surface	glabrous	glabrous	glabrous
awn length of lemma	awnless or extending from mid-nerve as a tiny point	awnless	awnless or extending from mid-nerve as a tiny point

11. *Muhlenbergia mutica* (Rupr. ex Fourn.) Hitchc. N. Amer. Fl. 17(6):459. 1935.

*Epicampes mutica* Ruprecht. Bull. Acad. Roy. Sci. Bruxelles, Belg. IX(2): 230. 1842. Nomen nudum. (*Galeotti* 5797, savanes de Mirador, Zacuapan, et Cantaranas près du Puente Nacional, Veracruz, Mexico.)

*Epicampes mutica* Rupr. ex Fourn. Mex. Pl. 2:87. 1886.

Strongly caespitose, robust perennial; culms stout, thick, glabrous, 2 meters or more tall; nodes 3, glabrous below; basal sheaths strongly compressed-keeled, glabrous; ligule membranous, undivided at the base, lacerate above, about 1 cm. long; sheath auricles lacking; blades of the culm 35 cm. long (in specimen examined), 4–5 mm. wide, the upper and lower surfaces of the blades scaberulous to scabrous; upper throat scaberulous; collar glabrous.

Panicle very large and open, the branches weak and lax, brownish or purplish brown, about 1 m. long and 30 cm. or wider; the primary branches as much as 30 cm. long, the secondary branches 6–12 cm. long, the tertiary branches 1.5–2 cm. long, quaternary branches lacking; axis scaberulous; pedicels shorter than the spikelet, those of the terminal spikelets longer than those of the lateral ones, scaberulous, becoming more scabrous just beneath the spikelet; spikelets 2.1–3.1 (mostly 2.5–2.8) mm. long; glumes about equal, much longer than the floret, scaberulous, acute, awnless, nerveless or indistinctly 1-nerved; lemmas 1.9–2.2 mm. long, glabrous, roundish at the tip, obscurely 3-nerved, awnless; palea a little shorter than the lemma, glabrous.

Fragment of type (ex P) in the U.S. National Herbarium, collected in "savanes de Mirador, Zacuapan, et Cantaranas près du Puente Nacional, Veracruz, México," by *Galeotti* (no. 5797). This specimen was cited by Ruprecht in 1842 without description. In his description of the species, Fournier (Mex. Pl. 2:87. 1886) cited this specimen, along with several other syntypes. *Galeotti* 5797 (P) is here designated as the lectotype.

DISTRIBUTION: Open rocky hillsides, at elevations of about 4,000–6,300 ft. Known only from Mexico in the states of Veracruz and Chiapas. Apparently rare.

MEXICO: VERACRUZ: Orizaba, *Botteri* 111 (US fragment, ex P), 729 (US fragment); *Botteri & Sumichrast* 104 (US fragment, ex P); *Hitchcock* 6348 (US). Mirador, Zacuapan, and Cantaranas, *Galeotti* 5797 (US fragment of lectotype, ex P). CHIAPAS: El Pozo to Oxchuc, *Hernández & Sharp* X-616 (US).

*Muhlenbergia mutica* is distinguished by its nonauriculate sheaths, large, wide-spreading panicle, and acute glumes much longer than the floret. It is most closely related to and doubtfully distinct from *M. gigantea*. The only character to separate the two is the length of the glumes in relation to the floret: In *M. gigantea* the glumes equal the floret, but in *M. mutica* the floret is exceeded by the glumes. Until

more material is available to study this character critically, I prefer not to combine the two species.

**12. *Muhlenbergia inaequalis* Soderstrom, sp. nov.**

Perennis caespitosa, culmis angustis erectis glabris vel scaberulis 50–70 cm. altis, nodis 3–4 glabris, vaginis inferioribus compressis et carinatis; ligula membranacea-firma, 0.5–1.5 mm. longa; laminis culmi angustis attenuatisque conduplicatis vel planis utrinque scaberulis, ca. 15–26 cm. longis, 2–3 mm. latis; collis glabris; panicula laxa, 25–30 cm. longa, usque ad 10 cm. lata, axe scaberulo, ramis primariis usque ad 8 cm. longis, secundariis usque ad 3 cm. longis, pedicellis scaberulis; spiculis 2.5–3.1 (plerumque 3) mm. longis, glumis acutis, inaequalibus, quam flosculo brevioribus, glabris, nervis 0 vel 1, indistinctis, lemmatibus acutis, 2.5–3(3) mm. longis, inferne brevi-pilosis, infra apicem aristatis, aristis 1–2 cm. longis.

A *M. emersleyi* Vasey ligulis brevioribus, glumis inaequalibus quam flosculo brevioribus, et lemmatibus inferne brevi-pilosis differt.

Caespitose perennial; culms erect, narrow, glabrous to scaberulous about  $\frac{1}{2}$ – $\frac{3}{4}$  m. tall; nodes 3–4, glabrous; basal sheaths compressed-keeled, glabrous to scaberulous; ligule a short, brown, firm membranous rim 0.5–1.5 mm. long; sheath auricles lacking; blades of the culm 15–26 cm. long, 2–3 mm. wide, flat or folded, the upper and lower surfaces scaberulous; upper throat scaberulous; collar glabrous.

Panicle pyramidal, lax above, the branches loosely ascending or spreading, purplish to purplish tan, 25–30 cm. long, 5–10 cm. wide; axis scaberulous; branches naked below, the lower primary branches of the panicle 5–8 cm. long, the secondary branches 2–3 cm. long; pedicels scaberulous, those of the lateral spikelets 0.5–1.8 (1–1.2) mm. long, those of the terminal spikelets longer; spikelets 2.5–3.1 (mostly 3) mm. long; glumes acute and some awn-tipped, unequal and shorter than the floret, the first about three-fourths as long as, and narrower than, the second, 1.6–2.5 (1.9) mm. long, the second 2–3 (2.4–2.5) mm. long, glabrous or scaberulous, nerveless or indistinctly 1-nerved; lemmas acute, 2.5–3(3) mm. long, short-pilose over the lower part and especially on the midnerve one-half to three-fourths its length, the lemma 3-nerved, the middle nerve excurrent from below the tip as a flexuous awn 1–2 cm. long; palea about equaling the lemma, short-pilose between the keels for one-half to three-fourths its length; anthers yellow, 1.1–1.2 mm. long.

Holotype in the U.S. National Herbarium, no. 2380325, collected in Quebrada de Durí, Estado de Trujillo, Venezuela, November 11, 1939, by A. Müller (no. 973). Isotypes at VEN.

DISTRIBUTION: Mountains to the south and southwest of Lago de Maracaibo, in Venezuela and Colombia.

VENEZUELA: TRUJILLO: Quebrada de Durí, Müller 973 (US holotype, VEN isotypes). MÉRIDA: Funck & Schlim 1017 (US fragment ex Herb. Boissier).

COLOMBIA: (?) Mutisi 1760-1808 (US fragment ex MA). NORTE DE SANTANDER: Ocaña Schlim 190 (US fragments ex Herb. Boissier and K).

*Muhlenbergia inaequalis* has the habit of *M. emersleyi* and possesses features of other species closely related to that species. The pyramidal panicle of long-awned spikelets looks much like typical *M. emersleyi* but the spikelets differ in important respects. The glumes are unequal and shorter than the floret, as in *M. scoparia*. The lemma is short-pilose over the lower part, on and between the nerves, somewhat as in *M. versicolor*. The ligule is a short, membranous rim as in *M. breviligula*. The short ligule, unequal glumes shorter than the lemma, and pubescence on and between the nerves of the lemma readily distinguish this species.

The collection of José Celestino Mutis, 1760-1808, is represented in the U.S. National Herbarium by only a panicle. Tentatively it is assigned to this species, as the glumes are unequal and shorter than the floret. However, the glumes are broader and more scabrous and less acute than those of the type and the panicle is more compact. The lemmas are short-pilose like those of the type, but shorter. The spikelets of the Schlim, and Funck and Schlim collections match closely those of the type specimen.

The name "inaequalis" refers to the very unequal glumes, an unusual feature in *Epicampes*.

**13. *Muhlenbergia scoparia* Vasey.** Contr. U.S. Nat. Herb. 1:283. 1893.

*Muhlenbergia carinata* Mez. Repert. Sp. Nov. Fedde 17:213. 1921. (Based on Pringle 2350, which is also the lectotype of *Muhlenbergia scoparia* Vasey [1893].)

Caespitose perennial; culms 55-88 (usually about 75) cm. tall, glabrous to scaberulous; nodes glabrous, covered by the sheaths; basal sheaths compressed-keeled, glabrous, becoming scaberulous toward the collar, the old sheaths and blades at the base curled, generally reddish-brown, fibrillose; ligule membranous throughout, usually hidden between the folded blade above, 8-16 (usually 10 or more) mm. long; sheath auricles lacking; blades of the culm 25-50 (mostly about 50) cm. long, flat or folded, 1-4.5 mm. wide when flat (mostly 2.5-3 mm. wide), the edges of the blade slightly saw-toothed, upper and lower surfaces of the blade scaberulous to scabrous; upper throat scabrous; collar glabrous to scaberulous (mostly scaberulous).

Panicle loose, nodding, the branches narrow, borne in groups at intervals along the axis, light green to purplish or brownish green, 22-30 cm. long, 1.5-5 cm. wide; axis scaberulous to very scabrous, strongly ribbed; primary branches 3.5-14 (mostly 4-9) cm. long,

naked below, the secondary branches 1–5.5 cm. long, tertiary branches lacking or, when present, 1–2 cm. long; pedicels of the lateral spikelets 0.6–1.2 mm. long, those of the terminal spikelets to 3 mm. long, scaberulous scabrous, especially below the spikelet; spikelets 1.5–2.2 (averaging 2) mm. long, excluding the awn tips; glumes very acute, first glume shorter than the second, awn-tipped (especially the second), the awn sometimes as much as 1 mm. long, glumes glabrous to scabrous, hyaline, nerveless or indistinctly 1-nerved; lemmas 1–2 (usually 1.5–2) mm. long, exceeding the glumes by a few mm., glabrous or scaberulous dorsally, the lower margins of the lemma conspicuously short-pilose, bearing short straight hairs to one-third the length of the lemma; lemmas acutish at the tip, 3-nerved, awned from just below the tip, the awn 6–15 mm. long; palea a little shorter than the lemma, glabrous.

Lectotype in the U.S. National Herbarium, no. 999089, collected on rocky hills near Guadalajara, Jalisco, Mexico, Nov. 10, 1889, by C. G. Pringle (no. 2350).

Vasey cited two specimens in the original description and remarked, "collected at Batopilas by Dr. Edward Palmer in 1885, and at Guadalajara (No. 2350) by C. G. Pringle in 1889." Of these syntypes, Hitchcock (1935b, p. 457) cited the latter as the type, thus effectively choosing it as lectotype. A note by Dr. Agnes Chase on the sheet of *Pringle* 2350 reads "second of the 2 specimens cited, but first is incomplete, description of habit, height, leaves, etc. must have been drawn from this."

**DISTRIBUTION:** Exposed rocky mountainsides and open areas in the oak zone, at elevations of 2,500–6,000 ft. Mexico, from Chihuahua, Sonora, and Sinaloa, south to Michoacán. Apparently infrequent.

**MEXICO:** *Palmer*, in 1886 (DS, ILL, NY). **SONORA:** Canyon Sapopa, Río Mayo, *Gentry* 1289 (GH, MO). Sierra Tecurahui, *Barclay & Arguelles* 19387 (US). **CHIHUAHUA:** Batopilas, *Palmer*, in 1885 (ARIZ, US, isosyntypes). **SINALOA:** Mesa Malqueson, Cerro Colorado, *Gentry* 5178 (ARIZ, F, GH, MO, NY, UC). Loc.? *Ortega* 1120 (F, US). 10 mi. E. of Santa Lucía (road from Villa Union to Durango), *Reeder & Reeder* 2451 (YU). **NAYARIT:** La Barranca, *Jones* 23446 (CAS, GH, MO, UC), Feb. 21, 1927 (NY, POM). Mina Esperanza, Rosa Morada, *Ortega* 6672 (CAS, US), Acaponeta, *Rose*, Aug. 2, 1897 (US). **JALISCO:** Km. 211 Guadalajara to Barra de Navidad *Aquilera* in 1958 (CHAP). 3 mi. N. of Pihaumo, *McVaugh & Koelz* 1394 (MICH, US). San Sebastián, trail to Monte Oscuro, Sierra Madre Mountains, *Mexia* 1644 (CAS, DS, F, GH, MICH, MO, NY, UC, US). Guadalajara, *Pringle* 2350 (F, LL, MEXU, US, isolectotypes). **MICHOACÁN:** Coalcomán, *Hinton* 12699 (ARIZ, GH, LL, MO, NY, TEX, US).

*Muhlenbergia scoparia* is distinguished by its unequal, awn-tipped glumes that are shorter than the floret. It is probably most closely related to *M. grandis*, sharing the features of reddish-brown basal

sheaths, short spikelets, and long-awned, comparatively glabrous lemmas with a short pilose callus. In *M. grandis*, however, the glumes are about equal, not awn-tipped, and the ligule is shorter, usually no more than 6 mm. Both species have a range farther west in Mexico than the majority of species of *Epicampes*, occurring in the states of Sinaloa, Nayarit, and Jalisco. *Muhlenbergia scoparia* also has a more extensive north-south range, from Chihuahua and Sonora to Michoacán.

14. *Muhlenbergia iridifolia* Soderstrom, sp. nov.

Perennis caespitosa, culmis erectis glabris  $1\frac{1}{4}$  m. altis, nodis 4 glabris, vaginis inferioribus forte compressis et carinatis; ligula membranacea-firma, 5-7 mm. longa; laminis culmi latis acutisque conduplicatis vel planis utrinque glabris, 30-70 cm. longis, 4-7 mm. latis; callis glabris; panícula supra laxa, 45 cm. longa, 3 cm. lata, axe glabro, ramis primariis 7-8 cm. longis, secundariis ca. 3 cm. longis, pedicellis glabris; spiculis 4-4.2 mm. longis, glumis angustis minute aristatis, quam flosculo paulo longioribus, glabris, nervis 0 vel 1, indistinctis, lemmatibus angustis, 4 mm. longis, 3-nervis, glabris, inferne brevipilosis, infra apicem aristatis, aristis 2-2.5 cm. longis.

Caespitose perennial; culms erect, glabrous, about  $1\frac{1}{4}$  m. tall; nodes 4, glabrous; basal sheaths strongly compressed-keeled, glabrous, spreading outward in a distinct flabellate fashion; ligule brown, firm-membranous, lacerate but rather blunt or truncate, conspicuous from side view, 5-7 mm. long; sheath auricles lacking; blades of the culm 30-70 cm. long, 4-7 mm. wide, the older blades folded but younger blades mostly flat, the upper and lower surfaces glabrous except for the scabrous, saw-toothed margins and midnerve on the undersurface; upper throat glabrous; collar glabrous.

Panicle lax above, the branches loosely ascending or spreading, purple, 45 cm. long, 3 cm. wide; axis completely glabrous; branches naked below, the lower primary branches of the panicle 7-8 cm. long, the secondary branches about 3 cm. long; pedicels glabrous, the swollen portion just beneath the spikelet puberulent, mostly 1-2 mm. long, those of the terminal spikelets longer and more variable in length; spikelets 4-4.2 mm. long; glumes purple, narrow, acute, minutely awn-tipped, the second a little longer than the first, just exceeding the floret, glabrous, nerveless or indistinctly 1-nerved; lemmas narrow, acute, about 4 mm. long, glabrous, short-pilose at juncture of lemma and callus at the base on palca side, the hairs about one-fourth the length of lemma, 3-nerved, the middle nerve excurrent from just below the tip as a slightly flexuous purple awn 2-2.5 cm. long; palea a little shorter than lemma, completely glabrous.

Holotype in the University of Michigan herbarium, collected in Jalisco, Mexico, in "Steep mountains 11-12 miles south of Talpa de Allende, in the headwaters of a west branch of Río de Talpa; barranca above a rapid clear stream, in dense forest of *Quercus*, *Carpinus*, *Distylium*, *Magnolia*, *Podocarpus*, with pine forest on the ridges above; abundant in the pine forest; in clumps, inflorescence purple; alt. 1200-1700 m., 23-25 November 1960," by Rogers McVaugh (no. 21313). Isotype at US. Known only from the type collection.

Although I would prefer to have additional collections at hand in describing this new species, there is little doubt that it is distinct. The habit of the inflorescence and spikelets with awn-tipped glumes and lemmas glabrous except for the short-pilose base, suggest a relationship with *M. scoparia*. The distinct fan-shaped appearance of sheaths and the stiff, rather wide, flat blades ascending erectly much like an iris suggested the name "iridifolia." The firm brown ligules are conspicuous and appear to be chopped off, leaving a firm brown base about 5-7 mm. long. The combination of long spikelets (4 mm.), awn-tipped glumes, and lemmas glabrous except at the base where the callus is short-pilose, readily distinguishes this species from all others in *Epicampes*.

15. *Muhlenbergia speciosa* Vasey. Bull. Torrey Club 13 (12):231. 1886.

*Bealia speciosa* (Vasey) Beal. Grasses N. Amer. 2:268. 1896. Based on *Muhlenbergia speciosa* Vasey.

*Epicampes speciosa* (Vasey) Jones. Contr. West. Bot. 14:7. 1912. Based on *Muhlenbergia speciosa* Vasey.

Caespitose perennial; culms pubescent or villous, the pubescence present as broad bands on the culm, glabrous between the bands, 95-129 cm. tall; nodes 5, densely pubescent to villous below and usually above; basal sheaths compressed-keeled, glabrous below and becoming villous toward the collar, or villous throughout, especially along the edges; ligule a membranous rim, 0.3-1.1 mm. long; sheath auricles lacking; blades of culm 36-52 cm. long, 2.5-4 mm. wide when flat, the blades usually folded with the edges rolled backward on the lower (abaxial) surface, upper surface of the blade villous (or scabrous) at the base near the ligule, the pubescence becoming sparse toward the distal end, here the surface scaberulous, or scaberulous with scattered long hairs, the lower surface of blade generally more villous than the upper surface and for the greater part of its length, especially villous near the ligule, becoming less so distally, here the surface scabrous; upper throat densely villous.

Panicle large and plumose, the branches ascending or opening outward, whitish or purplish white, 41-62 cm. long, 5-11 cm. wide; axis glabrous to scabrous with scattered long hairs; lower primary branches 9-13 cm. long, naked below; secondary branches 3.5-5 cm. long,

naked below; tertiary branches 1.3–3 cm. long; quaternary branches, when present, to 0.8 cm. long; pedicels of the lateral spikelets 0.5–2 mm. long, of the terminal spikelets relatively long, 1.5–5.5 mm., glabrous to scaberulous, often with scattered long hairs on the surface; spikelets 1.2–2.2 (averaging less than 2) mm. long; glumes equal or the second a little longer than the first, 1.4–2.3 mm. long, usually a little longer than the floret, mostly villous, rounded or lobed at the tip or rarely with an awn tip, hyaline, nerveless, white; lemmas 1.2–2.2 mm. long, villous throughout, especially on the lateral margins, 3-nerved, the nerves purple and become thickened toward the tip, awn of the lemma to 17 mm. long; callus of the lemma short and densely pilose; palea obtuse, a little shorter than the lemma, villous, especially between the keels.

Type in the U.S. National Herbarium, no. 999062, collected in "southwestern Chihuahua, Mexico," August to November 1885, by Dr. Edward Palmer (no. 30). Isotypes at GH and MEXU.

**DISTRIBUTION:** Found only in Mexico, where it is confined to rocky slopes in the pine-oak zone and in arroyos, at elevations of about 1,000–6,600 ft. From southwestern Chihuahua through western Durango, Sinaloa, Nayarit, and into Jalisco. Apparently infrequent.

**MEXICO:** *Palmer*, in 1886 (TAES). **CHIHUAHUA:** *Palmer* 30, Aug. to Nov. 1885 (US holotype, GH, MEXU, isotypes). **SINALOA:** Culiacán, *Cofradía Brandegees*, Oct. 26, 1904 (POM, UC, US). Palmito and vicinity along Durango-Sinaloa highway, *Gentry & Arguelles* 18201 (LL, US). Santa Lucía, *Meria* 490 (CAS, MO, UC, US). **DURANGO:** La Bajada, Tamazula, *Ortega* 4335 (US). 21 mi. E. of Santa Lucía, *Reeder & Reeder* 2476, aff. *M. speciosa* (YU). **NAYARIT:** Tepic, *Jones* 23438 (CAS, GH), Feb. 10, 1927 (NY). 9 mi. N. of Compostela, *McVaugh & Koelz* 575 (MICH). Ca. 5.5 mi. SW. of Jalisco, road to El Malinal, *McVaugh & Koelz* 668 (MICH). "Along banks of arroyos," *Palmer* 1919, in 1892 (GH, MO, NY, US). 7 mi. NW. of Tepic, *Reeder & Reeder* 4210 (US, YU), 4211 (US, YU). **JALISCO:** SW. Autlán, *Hernández* 4638 (CHAP, US). 4 mi. N.-NE. of Talpa de Allende, *McVaugh* 20102 (MICH, US). Ca. 8 mi. SW. of La Resolana, *McVaugh* 21105 (MICH, US). 3–5 road mi. above (N. of) La Cuesta, road to Talpa de Allende, *McVaugh* 21226 (MICH, US).

*Muhlenbergia speciosa* is distinguished by the more or less villous sheaths, blades, and culms, the very short ligule (about 1 mm. or less), a large plumose panicle, and small spikelets (mostly less than 2 mm. long), the lemmas long-awned. It appears to be most closely related to *M. pubescens*. Both species are generally villous throughout, the ligule is relatively short, and the glumes, lemmas, and paleas are more or less villous. *Muhlenbergia pubescens* differs in the longer ligule (2–3 mm.), a denser panicle with larger spikelets (mostly 2.4–2.6 mm.), and the shorter awns of the lemmas. The ranges of both overlap in southwestern Chihuahua and western Durango, Mexico, and some hybridization may possibly occur. One specimen, *Reeder & Reeder* 2476, from western Durango, seems to be somewhat intermediate

between these two species and perhaps represents such a hybrid. The long spreading branches of the panicle in this specimen and the very short ligule are characters of *M. speciosa*. The 2.5 mm. long spikelets and the short-awned lemmas are features of *M. pubescens*. The habit and overall appearance are those of *M. speciosa*, to which it appears to be more closely allied. The extent of such putative hybrids cannot be determined until many more collections are made in this region. Comparison may also be made with *M. grandis* which is similar in habit and occupies a similar range. Unlike *M. speciosa* it has glabrous culms, foliage, and glumes, and longer ligule (1.5–6 mm.)

**16. *Muhlenbergia pubescens*** (H.B.K.) Hitchc. N. Amer. Fl. 17(6):460. 1935, as to type, not as to description (see *M. distans* Swallen).

*Agrostis pubescens* H.B.K. Nov. Gen. & Sp. I:136. 1815. Basis of *Muhlenbergia pubescens* (H.B.K.) Hitchc. (Type collected in "scopulosis juxta Villalpando, Santa Rosa, et Cerro del Cubilete," 7800–8760 ft. [mining areas around the city of Guanajuato, Guanajuato, Mexico].)

*Agrostis lanata* H.B.K. Nov. Gen. & Sp. I:136. 1815. (Type from same localities as preceding.)

*Cinna?* *pubescens* (H.B.K.) Kunth. Rev. Gram. 1:67. 1829. Based on *Agrostis pubescens* H.B.K.

*Cinna?* *lanata* (H.B.K.) Kunth. Rev. Gram. 1:67. 1829. Based on *Agrostis lanata* H.B.K.

*Epicampes pubescens* (H.B.K.) Presl ex Kunth. Enum. Pl. 1:209. 1833. Based on *Agrostis pubescens* H.B.K.

*Epicampes lanata* (H.B.K.) Presl ex Kunth. Enum. Pl. 1:209. 1833. Based on *Agrostis lanata* H.B.K.

*Epicampes pubescens* (H.B.K.) Jones. Contr. West. Bot. 14:7. 1912. Based on *Agrostis pubescens* H.B.K.

*Muhlenbergia lanata* (H.B.K.) Hitchc. N. Amer. Fl. 17(6):459. 1935. Based on *Agrostis lanata* H.B.K.

Caespitose perennial; culms erect, 57–154 (usually about 100–125) cm. tall, sparsely to densely villous, especially on the lower part; nodes 3–4, sparsely to densely villous, especially below; basal sheaths compressed-keeled, villous (rarely scabrous with long sparse hairs); collar villous or scabrous with sparse long hairs; ligule membranous, usually finely lacerated, 1.5–6 (usually 2–4) mm. long; sheath auricles lacking; blades 12–61 (usually 25–50) cm. long, usually short on the upper part of the culm, 2.5–6.5 (usually 3–4) mm. wide, flat or folded, upper surface villous at base, becoming less villous toward the tip (rarely only scabrous with long scattered hairs), upper surface villous throughout or sometimes scabrous with long scattered hairs; blades of the culm constricted and villous at point of attachment to sheath; upper throat villous.

Panicle erect, columnar, densely flowered, gray or purplish gray, 12–49 (usually 20–40) cm. long, 2–7 (usually 3–7) cm. wide, the branches of the panicle ascending, floriferous to base; axis villous, rarely sparsely so; primary branches 3–11.5 (usually 5–8) cm. long,

secondary branches 1-5 (usually 1-2) cm. long, tertiary branches rarely to 1.5 cm. long; pedicels shorter than the spikelets, villous (sometimes sparsely so), 0.3-1 mm. long; spikelets 2.5-3 mm. long; glumes broadly acute at the tip, longer than the floret, almost equal or the first 1-2 mm. shorter than the second, sparsely to densely villous, nerveless, gray, often purplish at the base; lemma 2.2-3 (usually 2.4-2.6) mm. long, sparsely to densely villous throughout except at tip, 3-nerved, the median nerve often extending as an awn from just below the tip, 1-10 (usually 6-7) mm. long, straight or somewhat flexuous; palea villous throughout, rarely sparsely so.

Fragment of panicle of possible type marked "*Agrostis pubescens*" (in Kunth's script) in the U.S. National Herbarium, ex Herb. Humboldt & Bonpland (P), collected near Guanajuato, Guanajuato, Mexico, "in scopulosis juxta Villalpando, Santa Rosa, et Cerro del Cubilete," 7800-8760 ft. A photograph of the specimen is with the fragment.

**DISTRIBUTION:** Common on rocky mountain slopes and ledges and in rocky ravines, canyons, and barrancas, at elevations of about 5,600-8,000 ft. Known only from Mexico, from Chihuahua and Durango south to Puebla. A collection from Oaxaca is doubtfully referred to this species.

**MEXICO: CHIHUAHUA:** Hills near Chihuahua, *Pringle* 391 (F, GH, MO, US), 983 (MEXU, NY). 37 mi. S. of Villa Matamoros, *Reeder, Reeder, & Soderstrom* 3451 (US, YU). **DURANGO:** Canyon Cantero, Sierra de Gamón, *Gentry* 8406 (GH, MEXU, MICH, UC, US). 40 km. S. of Durango, *Hernández, Ruppert, & Guevara* X-2561 (US). 20 km. S. of Durango, *Hernández, Ruppert, & Guevara* X-2576 (US). Km. 1395, Carretera Juárez, Parral-La Zarca, *Hernández & Tapia* N-589 (CHAP). Durango, *Hitchcock* 7587 (ILL, US), 7652 (NY, US). SW. of Durango on Durango-Mazatlán road, *Soderstrom* 763 (US, YU), 768 (US, YU), 769 (US, YU), 773 (US, YU), 774 (US, YU). N. of Durango on Durango-Juárez road, *Soderstrom* 788 (US, YU). 23 mi. W. of Durango, *Reeder & Reeder* 2548 (YU), 2592 (YU). 31 mi. W. of Cd. Durango, *Reeder & Reeder* 2578 (YU), 2590 (YU). 6 mi. W. of Navíos, *Reeder, Reeder, & Soderstrom* 3377 (US, YU), 3411 (US, YU), 3412 (US, YU), 3413 (US, YU), 3414 (US, YU). Sierra Madre Occidental, W. of Cd. Durango, *Reeder, Reeder, & Soderstrom* 3428 (US, YU). 3 mi. E. of Navíos, *Reeder, Reeder, & Soderstrom* 3429 (US, YU), 3430 (US, YU). 5 mi. E. of Navíos, *Reeder, Reeder, & Soderstrom* 3433 (US, YU), 3434 (US, YU), 3435 (US, YU). 11 mi. W. of Durango, *Reeder, Reeder, & Soderstrom* 3444 (US, YU). **ZACATECAS:** 2 mi. W. of Sombrerete, *Soderstrom* 733 (US). **SAN LUIS POTOSÍ:** 22° N. Lat., *Parry & Palmer* 933 (F, GH, MO, US). 20 mi. SW. of San Luis Potosí, *Reeder, Reeder, & Soderstrom* 3304 (US, YU). *Schaffner* 190 (US). "Ex convalli S. L. P.," *Schaffner*, in 1876 (GH). San Francisco in the Sierra de San Miguelito, *Sohns* 1049 (US). Canyon del Lobo, Sierra de San Miguelito, *Sohns* 1158 (US). Canyon del Muerto, Sierra de San Miguelito, *Sohns* 1319 (US), 1327 (US). **AGUASCALIENTES:** 7 mi. E. of Ojo Caliente, *Reeder & Reeder* 4193 (US, YU). Mountains above Presa Calles, *Shreve* 9258 (ARIZ, US). **JALISCO:** San Juan de los Lagos, *Hernández* X-4608 (CHAP, US). Ojuelos-Aguascalientes, *Hernández, Ruppert, & Guevara* X-2513

(US), X-2515 (US). Road to León, Gto., 5 mi. SE. of junction at Lagos de Moreno, *McVaugh* 17800 (MICH). 7 mi. SE. of Lagos de Moreno, *Reeder & Reeder* 2306 (YU). 15 mi. SE. from Encarnación de Díaz on highway 45 to Lagos de Moreno, *Soderstrom* 692 (US), 693 (US), 694 (US), 696 (US), 698 (US). GUANAJUATO: About 9 mi. from Guanajuato, *Moore* 1355 (GH, MICH, UC, US). 695 (US), 12 mi. E. of Guanajuato, *Reeder & Reeder* 3088 (YU). 13 mi. NE. of Guanajuato, *Reeder & Reeder* 3093 (YU). 2-4 km. E. of Guanajuato, *Sohns* 298 (US). About 6 km. E. of Guanajuato, *Sohns* 302 (US), 313 (US). About 8 km. W. of San Felipe, *Sohns* 433. PUEBLA: 5 mi. NE. of Zacatepec, *Soderstrom* 483 (US, YU). TLAXCALA: Santa Ana Chiautempan, *Arsène* 1715 (GH, MO, NY, US). MEXICO: About 45 mi. S. of San Juan del Río, *Reeder & Reeder* 2235 (YU). El Pedregal, just S. of Mexico, City *Reeder & Reeder* 3047 (YU). OAXACA: (?) 27 mi. NW. of Cd. Oaxaca, *Reeder & Reeder* 2184, aff. *M. pubescens* (YU).

*Muhlenbergia pubescens* appears to be most closely related to *M. speciosa* and like that species has moderately to densely villous vegetative parts, a relatively short ligule, and blades usually constricted at the base. It is distinguished from *M. speciosa* by the denser panicles with the branches more appressed, longer spikelets (usually 2.4-2.6 mm. in contrast to 2 mm.), and shorter awns on the lemmas (7 mm. or less as opposed to 10 mm. or more).

In 1815 Kunth described two species of *Agrostis*, *A. pubescens* and *A. lanata*, and indicated that the latter might be a variety of the former. *Agrostis pubescens* was described as 3-4 ft. tall, generally glabrous throughout, pubescent under the nodes, having a short, lacerate ligule, white, nerveless, punctate-scabrous glumes, and lemmas pubescent at the base. *Agrostis lanata* was described as 3 ft. or taller, generally lanate throughout, having pubescent nodes, a short, lacerate ligule, and pilose glumes, lemmas, and paleas.

Presl (1830), along with his description of the original species of *Epicampes*, mentioned that these two species of *Agrostis* probably belonged with his new genus and added that *A. lanata* might be a variety of *A. pubescens*, but he made no transfers. Kunth (1833), following the opinion of Presl, formally transferred them to *Epicampes*. Jones (1912), commenting on *E. pubescens*, stated: "This is *Agrostis pubescens* H.B.K. . . . *A. lanata* is a synonym." He is the only author who stated, without reservation, that they are clearly synonymous and are not worthy of recognition as varieties within one species. Hitchcock (1935) transferred *E. pubescens* and *E. lanatus* to *Muhlenbergia* and, following the lead of Kunth and Presl, indicated that *M. lanata* might be a variety of *M. pubescens*.

*Muhlenbergia lanata*, as based upon *Agrostis lanata*, refers to a widespread plant characterized by villous lemmas, a very short ligule (about 3 mm. long), and moderately to densely villous glumes, culms, and sheaths. *Muhlenbergia pubescens*, as circumscribed by Hitchcock, is characterized by lemmas pubescent over the lower half,

a ligule 5-10 mm. long (or a little longer), and relatively glabrous glumes, culms, and sheaths.

The type collections of "*A. pubescens*" and "*A. lanata*" are from the same locality, near the city of Guanajuato. The majority of specimens from this area of Mexico are quite villous throughout, although occasionally the pubescence is confined mostly to the lemma, appearing more sparsely on the glumes and remainder of the plant. According to the original description these plants with sparse pubescence would be referred to "*A. pubescens*." The very short ligule, short blades, and at least some pubescence on the other vegetative parts seem to indicate a less pubescent form than "*A. lanata*," but certainly not a distinct species.

A fragment of a specimen marked *Agrostis pubescens*, in Kunth's handwriting (Mn. 5225, from the H.B.K. herbarium, P), and accompanying photograph in the U.S. National Herbarium are those of "*A. lanata*" of the original description. An annotation on the same sheet by Dr. Agnes Chase, dated 1935,<sup>12</sup> reads: "No specimen named '*A. lanata*' by Kunth has been found and no other named '*A. pubescens*.'" This fragment is mentioned above as the possible type of *Agrostis pubescens*, but the spikelets have villous rather than punctate-scabrous glumes as *A. pubescens* should have from the description, and so it is likely that this specimen is actually the type of *A. lanata*, and that the type of *A. pubescens* has not been found.

From the descriptions of Kunth, the amount of pubescence on the plant separated "*Agrostis pubescens*" from "*A. lanata*." The former was described as mostly glabrous except below the nodes and the lemmas as pubescent toward the base; the latter as having pubescent basal sheaths, nodes, and spikelets.

A large number of specimens of both types were collected by the author and Prof. and Mrs. J. R. Reeder in the autumn of 1960 in central Mexico. Specimens referable to both "species" were collected near each other, in addition to specimens intermediate in amount of pubescence between the two. This leaves little doubt that the amount of pubescence is a variable character in these species and that both types are representatives of one species, *M. pubescens*. Special reference is made to the following comparison of specimens, showing extreme and intermediate types of pubescence. All specimens were collected in the same locality, 6 miles west of Navíos, Durango, Mexico.

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<sup>12</sup> In 1935, Dr. Agnes Chase, of the United States National Herbarium, critically studied and made notes on type specimens of grasses in many European herbaria.

<i>Reeder, Reeder, &amp; Soderstrom number</i>	<i>Pubescence of sheaths</i>	<i>Pubescence of culm</i>	<i>Pubescence of blades</i>	<i>Ligule</i>	<i>Glumes</i>	<i>Lemma</i>	<i>Axis of panicle</i>	<i>Fits original description of Agrostis</i>
3411	only at base	sparsely pubescent; very pubescent around nodes	scabrous and with sparse long hairs	3 mm.	scaberulous only	villous on lower half	scabrous, not villous	<i>pubescens</i>
3412	villous	glabrous or with sparse long hairs: densely pubescent below nodes	villous	2 mm.	villous	villous through- out	lightly villous	<i>lanata</i>
3413	villous	glabrous or sparsely hairy, densely pubescent below nodes	sparsely villous	2 mm.	villous	villous on lower half	scabrous	<i>lanata</i>
3414	scabrous, some sparse pubescence	glabrous below, be- coming densely pubescent below nodes	scabrous	3 mm.	sparse hairs	sparsely pubes- cent below	scabrous	<i>pubescens</i>

When correctly understood, *M. pubescens* embraces short to medium-sized plants, the ligule is short (about 3 mm.), the usually short blades of the culm are constricted and villous at the base, and the lemma is pubescent on and between the nerves. The basal sheaths, blades, and other parts are often densely villous, but the amount varies and is often restricted to the lower part of the basal sheaths or as sparse hairs over the various parts. Hitchcock (1935) misinterpreted *M. pubescens*; the plants he described have relatively long ligules, glabrous vegetative parts, relatively long brownish spikelets, and awnless or short-awned lemmas pubescent over the lower part, on and between the nerves. Such specimens appear to belong properly to *M. distans*. The two species, as treated in this work, may be distinguished as follows:

	<i>M. pubescens</i>	<i>M. distans</i>
spikelets	about 2-3 mm. long, white to purplish	averaging 3 mm. long
glumes	sparsely to densely villous, obtusish	glaucous, with roughed surface, acute
lemma	usually densely pubescent throughout	pubescent over lower part
ligule	usually 2-3 mm. long, membranous throughout	5-10 mm. long, firmer and browner at base than above
blades of culm	constricted and villous at base	not constricted and villous at base
nodes	pubescent below	glabrous to scaberulous below; rarely pubescent
basal sheaths	villous, or at least slightly pubescent, with scattered long hairs	glabrous to scaberulous

17. *Muhlenbergia robusta* (Fourn.) Hitchc. N. Amer. Fl. 17(6):462. 1935.

*Epicampes strictus* J. S. Presl. Rel. Haenk. 1:235. 1830. Basis of *Muhlenbergia presliana* Hitchc. (Mexico: without precise locality, *Haenke*).  
Not *M. stricta* (Presl) Kunth. 1833.

*Epicampes berlandieri* Fourn. Mex. Pl. 2:89. 1886. Basis of *Muhlenbergia fournieriana* Hitchc. (Mexico: without precise locality, *Berlandier* 670).  
Not *M. berlandieri* Trin. 1841.

*Epicampes robusta* Fourn. Mex. Pl. 2:89. 1886. Basis of *Muhlenbergia robusta* (Fourn.) Hitchc. Fournier cites the following specimens in the original description:

*Bourgeau* 683, supra Tacubaya (state of Mexico). He also cites this collection under *Epicampes stricta* Presl (p. 89). Hemsley (1885) likewise cites it under *E. stricta* Presl. The lemmas are pubescent over the lower half and from a study of a fragment it appears to be *Muhlenbergia distans*.

*Bourgeau* 1153, Santa Fé, vallée de Mexico. A complete specimen ex P is in the U.S. National Herbarium. The lemmas are glabrous except for a few minute hairs at the base. Fragments in an envelope labeled *Bourgeau* 1153 ex LE consist of two elements. In one, probably *M. distans*, the lemmas are pubescent on the lower half and are awned. The other has

awnless lemmas but is pubescent on the lower midnerve and margins. Neither of these can be *Bourgeau* 1153.

*Hahn* 420, Cuernavaca, [Morelos], Mexico. Not seen.

*Muhlenbergia fournieriana* Hitchc. Journ. Washington Acad. Sci. 23:453. 1933. Based on *Epicampes berlandieri* Fourn.

*Muhlenbergia presliana* Hitchc. N. Amer. Fl. 17(6):462. 1935. Based on *Epicampes strictus* Presl.

Strongly caespitose perennial; culms stout, thick, erect, glabrous, 1–3 meters tall; nodes usually 4, glabrous below, the nodes covered by the sheaths; basal sheaths strongly compressed-keeled, glabrous (rarely scaberulous); ligule short, membranous, finely lacerated into narrow strands and hairs, 1.5–5 (usually 2–4) mm. long, longer on the innovations; rudimentary sheath auricles present, 1.5–5 (mostly 2–4.5) mm. long, rarely lacking or more than 5 mm. long; blades about 25–50 (mostly 30–50) cm. long, 3.5–6 (usually 4–5) mm. wide, the upper and lower surface scabrous, usually strongly so, the edges of the blades sharply saw-toothed; upper throat scabrous; collar glabrous, rarely scaberulous.

Panicle large, densely flowered, erect, purplish or greenish gray, columnar before anthesis, the branches spreading at flowering and becoming appressed at seed-set, 30–60 (usually 40–60) cm. long, rarely as much as 70–80 cm. long, 2–4 cm. wide (on herbarium specimen, much wider in field), the branches of the panicle naked below or floriferous to the base; axis thick, angled, scaberulous or scabrous; primary branches 4.5–17 (usually 5–8) cm. long, the secondary branches 1.3–6 (usually 1.5–3) cm. long, the tertiary branches 0.7–2.5 (usually 1 or less) cm. long; pedicels scaberulous or scabrous, those of the lateral spikelets very short, less than 1 mm. long, of the terminal spikelets a little longer; spikelets about 1.8–3.3 (mostly 2.1–2.8) mm. long, rarely longer; glumes acute to obtuse at the tip, equaling each other or the second a little longer than the first, glabrous to even scaberulous, purplish or greenish gray, longer than the floret, 1-nerved, often indistinctly so; lemma acutish, glabrous or evenly scaberulous, at most a few hairs at the base of the midnerve and margins, 3-nerved, the median nerve often extending into a rudimentary awn from just below the tip, usually less than 1 mm. long; callus of lemma glabrous or with only a few hairs; palea a little shorter than the lemma, glabrous or, at most, a few hairs between the keels toward the base.

Isolectotype in the U.S. National Herbarium, no. 999036, collected in "Barranca près Santa Fée, vallée de Mexico," Oct. 3, 1865, by E. Bourgeau (no. 1153).

Fournier cited three specimens in the original description. Of these Hitchcock (1935b, p. 462) cited *Bourgeau* 1153 as the type, and thus this is the lectotype.

**DISTRIBUTION:** Steep rocky mountainsides, slopes of canyons and barrancas, and eroded areas, at elevations of 3,000–7,000 ft., occurring most frequently at 5,000–6,000 ft. The most common species of *Epicampes* in southern Mexico, extending from Nayarit and Jalisco to Chiapas and into Guatemala and Nicaragua.

**MEXICO:** *Berlandier* 670 (US fragments of type of *E. berlandieri*, ex LE, P, W). *Haenke* (US fragment of type of *E. strictus*). *Palmer*, in 1884 (DS, NY, US). "Near river bank," *Schumann* 1754 (US). **NAYARIT:** SE. of Tepic, *McVaugh* 13393 (MEXU, SMU, US). **JALISCO:** Entre Pequeros y Tepatitlán, *Hernández* 4609 (CHAP). Zapotlán, *Hitchcock* 7172 (US), 7173 (US). Barranca de Oblatos, *Hitchcock* 7335 (ILL, NY). La Barranca, *Jones* 27658 (MO). N. of Autlán, *McVaugh* 19698 (MICH, US). SW. of Autlán, *McVaugh* 19899 (MICH, US). Río Blanco, *Palmer* 518, in 1886 (GH, MEXU, MO, NY, US). Guadalajara, *Pringle* 2321 (F, GH, MO, NY, UC, US), 11746 (CAS, F, GH, MO, US). 18 mi. S. of Guadalajara, *Reeder & Reeder* 2343 (YU). 3 mi W. of Tequila, *Reeder & Reeder* 4206 (US, YU). Sierra Madre, W. of Bolaños, *Rose* 2997 (GH, US). Ciudad Granja, W. of Guadalajara, *Soderstrom* 643 (US), 644 (US). SE. of Guadalajara, on road to Aguascalientes, *Soderstrom* 653 (US), 654 (US). 6 mi. E. of Santa Cruz, *Soderstrom* 566 (US), 567 (US), 568 (US), 569 (US), 570 (US), 571 (US), 572 (US). W. of Guadalajara on road to Tepic, *Soderstrom* 603 (US), 606 (US), 634 (US), 635 (US). 8 mi. E. of Guadalajara, near Barranca de Oblatos, *Soderstrom* 678 (US), 679 (US), 680 (US). **GUANAJUATO:** Guanajuato, *Kenoyer* 1765 (*M. robusta* X *M. emersleyi*?) (GH). 11 mi. NE. of Guanajuato, *Reeder & Reeder* 3081, aff. *M. robusta* (YU). 2–4 km. E. of Guanajuato, *Sohns* 297 (*M. robusta*?) (MICH). **VERACRUZ:** Orizaba, *Müller* 2130 (US). **PUEBLA:** Cerro Chiquihuite, *Arsène* 115 (US). Puebla: Cerro et fort de Guadalupe, *Arsène* 1186 (US). Mayorazgo, *Arsène* 1275 (MO, US). Cholula, *Arsène & Nicolas* 5441 (US); *Nicolas*, Sept. 15, 1910 (F). Rancho Posada near Puebla, *Nicolas* 303 (US). Esperanza, *Nicolas*, Sept. 8, 1909 (NY). Acatzingo, *Nicolas*, in 1909 (US). La Venta, *Sharp* 441664 (US). 6 mi. E. of Puebla, *Soderstrom* 387 (US), 388 (US), 389 (US), 390 (US). Zacatepec, *Soderstrom* 484 (US), 485 (US). **MORELOS:** Tauteppec, *Gándara*, in 1935 (US). Atlatlahucan, *Gándara* (US). Teposteco, *Lyonnet* 2553 (US). Sierra de Ocuila rumbo Mexicapa, *Lyonnet* 2872 (US). Casa de Tepoztero, *Seler* 4320 (GH). **MEXICO:** Santa Fe (as Santa Fé), *Bourgeau* 1153 (US lectotype, fragments ex LE, P). Carboneras, Temascaltepec, *Hinton* 1853 (GH, NY). Rincón del Carmen, Temascaltepec, *Hinton* 1959 (MO, NY, US). Temascaltepec, Temascaltepec, *Hinton* 2053 (LL, MO, NY, US). Anonas, Temascaltepec, *Hinton* 2591 (CAS, LL, MICH, MO, NY, US). Sultepec, Sultepec, *Hinton* 3219 (NY). Luvianos, Temascaltepec, *Hinton* 5302 (NY). Tenango, *Matuda* 18846 (US). Guajimalpa to Río Hondo, *Matuda* 21811 (US). Valle de Bravo, *Matuda* 27232 (MO). Carretera México-Cuautla, *Ortega & Vázquez*, Oct. 12, 1960 (CHAP). 5 mi. N. of Tenancingo, *Reeder & Reeder* 4173 (US, YU). Santa Fe, *Rose & Painter* 8009 (US). 3 mi. NW. of Tlamanalco, *Soderstrom* 380 (US), 382 (US). **DISTRITO FEDERAL:** Chalco region, *Collins*, Oct. 4, 1921 (US). Pedregal, *Hitchcock* 5939 (SMU, US). Near Chapultepec Castle, *Hitchcock* 7839 (US). ¼ mi. S. of La Cima R.R. Station, *Iltis, Koeppen, & Iltis* 146 (US, WIS). Pedregal de San Angel, *Juzepczuk* 216 (US); *Lyonnet* 1670 (US); *Matuda* 19479 (US). Churubusco, *Orcutt* 4317 (GH, US). Coyoacán, *Ortega & Vázquez*, Oct. 9, 1960 (CHAP). Lava fields above the Valley of México, *Pringle* 9077 (GH, MO, US). El Pedregal, *Reeder & Reeder* 3053 (YU). Huipulco, *Rzedowski* 1350 (IPN). Between Ixtle and El Conejo,

*Rzedowski* 1929 (IPN). Eslava, *Rzedowski* 1999 (US). Sobre el Ixtle, *Rzedowski*, Dec. 21, 1952 (IPN). About 5 km. W. of San Andrés, *Sohns* 183 (US). Pedregal, *St. Pierre* 804 (MICH, US), 805 (MICH, US). Dolores, *St. Pierre* 869 (US). Ciudad Universitaria, *Tateoka* 1106 (US). MICHOACÁN: Lomas de la Huerta, *Arsène* 2628 (ILL, MO, NY, US), Oct 15, 1909 (GH). Barranca NW. de Punguato, *Arsène* 2673 (ILL, MO, NY, US), 3145 (ILL, NY, TEX, US), Oct. 18, 1909 (GH). Loma Santa María, *Arsène*, Sept. 2, 1909 (US). Zitácuaro-Coyota, *Hinton* 13409 (DS, GH, NY, US). 5 mi. N. of Cotija and 22 mi. S. of Jiquilpan, *King & Soderstrom* 4648 (MICH, SMU, TEX, US). 22 mi. S. of Uruapan, *King & Soderstrom* 4859 (MICH, US). Below Tecambaro on road to Chipio, *Moore, Hernández, & Porras* 5616 (UC, US). Between Mil Cumbres and Ciudad Hidalgo, *Moore, Hernández, & Porras* 5774 (US). Road from Lorelia to Toluca, *Reeder, Reeder, & Goodding* 1476 (YU). Zacapú, *Ruppert & Guevara* X-2830 (US). 3 mi. E. of Morelia, *Soderstrom* 544 (US), 545 (US), 545a (US). Quiroga, *Soderstrom* 552 (US), 553 (US). Uruapan to Nueva Italia, *Sohns* 865 (US). OAXACA: Oaxaca, *Hitchcock* 6141 (US), 6154 (US). Reyes, *Nelson* 1778 (GH, US). 27 mi. NW. of Cd. Oaxaca, *Reeder & Reeder* 2183 (YU). Huajuapán de León, *Soderstrom* 412 (US). Loc.?, *Tateoka* 1107 (US). CHIAPAS: Km. 1134, *Baldwin* 14345 (US). 15 mi. S. of Comitán, *Reeder & Reeder* 2096 (YU). 20 mi. E. of Chiapa de Corzo, *Reeder & Reeder* 2128 (YU).

GUATEMALA: HUEHUETENANGO: Huehuetenango, *Melhus & Goodman* 3562 (F). 10 km. W. of Aguacatán, *Williams, Molina, & Williams* 21848 (US). QUEZALTENANGO: Aguascalientes, *Seler* 3236 (GH). GUATEMALA: *Aguilar* 311 (F). Guatemala City, *Hitchcock* 9035 (CAS, US), 9063 ½ (US). Eureka, *Hitchcock* 9081 (MICH, US). Between Antigua and Guatemala City, *Hitchcock* 9146 (US). N. of Guatemala City, *Popenoe* 738 (US). SACATEPÉQUEZ: Santa María, *Hitchcock* 9129 (US). Antigua, *Standley* 61698 (F, US). CHIMALTENANGO: Alameda, *Johnston* 976 (F). Finca La Alameda, near Chimaltenango, *Standley* 59136 (F, US). SE. of Patzún, *Standley* 61596 (F, US). Finca La Alameda, near Chimaltenango, *Standley* 79806 (F), 79729 (F). SOLOLÁ: Cerca del Lago Atitlán, *de Koninck* 145 (US). SANTA ROSA: Naranjo, *Heyde & Lux* 3932 (GH, MO, NY, US).

NICARAGUA: *Garnier* 1953 (GH, US). MANAGUA: Sierra de Managua, *Garnier*, "about 1930-1940" (F).

*Muhlenbergia robusta* is distinguished by its robust habit, very short fimbriate ligule, rudimentary sheath auricles, and awnless or short-awned, mostly glabrous, lemmas. Its closest relative appears to be *M. virletii*, which has a longer ligule (4-8 mm. rather than 2-4 mm.), rudimentary sheath auricles lacking, longer spikelets (mostly 3.5-3.6 mm. as opposed to 2.1-2.8 mm.), and the lemmas pubescent toward the base of the margins. The sheath auricles, short ligule, glabrous lemmas, and robust habit of *M. macrotis* also suggest a close relationship with *M. robusta*.

*Muhlenbergia robusta* is the dominant species of *Epicampes* found on rocky mountainsides in southern Mexico and might be thought of as the counterpart of *M. emersleyi* Vasey which is dominant in northern Mexico and southwestern United States. As in the latter species, *M. robusta* varies widely and some of the extreme forms have been described as species. Hitchcock (1935b) recognized two species, *M.*

*robusta* and *M. presliana*, the latter based on the type of *Epicampes*, *E. strictus* Presl.

The present study indicates that *M. presliana* and *M. robusta* are members of one polymorphic species. A comparison of characters from Hitchcock's descriptions discloses that the major distinction between the two species is spikelet size; in *M. robusta* it is 2.5–3 mm. long and only 2 mm. in *M. presliana*. Spikelet size is a variable character in all species of *Epicampes*. Within the *M. robusta* complex the spikelets vary in size from 1.8–3.3 mm., although usually 2.1–2.8 mm. long. The spikelets of a fragment of the type of *M. presliana* are mostly 2 mm. long, a few are 2.3 mm. Specimens with spikelets 2 mm. long are similar to specimens of *M. robusta* with longer spikelets and exhibit no other characters to delimit them as a distinct species.

In addition to variations of spikelet size and glume surface, the branches of the panicle are naked at the base in some specimens and in others floriferous to the base. Specimens exhibiting various combinations of these characters and intergrading forms have been found. Nevertheless, all possess the robust habit, relatively glabrous lemmas, short fimbriate ligule, and characteristic rudimentary sheath auricles generally about 3 mm. in length. In view of the lack of correlation of characters, it seems more realistic to regard *M. robusta* and *M. presliana* as members of a single variable species.

A rather unusual specimen, Kenoyer 1765 (Guanajuato, Mexico), may possibly be a hybrid between *M. robusta* and *M. emersleyi*. The Gray Herbarium specimen, the only one I have seen, has an incomplete culm and complete inflorescence. The latter is about 45 cm. long with ascending branches. The ligule is short-lacerate and small auricles are present, as in *M. robusta*, and the panicle is typical of that species. Although the shape and appearance of the spikelets are of that species, the lemmas are awned and slightly pubescent, in the pattern of *M. emersleyi*.

18. *Muhlenbergia virletii* (Fourn.) Soderstrom, comb. nov.

*Epicampes virletii* Fourn. Mex. Pl. 2:88. 1886. (*Virlet* 1415, San Luis de Potosí, Mexico)

Caespitose perennial; culms stout, erect, glabrous to scaberulous, about 1 m. tall; basal sheaths strongly compressed-keeled, glabrous to finely scaberulous; ligule membranous, lacerate above, 4–12 (usually 4–8) mm. long; sheath auricles lacking; blades of the culm folded, about 30–40 cm. long, 2.5–6 (usually 2.5–3.5) mm. wide, the upper and lower surfaces scabrous, the margins sharply saw-toothed; upper throat scabrous; collar scaberulous.

Panicle erect, dark green, 29–55 (usually 30–50) cm. long, 1.5–4 (usually 2–4) cm. wide, the branches ascending or spreading, naked

below, the spikelets clustered above; axis scabrous, primary branches 6–16.5 cm. long, secondary branches 2.5–5.5 cm. long; tertiary branches 1–1.5 cm. long; pedicels shorter than the spikelets, 0.7–2 mm. long, scabrous; spikelets 3–4 (mostly 3.5–3.6) mm. long; glumes equal to or longer than the floret, usually equal to each other, or the second glume 1–2 mm. longer than the first, green-translucent, often punctate-roughened, acute at tip, indistinctly 1-nerved; lemmas acuminate, 2.7–3.8 mm. long, sparsely to densely pubescent on the lower margins, glabrous dorsally (rarely a few sparse hairs on the midnerve below), 3-nerved, awnless or the awns rudimentary, no more than 0.5 mm. long; callus of lemma pilose; palea shorter than the lemma, glabrous or with a few hairs between the nerves.

Fragments of panicle of type, ex P-CO and Fournier herbarium (P) in the U.S. National Herbarium, no. 73225, collected in "Mexique, Prov. de San Luis," in 1851, by Virlet d'Aoust (no. 1415).

DISTRIBUTION: Arroyos and rocky hillsides in the pine-oak zone, at elevations of about 6,600–8,400 ft. Infrequent from San Luis Potosí in central Mexico, south to Puebla. A single collection from Durango is doubtfully referred to this species.

MEXICO: DURANGO: Km. 143 Durango-Mazatlán, *Hernández & Tapia* N-849 (*M. virletii* vel aff.) (CHAP). SAN LUIS POTOSÍ: *Virlet* 1415 (US fragment of type, ex P). PUEBLA: Manzanilla, *Arsène* 1693 (GH, ILL, MO, NY, US). Km. 47, camino de Puebla, *Matuda* 18611 (US). MORELOS: Lagunas Zempoala, *Lyonnet* 2515 (US). MEXICO: Comunidad, Temascaltepec, *Hinton* 2439 (MICH, NY, US). Sultepec, Sultepec, *Hinton* 3219 (ILL, MO, NY, US). 23 mi. SE. of México on highway 190, *Pratt* 751 (TEX). Near Santa Fe, *Rose & Painter* 8010 (NY, US). E. of Ixtlahuaca, *Soderstrom* 512 (US). DISTRITO FEDERAL: Desierto de Leones, *Matuda* 25930 (US). Cerca del Xitle, *Rzedowski* 2167 (IPN). Western part of the Pedregal, *Rzedowski* 2242 (US). Eslava, *St. Pierre* 813 (US). MICHOACÁN: Quinceo, *Arsène* 3201 (ILL, MO, NY, US). Morelia, *Arsène* 6999 (US). Ca. 18 mi. S. of Pátzcuaro, *King & Soderstrom* 5200 (US).

*Muhlenbergia virletii* is distinguished by the very long green spikelets, the lemmas glabrous except toward the base of the margins, the medium ligule, and the absence of sheath auricles. In its nearest ally, *M. robusta*, rudimentary sheath auricles are usually present, the spikelets are shorter, the lemmas are mostly glabrous throughout, and the ligule is shorter (mostly 2–4 mm. as opposed to 4–8 mm. long). The glumes of *M. robusta* are generally purplish or ashy gray; those of *M. virletii* are dark green and appear translucent.

Glume surface is more or less glabrous in some specimens, in others scaberulous or scabrous. Specimens collected in the same locality exhibit such differences. In spikelets of specimens previously referred to *M. presliana* the glumes are glabrous, although Hitchcock described them as scabrous. Specimens have been cited, however, with spikelets about 2 mm. long and the glumes scabrous, e.g., *Hitchcock* 9129

(Guatemala), *Gándara* (Morelos, Mexico), and *Moore, Hernández, & Porras* 5616 (Michoacán, Mexico). Furthermore, specimens were found with the glumes glabrous and the spikelets similar to those of the type of *E. strictus*, except larger, 2.5–3 mm. long, e.g., *Rzedowski* 1999 (México, D. F.). *Sohns* 183 (México, D. F.) has spikelets similar to those of *Rzedowski* 1999 but the glumes are scabrous.

19. *Muhlenbergia breviligula* Hitchc. N. Amer. Fl. 17(6):458. 1935.

Strongly caespitose perennial; culms stout, glabrous to scaberulous, 75–141 cm. tall; nodes 3, glabrous or slightly puberulent below, sometimes puberulent above the nodes; basal sheaths compressed-keeled, the old basal sheaths persistent, becoming brown, curled and fibrillose; ligule of the culm leaves a membranous rim of hairs 0.1–2 mm. long (usually negligible, less than 1 mm. long) those of the innovations sometimes over 1 cm. long; sheath auricles lacking or rudimentary, whitish, 1.5–6 mm. long when present; blades of the culm flat or folded 24–47 cm. long 2–3 (mostly 2.5) mm. wide when flat, the upper surface glabrous to scaberulous, the lower surface scaberulous to scabrous; upper throat scabrous, often pubescent; collar scabrous or puberulent.

Panicle nodding, rather dense, yellowish to purplish brown or purplish green, the branches ascending or opening outward, 30–51 (mostly 30–40) cm. long, 3–9 (mostly 3–5) cm. wide; axis scabrous, the primary branches 6–12 cm. long, the secondary branches 1.5–7 cm. long, the tertiary branches 0.5–3.5 cm. long; pedicels of the lateral spikelets 0.5–1.5 mm. long, those of the terminal spikelets to 3 mm. in length, scaberulous on the lower part, becoming scabrous just below the spikelet; spikelets 2–3 mm. long or sometimes longer (mostly 2.5–3 mm.); glumes about equal, equaling or a little longer than the floret, glabrous (scaberulous at the tips under high power), acute, often slightly awned (awns to 0.2 mm. long), hyaline, faintly 1-nerved; lemmas 2.5–2.6 (usually about 2.5) mm. long, 3-nerved, pubescent on the lower two-thirds of the midvein and lower margins (rarely with hairs between the nerves below), bearing an awn from below the tip, 0.7–1.7 (this usually more than 1) cm. long, flexuous; callus of lemma sparsely pilose; palea a little shorter than the lemma, sparsely pubescent on the lower two-thirds between the keels.

Holotype in the U.S. National Herbarium, no. 995888, collected on clay hill, Guatemala City, Guatemala, alt. 1,500 m., December 2, 1911, by A. S. Hitchcock (no. 9063).

DISTRIBUTION: Rocky hillsides and exposed pine-oak areas, at elevations of 2,000–4,500 ft. Apparently common in Guatemala and Honduras.

GUATEMALA: HUEHUETENANGO: W. of Aguacatán, on the road to Huehuetenango, *Standley* 81190 (F). ALTA VERAPAZ: Sequanquím, *Cook & Doyle*

60 (US). ZACAPA: Volcán Gemelos, *Steyermark* 43251 (F). CHIQUIMULA: Between Chiquimula and Montaña Barriol, 3-15 miles NW. of Chiquimula, *Steyermark* 30649 (F, US). JALAPA: Vicinity of Jalapa, *Standley* 76731 (F, US). GUATEMALA: Guatemala City, *Hitchcock* 9063 (US holotype); *Hitchcock* 9064 (US); *Hitchcock* 9109. JUTIAPA: Between Jutiapa and Plan de Urrutia, *Standley* 75582 (F).

HONDURAS: COMAYAGUA: Between Comayagua and Villa San Antonio, *Archer* 3842 (CAS). FRANCISCO MORAZÁN: 30 km. W. of Tegucigalpa, *Archer* 3846 (US). Río Yeguaré at about longitude 87° W. and latitude 14° N., *Molina* 1593 (US). Río Yeguaré a Danlí, *Rodríguez* 1564 (F, GH). Above El Zamorano, *Standley* 14630 (F); *Standley* 24850 (F). San Antonio del Oriente, above San Antonio, *Swallen* 10968 (US). Mt. Uyuca, beyond Las Floras, *Swallen* 11323 (US). EL PARAÍSO: Mt. Yuscarán, *Molina* 605 (F, GH, US). Güinope, *Rodríguez* 1848 (F). Las Casitas, road to Güinope, *Swallen* 11081 (US). Road to Danlí, beyond Río San Francisco, *Swallen* 11216 (US). Road to Yuscarán, *Swallen* 11359 (US); *Swallen* 11367 (US). 5 km. S. of Ojo de Agua, *Williams & Molina* 11220 (F, GH, US). CHOLUTECA: San Marcos, *Williams & Molina* 10921 (F, GH, MICH, MO, US).

*Muhlenbergia breviligula* is distinguished by the very short ligule, long-awned lemmas pubescent on the lower two-thirds of the midnerve and margins, and spikelets usually 2.5 mm. or longer. In overall aspect it resembles most closely *M. emersleyi*, but in that species the ligule is usually 1 cm. or longer, the blades are considerably broader at the base, and the basal sheaths are not so persistent and fibrillose when old. *Muhlenbergia aurea* is closely allied by the very short ligule and long-awned lemmas; however, its spikelets are small, 2-2.2 mm., and the lemmas are only pubescent toward the base.

20. *Muhlenbergia aurea* Swallen. Contr. U.S. Nat. Herb. 29:411. 1950.

Strongly caespitose perennial; culms stout, glabrous, becoming scaberulous to scabrous toward the panicle, about  $\frac{3}{4}$  m. tall, glabrous beneath the nodes; basal sheaths compressed-keeled, glabrous at the base, becoming scabrous toward the collar; ligule a short membranous rim appressed against the blade and hardly noticeable, 0.3-1.5 mm. long; sheath auricles rudimentary, 0.8-3 mm. long; blades of the culm to 42 cm. long, flat or folded, 2.5-5 mm. wide when unfolded, the upper surface scaberulous, the lower surface scabrous, the edges of the blade saw-toothed; upper throat scabrous; collar scabrous.

Panicle nodding, dense, golden yellow, about 36 cm. long, 7-9 cm. wide, the floriferous branches of the panicle appressed; axis scabrous; primary branches of the panicle 15-17 cm. long, secondary branches 4-6 cm. long, tertiary branches 1.5-2 cm. long; pedicels 1.5-2 mm. long, scabrous; spikelets 1.7-2.2 (mostly 2-2.2) mm. long; glumes about equaling the lemma, the second a little longer than the first, scabrous, very acute or slightly awn-tipped, especially the second glume, hyaline, 1-nerved; lemmas 1.9 mm. long, pubescent on the

lower third of the midvein and margins, acute, indistinctly 3-nerved, bearing an awn from just below the tip, mostly 1–1.5 cm. long; callus of the lemma with short hairs; palea a little shorter than the lemma, glabrous.

Holotype in the Field Museum of Natural History, no. 1057948, collected on lower south-facing slopes of Volcán Santa María de Jesús and Calahuache in thickets at base of vertical slopes along r. r., Dept. of Quezaltenango, Guatemala, alt. 1,300–1,500 m., Dec. 31, 1939, by J. A. Steyermark (no. 33175). A fragment of the holotype and photo are in the U.S. National Herbarium.

DISTRIBUTION: Known only from the type collection.

*Muhlenbergia aurea* is distinguished by the very short ligule, slightly awn-tipped glumes that equal the floret, and long-awned lemmas pubescent on the lower third of the midnerve and margins. In the original description the author remarked, "*Muhlenbergia aurea* is probably most closely related to *M. scoparia* Vasey, which differs in having much narrower sheaths and blades, an elongate ligule, a narrow, less densely flowered, purple panicle, and longer awns." Although related to *M. scoparia*, its closest relative appears to be *M. breviligula*, with which it shares the characteristics of a very short ligule and subequal slightly awn-tipped glumes (in *M. breviligula* the glumes are acute or occasionally somewhat awn-tipped). In *M. scoparia* the ligule is usually 1 cm. long or more and the glumes are unequal, a little shorter than the floret, and longer awn-tipped. *Muhlenbergia aurea* and *M. breviligula* occur much farther south than *M. scoparia*. *Muhlenbergia aurea* is known only from the type collection in Guatemala, *M. breviligula* from Guatemala and Honduras, and *M. scoparia* from northern and central Mexico.

21. *Muhlenbergia grandis* Vasey. Contr. U.S. Nat. Herb. 1:283. 1893.

*Epicampes grandis* (Vasey) Beal. Grasses N. Amer. 2:309. 1896. Based on *Muhlenbergia grandis* Vasey.

*Epicampes bourgaei* var. *grandis* (Vasey) Jones. Contr. West. Bot. 14:7. 1912. Based on *Muhlenbergia grandis* Vasey.

Caespitose perennial; culms glabrous, 88–164 (mostly 100–150) cm. tall; nodes 4, pubescent below (rarely above); basal sheaths compressed-keeled, glabrous, the old ones inflated, papery, brown or usually reddish brown, becoming fibrillose; ligule membranous, lacerate, 1.5–6 mm. long; sheath auricles lacking; blades of the culm 15–34 (mostly about 30) cm. long, flat or folded, 3–8 mm. wide when flat (usually 3–5 mm.), the upper surface of the blade scaberulous to scabrous, the lower surface scaberulous to scabrous, the upper and lower surfaces of the same blade alike; upper throat pubescent; collar a fringe of short white appressed hairs, rarely glabrous.

Panicle erect or somewhat nodding, usually very dense, the panicle branches mostly appressed, the groups of branches borne at intervals along the axis, yellowish or yellowish brown, 30-63 (usually 30-50) cm. long, 2-8 (usually 4-5) cm. wide; axis scaberulous, sometimes with a few hairs, ribbed, the primary branches to 9 (usually 7-9) cm. long, the secondary branches 1.5-4.5 cm. long, the tertiary branches 1-2 cm. long; pedicels of the lateral spikelets 0.5-1.5 mm. long, those of the terminal spikelets longer, to 2.5 cm., glabrous to scabrous, at least scaberulous under the spikelet; spikelets 1.3-2.5 (usually 1.5-2) mm. long; glumes usually about equal to the floret, equal or subequal (the second a little longer than the first), glabrous to scaberulous, roundish at the tips, somewhat erose at the tips (under high power), awnless, hyaline, nerveless; lemmas 1.5-2.2 (usually 1.8-2.1) mm. long, glabrous except for hairs on the lower part of the midnerve, acutish at the tip, 3-nerved, bearing a flexuous awn from below the tip, 6-19 (usually more than 10) mm. long; callus of lemma conspicuously short-pilose; palea a little shorter than the lemma, glabrous or with a few hairs at the base between the keels.

Type in the U.S. National Herbarium, no. 73222, collected in Río Blanco, Jalisco, Mexico, 1886, by Edward Palmer (no. 515).

DISTRIBUTION: Rocky mountainsides and rocky slopes of barrancas and canyons, at elevations of 3,000-5,000 ft. Of limited distribution in western Mexico, occurring from Sonora, south into Nayarit and Jalisco.

MEXICO: *Palmer* 170, in 1885 (TAES), in 1885 (GH, NY). SONORA: Cañon Estrella, Dist. Alamos, *Gentry* 332 M (MICH). NAYARIT: 10 mi. SE. of Tepic, *McVaugh* 13377 (MEXU, SMU, US). 10 mi. SE. of Ahuacatlán, *McVaugh & Koelz* 743 (MICH). JALISCO: SW. Autlán, *Hernández* 4637 (CHAP, US). 1-2 mi. N. of Ahuacapán, *McVaugh* 19531 (MICH, US). Ca. 8 mi. S. of La Resolana, *McVaugh* 21086 (MICH, US). Río Blanco, *Palmer* 415, in 1886 (F), 515, in 1886 (US type), 515a, in 1886 (GH, MO, US), 682, in 1886 (GH, NY, US). Guadalajara, *Pringle* 1760 (F, UC, US, paratypes), 2362 (ARIZ, CAS, GH, MICH, SMU, UC, US), 2765 (F, MO, UC, US fragment), 11751 (CAS, F, GH, MICH, MO, US). 2 mi. W. of Tequila, *Reeder & Reeder* 4205 (US, YU).

*Muhlenbergia grandis* is distinguished by the reddish-brown basal sheaths, collar a dense fringe of short hairs, the short spikelets, and long-awned lemmas short-pilose on the callus. It appears to be most closely related to *M. scoparia* with the reddish-brown sheaths unique to both species; the short spikelet, long-awned lemma, and short-pilose callus are features of both. The glumes of *M. grandis* are about equal and shorter than the floret, but are unequal in *M. scoparia*, long-awned, and about equal to the floret. The ligule of *M. grandis* is usually no more than 6 mm., as opposed to 8-16 mm. long in *M. scoparia*.

22. *Muhlenbergia distans* Swallen. N. Amer. Fl. 17(6):461. 1935

*Muhlenbergia pubescens* (H. B. K.) Hitchc. N. Amer. Fl. 17(6):460. 1935 (as to description only, not as to name).

Caespitose perennial; culms erect, 66–154 cm. tall, glabrous below, becoming scaberulous or scabrous below the panicle; nodes 2–4 on the lower part of the culm, puberulent to pubescent below, especially of the lower nodes; basal sheaths compressed-keeled, glabrous, the keels scaberulous; ligule membranous, firmer below but not decurrent, lacerate above, 0.5–1.5 cm. (usually 5–10 mm.) long; sheath auricles lacking; blades of the culm 11–62 (usually 25–40) cm. long, folded, narrow, 1–5 (mostly 2–3) cm. wide when flat, the edges saw-toothed; upper surface of blade mostly scaberulous, the lower surface mostly scabrous; upper throat scaberulous to scabrous; collar scaberulous to scabrous (mostly scaberulous).

Panicle erect, narrow, greenish brown, 24–40 cm. long, 1.5–4 (usually 2–4) cm. wide, the densely flowered branches ascending, floriferous almost to the base; axis scabrous; primary branches 5.5–9 cm. long, the secondary branches 1–5 (mostly 2–3) cm. long, the tertiary branches mostly 0.5 cm. long; pedicels scabrous, especially just below the spikelet, shorter than the spikelet, those of the lateral spikelets about 1 mm. long, those of the terminal spikelets 1.5–2 mm. long; spikelets 2.7–3.6 (usually 3–3.3) mm. long; glumes broadly acute at the tip, rarely a bit dentate, glabrous-appearing with a roughened surface, the second glume 1–4 mm. longer than the first, indistinctly 1-nerved; lemmas acutish, 2.7–3.4 mm. long, shorter than the glumes, lightly pubescent on and between the nerves over the lower part, the upper part scabrous, the lateral margins densely pubescent toward the base, 3-nerved, the median nerve in many or all of the florets of the panicle extending from below the tip into a short awn, 1.5–5 (at least less than 5) mm. long; palea pubescent on the lower part.

Holotype in the U.S. National Herbarium, no. 746297, collected on dry hills, Las Sedas, Oaxaca, Mexico, alt. 6,000 ft., Sept. 15, 1894, by C. G. Pringle (no. 5575). Isotype at F.

DISTRIBUTION: Rocky slopes and barrancas, in the pine-oak zone, at elevations of 5,000–8,500 ft. Ranging in Mexico from Durango and San Luis Potosí southeastward into Guatemala. Apparently infrequent.

MEXICO: DURANGO: (?) Navíos, *Reeder, Reeder, & Soderstrom* 3379 (US, YU). (?) Llano Grande, *Reeder, Reeder, & Soderstrom* 3396 (US, YU), 3397 (US, YU), 3398 (US, YU). ZACATECAS: W. of Zacatecas on highway to Villanueva, *Soderstrom* 724 (US). SAN LUIS POTOSÍ: 8 mi. W. of Santa Catarina, *Reeder & Reeder* 4103 (US, YU). SW. of San Luis Potosí on road to Aguascalientes, *Reeder, Reeder, & Goodding* 1387 (YU). SW. of San Luis Potosí, *Reeder, Reeder, & Soderstrom* 3327 (US, YU), 3331 (US, YU). Puerta Huerta in the Sierra de

Alvarez, *Sohns* 1044 (US). JALISCO: Paso de Troje, SW. of Ojuelos on road to Aguascalientes, *McVaugh* 16801 (MICH, US). HIDALGO: Pachuca, *Hitchcock* 6708 (US); *Purpus*, Sept. 1905 (UC). Ixmiquilpan, *Purpus* 1466 (UC). Puebla: Cerro Tepoxuchil, *Arsène* 1901 (GH, MO, US). Acatzinco, Distrito de Tepeaca, *Arsène (Bro. Amable)* 2265 (MO, US). Fort de la Guadalupe, *Arsène (Bro. Nicolas)* 5436 (US). Between haciendas Santa Barbara and Cristo, *Arsène*, Aug. 1, 1907 (MO, US). Esperanza, *Hitchcock* 6485 (US). NE. of Zacatecas, *Soderstrom* 486 (US). TLAXCALA: Km. 70 de la carretera Apizaco-México, *Guerrero*, Sept. 25, 1962 (IPN). MEXICO: "Pédregal près Mexico," *Bourgeau* 683(?), 1865-1866 (US fragment ex P). Tenancingo, *Matuda* 28985 (US). DISTRITO FEDERAL: Xochitepec, *García* 86 (IPN). Lomas de Santa Fe, *Lyonnet* 55 (GH, MO, NY, US). Barrancas de Mixcoac, *Lyonnet* 2369 (US). Zacatepec, pedregal de Tlalpan, *Matuda* 21358 (US). Near Tlalpan, *Rose, Painter, & Rose* 8255 (US). On pedregal, *Rose, Painter, & Rose* 9456 (US). Tacubaya, *St. Pierre* 313 (MICH, US). Tacubaya, Dolores, *St. Pierre* 862 (MICH, US), 866 (MICH, US), 869 (US). Jajalpa, *St. Pierre*, 929 (CAS, MICH, US). MICHOACÁN: N. of Loma del Zapote, *Arsène*, Sept. 26, 1909 (MO, US). OAXACA: De Las Sedas a Felix Mahuaca, *Conzatti* 4870 (CAS). Las Sedas, *Pringle* 5574 (F), 5575 (US holotype, F isotype); *Smith* 916 (MO).

GUATEMALA: ZACAPA: Sierra de las Minas, below Finca Alejandria, *Steyermark* 29773 (F).

*Muhlenbergia distans* is distinguished by the greenish-brown spikelets, usually 3 mm. long or more, lemmas pubescent on the lower part, on and between the nerves, and ligules mostly 5-10 mm. long. The panicles are narrow, densely flowered, and have a distinctive brownish color. The basal sheaths are characteristically dark brown and firm when old. Apparently it is most closely related to *M. versicolor*, having in common the relatively greenish spikelets consisting of subequal glumes, lemmas pubescent on and between the nerves, and nodes pubescent below. In *M. versicolor* the glumes are often awn-tipped (especially the longer second glume) but only slightly dentate at the tip and not awned in *M. distans*. The lemmas of *M. versicolor* bear long awns on all the spikelets of the panicle; in typical *M. distans* short-awned and awnless spikelets occur in the same panicle. Moreover, *M. versicolor* is generally characterized by sheath auricles, which are lacking in *M. distans*.

*Muhlenbergia distans* was described from a specimen collected on dry hills, Las Sedas, Oaxaca, Mexico, in 1894 and has been known only from the type collection. It is a small tufted perennial with narrow culms and panicles with loosely ascending branches. The brownish spikelets range in length from 2.7-3.5 mm., the somewhat scaberulous glumes are acutish, and the short-awned lemmas are lightly villous on and between the nerves for a greater part of the length, with densely pubescent margins. Specimens previously referred to *M. pubescens* (H.B.K.) Hitchc. appear to belong to this species. As the name *M. pubescens* (H.B.K.) Hitchc. is untenable for these specimens, *M. distans* Swallen is the proper epithet. The majority of

cited specimens differ from the type of *M. distans* in being more robust and having thicker culms and denser panicles. However, the basic characters are similar, for the brownish spikelets are about 3 mm. long, the short-awned lemmas are pubescent on and between the nerves, although the pubescence is confined mostly to the lower half, and the ligules are about 5-10 mm. long. The holotype of *M. distans* appears to represent a smaller than typical and less robust representative of the species. *Conzatti* 4870, collected near the type locality, is more robust and has larger panicles than the type and is in all respects more like the majority of specimens referred to *M. distans*. Such differences as size and looseness versus denseness of panicles are variable characters within species of *Epicampes*. The spikelet and ligule are the more stable characters and are of greater importance in referring these specimens to *M. distans*.

Three collections (*Reeder, Reeder, & Soderstrom* 3379, 3396, and 3398) are doubtfully referred to *M. distans*. These specimens have long spikelets with the lemmas pubescent over the lower part and ligules about 1 cm. long. The habit of the panicles and plants, however, is more like that of *M. emersleyi* than of *M. distans*.

**23. *Muhlenbergia longiglumis* Vasey. Contr. U.S. Nat. Herb. 1:283. 1893.**

Caespitose perennial; culms glabrous,  $\frac{3}{4}$ -1 m. tall; nodes 2 (or 3?), pubescent below; basal sheaths compressed-keeled, glabrous, the old ones becoming brown and fibrous; ligule membranous, brownish and firmer on the lower part, thinner and lacerate above, 4-10 mm. or longer; sheath auricles lacking; blades of the culm 20-30 cm. long, folded, 1.5-2 mm. wide when flat; upper surface of the blade scaberulous to scabrous, the lower surface mostly scabrous (rarely glabrous); upper throat scabrous; collar scabrous.

Panicle erect or somewhat nodding, narrow, 20-40 (mostly about 30) cm. long, 1-2.5 cm. wide (excluding awns), the branches of the panicle about 3-3.5 cm. long, ascending, borne in verticils of approximate clusters of 2-6 at intervals along the axis, the body of the panicle light green, sharply contrasting with the dark purple awns; axis scaberulous, ribbed; pedicels of the lateral spikelets 2-3 mm. long, those of the terminal longer, scabrous on the narrow lower portion, pubescent on the swollen upper portion subtending the spikelet; spikelets 5-7 (mostly 6-7) mm. long; glumes about equal, a little longer than the floret, the surface with sparse short hairs, attenuate, awn-tipped (the awn 1 mm. long or less), grayish green, hyaline, 1-nerved; lemmas 4-5 mm. long, the margins densely pubescent on the lower  $\frac{1}{2}$ - $\frac{1}{3}$ , internerves glabrous or slightly pubescent near the base, remainder of lemma glabrous to scaberulous, lanceolate, 3-nerved, bearing a flexuous awn from below the tip, 2-6.5 cm. long;

callus of lemma bearing a dense ring of white hairs up to 1.5 mm. long; palea about equaling the lemma, glabrous or sparsely pubescent between the keels; anthers 3, yellow or greenish yellow, 2–3 mm. long.

Holotype in the U.S. National Herbarium, no. 2383429, collected near Guadalajara, Jalisco, Mexico, July–October 1886, by Edward Palmer (no. 766).

**DISTRIBUTION:** Rocky mountainsides in the pine-oak zone, at elevations of 5,000–7,000 ft. Apparently of limited distribution, all collections except one being from Jalisco; the one from Aguascalientes is from near the Jalisco border, and possibly on the Jalisco side.

**MEXICO:** *Palmer*, in 1886 (MO, may be part of *Palmer* 766 in 1886). **AGUASCALIENTES:** Sierra del Laurel, ca. 10 mi. SE. of Calvillo, *McVaugh & Koelz* 171 (MICH). **JALISCO:** 4–4.5 mi. NW. of Cuautla, road to Los Volcanes, *McVaugh* 20462 (MICH). Guadalajara, *Palmer* 766, in 1886 (US, holotype); *Pringle* 2365 (US), 11752 (GH, US).

*Muhlenbergia longiglumis* is distinguished by its awn-tipped, long glumes, light grayish green in contrast to the long dark purple awns of the lemmas, and lemmas glabrous except at the base. The purplish green panicle is not unlike that found in *M. versicolor*, although the species is probably most closely related to *M. emersleyi* with its long ligule, pyramidal panicle, and generally similar habit.

**24. *Muhlenbergia emersleyi* Vasey.** Contr. U.S. Nat. Herb. 3:66. 1892.

*Muhlenbergia distichophylla* sensu Vasey in Rothrock, Bot. Wheeler Surv. 283. 1878. Not *Podosaemum distichophyllum* J. S. Presl in K. B. Presl, Rel. Haenk. 1:231. 1830=*Muhlenbergia distichophylla* (J. S. Presl) Kunth. Description based on Rothrock 282 and 283.

*Muhlenbergia vaseyana* Scribn. Rep. Missouri Bot. Gard. 10:52. 1899. Based on *Muhlenbergia distichophylla* sensu Vasey, not *Podosaemum distichophyllum* J. S. Presl, 1830. Syntypes (by inference) Rothrock 282 and 283, from Rocky Canyon, Arizona, the basis of Vasey's description as cited above. Rothrock 282 is chosen as lectotype.

*Epicampes stricta* var. *distichophylla* sensu Jones, Contr. West. Bot. 14:6. 1912, in part as to the synonyms cited, *M. vaseyana* and *M. emersleyi*, not as to the basionym, *Podosaemum distichophyllum* J. S. Presl.

*Epicampes emersleyi* (Vasey) Hitchc. Bull. U.S. Dept. Agr. 772:144. 1920. Based on *Muhlenbergia emersleyi* Vasey.

*Epicampes subpatens* Hitchc. Bull. U.S. Dept. Agr. 772:144. 1920. (*Hitchcock* 13541, Guadalupe Mountains near Queen, New Mexico.)

Caespitose perennial; culms erect, narrow to thick, glabrous (rarely roughened), 1–1.5 meters, occasionally to 2 meters tall; nodes 3–4, glabrous or somewhat puberulent beneath; basal sheaths compressed-keeled, glabrous; ligule long, membranous, usually a little firmer at the base than above where thin and usually lacerated into narrow strands, ligules of the innovations long, narrow, and membranous throughout, conspicuous; sheath auricles lacking; blades of the culm 23–47 (mostly

20–40) cm. long, 2–6 mm. wide, flat or folded, the upper surface glabrous to scaberulous, the lower surface scabrous, at least the lower surface more scabrous than the upper surface of the same blade, the edges saw-toothed; upper throat scaberulous to scabrous (mostly scabrous); collar scaberulous.

Panicle typically lax above, the branches loosely ascending or spreading, the panicle pyramidal, light purplish to purplish tan, 20–40 (mostly 30–40) cm. long, 4–7 cm. wide (often much wider in the field); axis glabrous to scaberulous (rarely scabrous), the branches of all the orders naked below, the primary branches 9–17 (usually 9–12) cm. long, the secondary branches 3–9 (mostly 3–5) cm. long, the tertiary branches 0.5–4.5 (mostly 0.5–1.5) cm. long, quaternary branches sometimes present, as much as 2 cm. long; pedicels glabrous to scaberulous (sometimes scabrous), more scabrous just below the spikelet, pedicels of the lateral spikelets 0.5–1.5 mm. long, those of the terminal spikelets 1.5–3 mm. long; spikelets 2.2–3.2 mm. long, occasionally shorter or longer (usually 2.5–3, but most frequently 2.5–2.7 mm. long); glumes broadly acute, about equal to each other or the second glume 1–2 mm. longer than the first, mostly scaberulous to evenly scabrous, indistinctly 1-nerved; lemmas acutish, a little shorter than the glumes, pubescent on the midnerve and margins about one-half to three-quarters of the length, the pubescence varying from sparse to rather dense, that of the margins generally denser than that of the midnerve, the lemma 3-nerved, the middle nerve often excurrent from below the tip into an awn as long as 15 mm., generally purplish and flexuous, the awn persistent or deciduous, breaking off easily at the point of attachment to the lemma; palea a little shorter than the lemma, more or less pubescent between the keels for one-half to three-quarters of the length.

Type in the U.S. National Herbarium, no. 73223, collected in southern Arizona in 1890, "a coarse range grass that stock do not like," by J. D. Emersley (no. 46).

DISTRIBUTION: Rocky mountain slopes, barrancas, canyons, arroyos, and rocky ledges, at elevations of 4,500–7,500 ft., occurring most frequently at about 6,000–7,000 ft. The most common species of *Epicampes*, ranging from Texas to Arizona into northern Mexico, becoming less frequent south of Durango to Oaxaca.

UNITED STATES: TEXAS: Hucco, *Mulford* 80 (ILL, MO, NY). *Nealley*, in 1889 (DS, MICH, NY, UC, US), in 1890 (NY, US). "Common all over mts.," *Swallen* 1101 (US). Pine Spring, *Whitehouse* 8533 (US). "Expedition from western Texas to El Paso," *Wright* 729 (UC, US), 730 (GH, UC, US), 736 (US). BREWSTER COUNTY: Chisos Mountains, *Bailey* 392 (US). Green Gulch, *Berkman* Sept. 10, 1925 (TEX). Highway 223, *Brown* 30 (TEX). 6 mi. S. of Alpine, *Brown* 47 (TEX). N. of Alpine, *Carter* 19 (US). Blue Creek Trail, *Cory* 7272 (POM). Davis Mountains, 6 mi. W. of Alpine, *Cory* 40248 (TEX), 40413 (TAES).

Chisos Mountains, *Havard*, August 1833 (US). Alpine, *Hitchcock* 13594 (US). 5 mi. SW. of Marathon, *Johnston* 3336 (CAS, TEX). Elephant Mesa, *Johnston* 6427 (LL). Green Gulch, *Lundell* 13250 (LL, UC). Chisos Mountains, *Marsh* 56 (F). Lower Pine Canyon, *Marsh* 282 (GH, TAES, TEX), 322 (GH, TAES, TEX, US). Upper Pine Canyon, *Marsh* 351 (GH, TEX). Big Bend National Park, *Marsh* 51-1153 (TEX). Boot Spring, *Moore & Steyermark* 3181 (GH, MICH, MO, NY, UC, US). Emory Peak, *Mueller* 7850 (GH, MICH, NY, SMU, TAES, TEX, UC, US). Chisos Mountains, *Muller*, July 25, 1932 (DS, GH, UC). Blue Creek Canyon, *Parks & Cory* 7270 (TAES). Upper Blue Creek, *Parks & Cory* 7271 (TAES). Boot Ravine, *Parks & Cory* 30350 (TAES). Iron Mountain, *Parks & Cory* 30567 (TAES). Big Bend, *Reed* 90 (SMU), 99 (ARIZ). Iron Mountain, *Reed* 109 (UC), 112 (CAS). Hidden Valley, *Rose-Innes & Moon* 1266 (TEX). Big Bend National Park, *Shinners* 8799 (SMU). SR Hill, *Sperry* T487 (ARIZ, TAES). Green Gulch, *Sperry* 1805 (TAES). Casa Grande, *Warnock* 806 (DS, SMU). Mt. Emory, *Warnock* 12378 (TAES). McIntire Hill, *Warnock* 20270 (TEX). Split Tanks, *Warnock* 20766 (TEX). Baldy Peak, *Warnock* 20805 (TEX). Goat Mountain, *Warnock* 21470 (TEX). Old Marfa highway 2 mi. S. of Alpine, *Warnock* 21731 (TEX). S. of Alpine, *Warnock*, May 5, 1938 (ARIZ, GH). Blue Creek Canyon, *Wolff* 4693 (TAES), 4698 (F, TAES). Nail Place, *Young*, Aug. 7, 1915 (TEX). CULBERSON COUNTY: Guadalupe Mountains, *Bailey* 739 (US); *Havard*, in 1881 (US); *Silveus* 7674 (CAS, DS, SMU, TAES, TEX); *Young*, Sept. 5, 1916 (TEX). NE. of Pine Springs, *Correll & Johnston* 24231 (LL). McKittrick Canyon, *Moore & Steyermark* 3636 (CAS, DS, GH, MICH, MO, NY, UC, US); *Warnock* 10930 (ILL, LL, SMU), 12089 (LL, SMU). Mountains toward the Rio Grande, *Wright* 729 (GH). EL PASO COUNTY: Hueco Tanks, *Parks & Cory* 30973 (TAES); *Whitehouse*, Nov. 11, 1931 (TEX). Franklin Mountains, *Warnock* 14271 (LL, TEX). El Paso, *Whitehouse* 8531 (TEX). GILLESPIE COUNTY: *Reed*, January 1890 (MICH). HARDIN COUNTY: Camp Mountain, *Parks & Cory* 7093 (TAES). HUDSPETH COUNTY: Eagle Mountain, *Waterfall* 6341 (MO). JEFF DAVIS COUNTY: Davis Mountains, *Brown* 4213 (TEX); *Young* 20a (TEX), 40 (MO, US), Aug. 6, 1914 (TEX), Aug. 10, 1914 (GH, TEX). Fort Davis, *Carter* 61 (US); *Silveus* 7675 (CAS, SMU, TAES, TEX). Sawtooth Mountain, *Correll* 15008 (LL). Halloran, Nov. 29, 1940 (TAES). Mt. Livermore, *Hinckley* 101 (MICH), July 1936 (ARIZ, GH, NY), Aug. 27, 1939 (TEX). Limpia Canyon, *Nealley* 133 (DS, GH, ILL, MO, NY, POM, UC, US), in 1890 (US); *Reeder & Reeder* 4234 (YU); *Silveus* 294 (TAES, TEX). Castle Mountain, *Reeves* 1646 (TAES). Alpine-Ft. Davis, *Silveus* 824 (US). 15 mi. N. of Alpine, *Silveus* 825 (TAES, TEX). Mosquiz Canyon-Alpine-Ft. Davis road, *Silveus* 826 (CAS, TEX, US). McDonald Observatory, *Turner* 2970 (SMU). Scenic Loop of Davis Mountains, *Warnock* 9285 (LL, SMU). Mosquiz Canyon, *Warnock* 46557 (TEX). PRESIDIO COUNTY: Chinati Peak, *Correll & Johnston* 24378 (LL). 26 mi. SE. of Marfa, *Cory* 2852 (GH). KNOX CANYON, *Hinckley* 2039 (SMU), July 20, 1941 (TEX). NEVADA: *Wheeler*, in 1872 (US). CLARK COUNTY: Las Vegas, *Arsène*, October 1925 (NY). NEW MEXICO: Gray, *Goodding* M-251.1 (US). *Vasey* (NY). *Wright* 1990 (CAS, GH, MO, NY, TAES, US). BERNALILLO COUNTY: Sandia Mountains, *Rominger* 16 (UNM). CATRON COUNTY: Mangas Canyon, *Melcalfe*, Sept. 15, 1896 (US), November 1896 (US). Tularos Creek, *Olson* 439 (UC). Mogollon Mountains, *Rusby* 463 (ILL, MICH, MO, NY, UC, US), 597 (US). DONA ANA COUNTY: Dripping Springs, *Archer* 498 (MICH), *Dunn* 7284 (UNM). Organ Mountains, *Hitchcock* 3769 (US), 3795 (MICH, US); *Vasey*, August 1881 (US); *Wooton* 461 (DS, MO, NY, US), May 1891 (UNM), Sept. 17, 1893 (DS, UC, US), August 1894 (UNM), Sept. 17, 1903 (DS); *Wooton & Standley*, Sept. 23, 1906 (US). Mesilla Valley, *Fosberg* S-3674 (A, POM). Las

Cruces, *Griffiths* 7427 (US). Peña Blanca, *Standley*, Oct. 21, 1906 (US), Oct. 28, 1906 (US). Van Pattens Camp, *Wootton*, Sept. 10, 1899 (ILL). GRANT COUNTY: Mule Creek road, *Anderson & Rhinehart* 503 (TAES). Fort Bayard Watershed, *Blumer*, Nov. 18, 1905 (GH, NY, US). Black Range, *Goodding & Goodding* 381 (ARIZ). Silver City, *Greene* 439 (F, US), 440 (US). *Rusby*, in 1880 (US). Greenwood Cañon, *Smith*, Sept. 24, 1896 (US). "Copper-mines," *Wright* 1994 (GH, MO, NY, UC). HIDALGO COUNTY: Clanton Canyon, *Castetter* 10235 (UNM), 10244 (UNM). Little Hatchet Mountains, *Castetter* 10387 (UNM). Skeleton Canyon, *Castetter* 11256 (UNM). Coronado Forest S. of Animas, *Goodding* CG-14 (US). 20 mi. N. of Rodeo, *Goodding* M-248 (ARIZ, US). Below Animas Peak, *Goodding & Goodding* A-9775 (ARIZ, SMU), M-385 (ARIZ, LL). White Water, *Mearns* 352 (US). Dog Mountains, *Mearns* 2373 (US). Animas Valley, *Mearns* 2507 (US). LINCOLN COUNTY: S. of Fort Stanton, *Goodding & Goodding* M-183 (MO). OTERO COUNTY: Guadalupe ridge, *Chapline* 690 (US). Guadalupe Mountains, *Goodding & Goodding* M-201 (ARIZ, NY); *Hitchcock* 13541 (US holotype of *E. subpatens*). Gray's Ranch, *Goodding & Hardies* M-135 (MICH), M-136 (US), M-137 (ARIZ). Queen, *Hitchcock* 13500 (US), 13579 (US); *Amer. Gr. Nat. Herb.* 1382 (CAS, GH, LL, MO, UC), 1383 (CAS, GH, LL, MO, UC, US). SAN MIGUEL COUNTY: Las Vegas, *Aneet* 198 (GH, NY, US); *Arsène* 17968 (UC); *Drouet & Richards* 3224 (F). SIERRA COUNTY: Lake Valley, *Beals*, in 1914 (MICH, US). Black Range, *Metcalf* 1366 (CAS, F, GH, MO, NY, UC, US). SOCORRO COUNTY: Socorro, *Plank* 53 (US). 12 mi. S. of Magdalena, *Potter* 12 (UNM). ARIZONA: 3 mi. W. of Palominas, *Goodding*, Oct. 6, 1935 (ARIZ). Celero Mountains, *Griffiths* 6122 (MO, US). Stein's Pass, *Jones* 4219 (ARIZ, CAS, F, POM, UC, US). Wood's Ranch, *McDougal* 490 (US). Niggerhead Mountains, *Mearns* 1871 (US). *Miera* 1 (UNM). Devils Canyon, *Peebles, Harrison, & Kearney* 3200 (ARIZ). *Pringle*, June 17, 1884 (NY). Montezuma Wells, *Purpus* 8289 (MO, UC, US). "Explorations and surveys W. of the 100th. meridian," *Rothrock* 282 (GH syntype of *M. vaseyana*). "In all canyons," *Rusby* G(MO, NY). White Mountains, *Schroeder*, summer 1938 (ARIZ). *Vasey*, in 1889 (US). COCHISE COUNTY: Chiricahua Mountains, *Blumer* 68 (ARIZ). Paradise, *Blumer* 1698 (ARIZ, DS, F, GH, MO, NY, US). Upper Hunt Canyon, *Clark* 8457 (ARIZ). Upper Rhyolite Canyon, *Clark* 8510 (ARIZ). 8 mi. W. of Wilcox, *Darrow*, Sept. 10, 1942 (ARIZ, UC). Carr Canyon, *Darrow, Gould, Phillips, & Pultz* 1402 (DS), 2436 (ARIZ, CAS, UC, US). Black Canyon, *Goodding* 429-49 (ARIZ). Coyote Canyon, *Goodding* 1123-49 (ARIZ). Golden Eagle Box Canyon, *Goodding* 88-54 (ARIZ, UC), 30-55 (ARIZ). Huachuca Canyon, *Goodding* 709-58 (ARIZ). Huachuca Mountains, *Goodding* 251-62 (ARIZ); *Jones*, Sept. 3, 1903 (DS, POM). Guadalupe Canyon, *Gould & Haskell* 4540 (ARIZ, GH). Dragoon Mountains, *Griffiths* 1876 (ARIZ, US). *Pearce, Griffiths* 1957 (ARIZ, US). Ramsey Canyon, *Jones* 24736 (CAS, GH, MO, POM, UC), Sept. 30, 1929 (NY). Dos Cabezas, *McDougal* 778 (US). Pedregosa Mountains, *Mearns* 838 (US). San Simon, *Thorner* 2225 (ARIZ). Pine Canyon, *Toumey* 14 (US, YU), Sept. 10, 1896 (NY, US). Blue Canyon, *Toumey* 15a (US). Fort Huachuca, *Wilcox* 410 (US), 446 (TAES), in 1894 (NY, US). COCONINO COUNTY: Kaibab Forest, *Pase* 343 (US). GILA COUNTY: on road from Globe to Coolidge Dam, *Eastward* 16646 (CAS). Pocket Creek Canyon, *Gould* 3741 (ARIZ, GH, NY, UC, US). Parker Creek Canyon, *Gould & Hudson* 3867 (ARIZ). Pinal Mountains, *Shreve* 7454a (ARIZ). Pine, *Toumey* 67 (US), July 23, 1892 (ARIZ, DS, UC). GRAHAM COUNTY: 7 mi. S. of Stockton Pass road, *Anderson & Rhinehart* 603 (ARIZ). Clifton road, *Anderson & Rhinehart* 622 (ARIZ, TAES). Porter Springs, *Kessler* 485 (ARIZ, TAES). Graham Mountains, *Moeller* 186 (ARIZ, TAES). San Simon Valley, *Thorner*, Aug. 22, 1905 (ARIZ). MOHAVE COUNTY:

Hualpi Mountains, *Nichol*, Sept. 14, 1937 (ARIZ). PIMA COUNTY: Redington Pass, *Benson* 9216 (ARIZ, DS, POM). Sabino Canyon, *Benson* 10559 (POM). Happy Valley Trail, *Blumer* 3453 (F). Sabino Trail, *Carter*, Nov. 20, 1932 (ARIZ). Soldier Canyon, *Darrow*, Sept. 27, 1936 (GH). Fresnal Canyon, *Gilman* 11 (ARIZ). Baboquivari Canyon, *Gilman* 17 (DS, NY, US). Prison Road, *Ginter*, Oct. 6, 1941 (UC). Coyote Mountains, *Goodding & Lusher* 97-45 (ARIZ, NY). About 25 mi. E. of Tucson, *Gould* 2565 (ARIZ, MO, UC, US). Santa Rita Forest Reserve, *Griffiths* 3437 (US), 5936 (ILL, US). Santa Catalina Mountains, *Griffiths* 7043 (US), 7047 (US), 7048 (US), 7149 (ILL, US), 7164 (US); *Pringle*, May 14, 1883 (MO, YU); *Thorner* 9217 (ARIZ). Baboquivari Mountains, *Jones* 24737 (CAS, GH, MO, POM, TEX, UC), Sept. 19, 1929 (NY). Molina Basin, *Leader & Leader* 228 (ARIZ). Redding Pass Road, *Leader & Leader* 371 (ARIZ). Baboquivari Canyon, *Peebles* 532 (ARIZ). Mt. Lemmon, *Peebles & Harrison* 2293 (MO). Rincon Mountains, *Pringle*, July 19, 1884 (CAS, F, GH, LL, NY, US). Soldier Canyon, *Shreve* 5420 (ARIZ, GH). White House Canyon, *Stewart*, Sept. 23, 1942 (NY). Soldiers' Trail, *Stewart*, Oct. 10, 1942 (NY). Floritas Canyon, *Streik* S-32 (ARIZ). Rosemont, *Thorner*, Sept. 30, 1901 (ARIZ, DS, UC). Tucson, *Toumey*, in 1892 (NY, UC, US). Reddington Pass, *Young*, Oct. 2, 1939 (ILL). PINAL COUNTY: Oracle, *Thorner*, Sept. 9, 19(?) (ARIZ). SANTA CRUZ COUNTY: Santa Rita Mountains, *Arnold & Arnold*, Aug. 23, 1939 (UC); *Griffiths* 7257 (US); *Griffiths & Thorner* 46 (US); *Jones*, Aug. 24, 1903 (POM, UC); *Thorner & Griffiths* 46 (ARIZ). Box Canyon, *Arnold*, Sept. 16, 1936 (GH). White House (Madera) Canyon, *Benson* 9732 (POM); *Graham* 3635 (DS); *Parker* 7079 (ARIZ). Stone Cabin Canyon, *Culley* 36 (ARIZ); *Thorner* 188 (ARIZ, DS, MO, NY, POM, UC), 5245 (ARIZ), Sept. 14, 1903 (UC). Sycamore Canyon, *Goodding* M-258 (LL, SMU); *Goodding & Goodding* 431 (ARIZ); *Parker* 7381 (ARIZ, ILL). Nogales, *Harris*, Sept. 19, 1927 (MO, POM); *Peebles & Harrison* 4695 (ARIZ). Patagonia, *Hitchcock* 3689 (US), 3719 (US), 3720 (US); *Kearney & Peebles* 10050 (MICH, US). Coronado National Forest, *Killip* 40854 (US). YAVAPAI COUNTY: Granite Dells, *Benham* M-95 (ARIZ); *Darrow*, Sept. 3, 1939 (ARIZ, UC). Mingus Mountain, *Benham* M-109 (MICH, YU); *Goodding* 174-46 (ARIZ, NY). Fort Whipple, *Coues & Palmer* 424 (MO). 10 mi. S. of Prescott, *Featherly*, July 18, 1929 (SMU). Prescott, *Kearney & Peebles* 9735 (ARIZ, US); *Purchase* 527 (MICH); *Thorner* 8644 (ARIZ); *Williams* 3037 (US).

MEXICO: *Palmer*, in 1886 (ARIZ). *Wilkinson* 9601 (F, NY, US). BAJA CALIFORNIA: El Tasto, *Brandegge*, Sept. 13, 1893 (NY, UC, US), Nov. 1902 (UC). Sierra de San Francisquito, *Brandegge*, Sept. 24, 1899 (US), Sept. 29, 1899 (UC). Sierra de la Laguna, *Brandegge*, Oct. 4, 1899 (UC, US). Cerro de la Giganta, *Carter, Alexander, & Kellogg* 2025 (DS, GH, LL, MO, UC, US). Sierra de la Laguna, E. of Todos Santos, *Carter, Alexander, & Kellogg* 2382 (DS, GH, UC, US). SONORA: Cañon Estrella, *Gentry* 394 M (DS, MICH), Oct. 1, 1933 (US). Cerro del Capulin, NW. of Aribabi, *Harvey* 1688 (CAS, GH, MICH, MO, US). Estación de Tajo, *Hernández & Tapia* N-1569 (CHIAP). San José Mountains, *Mearns* 962 (US). Sierra de los Alamos, *Palmer* 409, in 1890 (CAS, GH, US). Colonia Morelos, *Santos* 30 (US) 174 (US). 20 mi. W. of La Angostura, *Santos* 1798 (GH). El Tigre to El Rancho de Robles, *Santos* 1925 (ARIZ, GH, MICH, MO, NY, SMU, TEX, US). El Rancho de Robles to Colonia Morelos, *Santos* 1974 (ARIZ). El Puerto del Cumarito, *Santos* 2090 (GH, SMU, TEX). El Cañon de la Bellota, *Santos* 2109 (DS, SMU, TEX). El Picacho del Pilar, *Santos* 2166 (GH, SMU, TEX). Cañon del Agua Amarga, *White* 3631 (MICH). 8 mi. S. of Nogales, Sonora, *Wiggins* 7535 (DS, MICH, US). CHIHUAHUA: Arroyo Mesteño, Sierra del Nido, *Christman* 170 (UC). 15 mi. S. of Encinillas, *Correll* 23294 (LL). Minas Nuevas, *Correll & Gentry*

22736 (LL). Between Guadalupe y Calvo and Tecolote, *Correll & Gentry* 23237 (LL). Guasaremos, *Gentry* 1874 (ARIZ, F, GH, MEXU, MO, UC). Rancho Carretas, *Harvey* 1627 (CAS, GH, MICH, MO, US), 1641 (MICH). Km. 1773 carretera Cd. Juárez, *Hernández & Mathus* N-1837 (GH). Sánchez, *Hitchcock* 7669 (US), 7669 ½ (NY, US), 7714 (ILL, US). Miñaca, *Hitchcock* 7742 (US). Pirámide, *Johnston* 8118 (GH). Guayanopa Canyon, *Jones*, Sept. 24, 1903 (NY, POM). Río Gavilán, *Leopold* 225 (US). Majalca, *Le Sueur* Mex-021 (GH, MO, SMU, TEX, US). Chuhuichupa, *Le Sueur* Mex-087 (TEX). NW. of Chihuahua, *Le Sueur* 0149 (CAS, GH, MO, SMU, UC, US). 20 mi. SW. of Chuhuichupa, *Muller* 3594 (GH, LL, MICH, UC). Sierra Gazachic, SW. of Miñaca, *Pennell* 18957 (US). 15 mi. S. of Madera, *Reeder & Reeder* 2640 (YU). 23 mi. SE. of Chuhuichupa, *Reeder & Reeder* 2670 (YU), 2671 (YU). 37 mi. S. of Villa Matamoros, *Reeder, Reeder, & Soderstrom* 3449 (US, YU). 4 mi. E. of Parral, *Reeder, Reeder, & Soderstrom* 3457 (US, YU). 1 mi. E. of Cuauhtémoc, *Reeder, Reeder, & Soderstrom* 3467 (US, YU). 16 mi. W. of Cuauhtémoc, *Reeder, Reeder, & Soderstrom* 3469 (US, YU), 3470 (US, YU), 3471 (US, YU), 3472 (US, YU). 12 mi. N. of Chihuahua, *Reeder, Reeder, & Soderstrom* 3482 (US, YU), 3485 (US, YU). 15 mi. W. of Flores Magon, *Reeder, Reeder, & Soderstrom* 3499 (US, YU). 12 mi. W. of Colonia Juárez, *Reeder, Reeder, & Soderstrom* 3502 (US, YU), 3503 (US, YU). S. of Hernández, *Reeder, Reeder, & Soderstrom* 3524 (US, YU), 3533 (US, YU). NE. of Cuesta Blanca, *Reeder, Reeder, & Soderstrom* 3542 (US, YU), 3543 (US, YU), 3548 (US, YU), 3549 (US, YU). Parral, *Soderstrom* 828 (US, YU). San Francisco de Oro, *Soderstrom* 870 (US, YU), 871 (US, YU). 13 mi. SW. of Cuauhtémoc, *Soderstrom* 917 (US, YU), 918 (US, YU). 12 mi. N. of Chihuahua, *Soderstrom* 930 (US, YU). Sierra Hechiceros near the Coahuilan border, *Stewart* 202 (GH). Organos, *Stewart & Johnston* 2066 (GH). Casas Grandes, *Townsend & Barber* 357 (CAS, F, GH, ILL, MO, NY, POM, UC, US). Santa Eulalia Hills, *Wilkinson*, Aug. 25, 1885 (F, US), Sept. 21, 1885 (UC). COAHUILA: Corte Blanco fork of Charretera Canyon, *Johnston* 8950 (GH, MO). 2 mi. NE. of Nava, *Johnston & Graham* 4166 (TEX). La Noria, *Johnston & Muller* 462 (GH, LL), 587 (GH, LL). Del Carmen Mountains, *Marsh* 624 (GH, TEX, US), 655 (GH, TEX, US). Santa Rosa Mountains, *Marsh* 1511 (F, GH, TEX). Sierra de la Gloria, *Marsh* 1948 (F, GH, TEX). 1 mi. S. of Cuesta Blanca, *Reeder & Reeder* 3227 (YU). 26 mi. E. of Saltillo, *Reeder, Reeder, & Soderstrom* 3289 (US, YU). Jaral, *Schumann* 1753 (US). La Noria, *Stewart* 1208 (GH). Sierra del Carmen, Villa Acuña, *Wynd & Mueller* 594 (US). NUEVO LEON: Dulces Nombres, *Meyer & Rogers* 3092 (MO, US). Monterrey, *Mueller & Mueller* 385 (GH). Ca. 10 mi. E. of Galeana, *Reeder & Reeder* 3973 (US, YU). Mt. Mirador, *Roybal* 60 (US). 8 mi. N. of Escondido, *Shreve & Tinkham* 9714a (ARIZ). TAMAULIPAS: (?)El Rosario, *Bartlett* 10882 (CAS, GH, MICH, NY, POM). 11 mi. W. of Victoria toward Jaumave, *Johnston & Graham* 4141 K (TEX). (?)Sierra de Tamaulipas, at Santa María de los Nogales, *Martínez & Borja* F-1939, aff. *M. emersleyi* (TEX), F-2083, aff. *M. emersleyi* (TEX). SINALOA: Cerro Babuyo, *Gentry* 11420 (US). Ortega 3118 (US). 18 mi. E. of Santa Lucía, *Reeder & Reeder* 2469 (YU). DURANGO: 40 mi. S. of Durango, *Hernández, Ruppert, & Guevara* X-2558 (US). Durango, *Hitchcock* 7621 (US); *Palmer* 542, in 1896 (CAS, F, GH, MO, UC, US). Otinapa, *Palmer* 344, in 1906 (F, GH, NY, US), 553, in 1906 (US). 25 mi. W. of Durango, *Reeder, Reeder, & Soderstrom* 3440 (US, YU), 3441 (US, YU). 27 mi. SE. of Durango, *Soderstrom* 756 (US), 758 (US). SW. of Durango on Durango-Mazatlán road, *Soderstrom* 767 (US), 772 (US), 775 (US). 6 mi. N. of Durango, *Soderstrom* 787 (US), 789 (US). ZACATECAS: 6 mi. SW. of Carboneras, *Gentry* 8522. 15 mi. W. of Zacatecas, *Soderstrom* 725 (US). 25 mi. NW. of Fresnillo, *Soderstrom* 728

(US), 729 (US). Sombrerete, *Soderstrom* 734 (US), 735 (US), 746 (US), 753 (US). SAN LUIS POTOSÍ: 8 mi. W. of Santa Catarina, *Reeder & Reeder* 4104. SW. of San Luis Potosí, *Reeder, Reeder, & Soderstrom* 3303 (US, YU), 3324 (US, YU), 3325 (US, YU), 3326 (US, YU), 3330 (US, YU). Sierra de San Miguelito, *Sohns* 1140 (US), 1151 (US), 1157 (US), 1320 (US), 1465 (US). Sierra de Alvarez, *Sohns* 1385 (US). AGUASCALIENTES: Rincón de Romos, *Reeder, Reeder, & Soderstrom* 3335 (US). JALISCO: Bolaños, *Rose* 3003 (US). 15 mi. SE. of Encarnación de Díaz, *Soderstrom* 694 (US), 697 (US). GUANAJUATO: Ojo de Agua, *Sohns* 252 (MICH, US). 6 km. E. of Guanajuato, *Sohns* 315 (MICH, US). HIDALGO: 18 mi. NE. of Zimapán, *Reeder & Reeder* 4121 (US, YU). PUEBLA: Cerro de Soluche, *Purpus* 4081 (F, GH, MO, NY, UC, US). MORELOS: Km. 53 Autopista México-Cuernavaca, *Espinosa* 66 (IPN). MEXICO: Naranjo, Temascaltepec, *Hinton* 1987 (NY, UC). DISTRITO FEDERAL: Mixcoac, *St. Pierre* 905 (MICH, US). MICHOACÁN: La Huerta, *Arsène*, Oct. 30, 1909 (NY). San Miguel, *Arsène*, Dec. 4, 1910 (NY). OAXACA: Huahuapan de León, *Soderstrom* 413 (US), 414 (US), 447 (US).

*Muhlenbergia emersleyi* is distinguished by the typically long membranous ligule, lemmas pubescent on the midnerve and margins, palea pubescent between the keels, and the purplish, flexuous, more or less pyramid-shaped panicle. It appears to be most closely related to *M. lehmanniana* with their similar overall habit, long ligules, and lemmas pubescent on the lateral margins. *Muhlenbergia lehmanniana* differs in that the midnerve of the lemma is usually glabrous or if pubescent the hairs are sparse and rather inconspicuous; the palea is glabrous between the keels, rarely a few hairs are present. The panicles of *M. lehmanniana* are golden yellow but usually purplish in *M. emersleyi*. The callus is blunt or truncate at the base in *M. emersleyi* but more or less acute in *M. lehmanniana*. *Muhlenbergia emersleyi* is most common in southwestern United States and northern Mexico and has not been collected south of the Isthmus of Tehuantepec. South of the Isthmus, in Chiapas through Central America, the specimens with yellowish panicles are referable to *M. lehmanniana*. Comparison may also be made with *M. breviligula*, its ligule only a short rim or almost lacking. However, long ligules are sometimes found on the leaves of the innovations in the same plants that have the typically short ligule on the culm leaves. This suggests, perhaps, the ancestral nature of a long ligule in this species and points to a close relationship with *M. emersleyi*.

The awned condition of the lemmas requires further study. Awned and awnless specimens, alike in all other respects, were collected side by side (e.g., *Pennell* 18957, *Greene* 439 and 440, awnless and awned forms; and *Nealley* 133, slightly awned and very long-awned specimens). In this species the condition of the awn is not correlated with other characters to separate the awned from the awnless plants. The length of the awn is also quite variable. The author has collected plants side by side; in one the awns were short (*Reeder, Reeder, &*

*Soderstrom* 3548) and in the other very long (*Reeder, Reeder, & Soderstrom* 3543). All of the specimens I have seen from Baja California and Sonora, Mexico, are long-awned.

An awnless form of this species from New Mexico (*Hitchcock* 13541) served as the type for *Epicampes subpatens* Hitchc. In the type specimen the spikelets are about 3 mm. long, the glumes whitish and scabrous, and the lemmas densely pubescent on the midnerve and margins. Although most of the spikelets are awnless, some bear a rudimentary awn from just below the tip. The branches of the panicle are stiffer than those of the type of *M. emersleyi* (*Emersley* 46) and the panicle is not lax. With this exception no basic difference exists between the two specimens. Hitchcock, who described *E. subpatens*, later placed it in synonymy with *M. emersleyi*.

Three specimens deserve special comment. *Bartlett* 10882 (Sierra de San Carlos, Tamaulipas, Mexico) has an inflorescence much like that of *M. emersleyi* with long-awned spikelets in which the lemmas have the typical pubescence pattern of the species. However, the basal sheaths in many specimens are not strongly compressed-keeled, the ligule is firm below and membranous above, and the blades are narrow and folded, reminiscent in these latter features of *M. gooddingii*. Although it looks distinctive, no basic characters separate this specimen from the *M. emersleyi* complex. Two additional specimens, *Martínez & Borja* F-1939 and F-2083 (Sierra de Tamaulipas), are quite distinctive, but I can find no good characters to separate them from the *M. emersleyi* complex. Further collections of *Epicampes* from the state of Tamaulipas may clarify the position of these unusual specimens. I have seen only four specimens from the whole state.

*Muhlenbergia emersleyi* is the most common species of *Epicampes* and the most variable. Attempts to segregate the forms into more than one species on the basis of morphology are unrewarding because of a thorough intergradation of characters among the specimens. An intensive cytological investigation of this species complex will be necessary before we can be certain of the precise nature and extent of the various races present.

#### 25. *Muhlenbergia xanthodas* Soderstrom, sp. nov.

Perennis caespitosa, culmis robustis erectis glabris 60-90 cm. altis, nodis 3 glabris, vaginis inferioribus compressis et robuste carinatis basin versus glabris adversum collum scaberulis; ligula membranacea (ad basin firma), margine versus apicem lacerata, usque ad 30 mm. longa; laminis culmi angustis attenuatisque conduplicatis utrinque scabris, ca. 70 cm. longis; collis scabris; panicula erecta angusta aurea, 23-27 cm. longa, usque ad 3 cm. lata, ramis appressis ad basin floescentibus, axe glabro, ramis primariis usque ad 4.5 cm.

longis, secundariis usque ad 1.5 cm. longis, tertiariis usque ad 5 mm. longis, pedicellis glabris infra spiculam scaberulis quam spiculis brevioribus; spiculis 2-3 (plerumque 2-2.5) mm. longis, glumis acutissimis fere aequalibus, quam flosculo paullo longioribus, glabris lucidis paene translucentibus enerviis, lemmatibus acutis, 2-2.7 mm. longis, glabris nisi quod puberulentis lateribus ad basin, nervis 3, infra apicem aristas, 6-10 mm. longas, aureas ferentibus, callo brevipiloso.

A *M. lehmanniana* Henr. ramis paniculae brevioribus et magis appressis, et glumis glabris lucidis (paene translucentibus) sine nervis differt.

Caespitose perennial; culms stout, erect, glabrous, 60-90 cm. tall; nodes 3, glabrous beneath; basal sheaths strongly compressed-keeled, glabrous below, becoming scaberulous toward the collar; ligule membranous (somewhat firm at the base), lacerate above, as short as 0.5 mm. on the lower culm leaves, to as much as 30 mm. on the higher culm leaves; sheath auricles lacking; blades of the culm to 70 cm. long, narrow and long-attenuate, tightly folded, 1.5-2 mm. wide when unfolded, the upper and lower surfaces scabrous; upper throat scabrous; collar scaberulous.

Panicle erect, narrow, golden yellow, 23-27 cm. long, to 3 cm. wide, the branches of the panicle strongly appressed, floriferous almost to the base; axis glabrous; primary branches to 4.5 cm. long, the secondary branches to 1.5 cm. long, the tertiary branches to 5 mm. long; pedicels shorter than the spikelet, glabrous, scaberulous beneath the spikelet; spikelets 2-3 (mostly 2-2.5) mm. long; glumes acute, about equal to each other, a little longer than the floret, glabrous, shining, almost translucent, nerveless; lemmas acute, 2-2.7 mm. long, glabrous except for short hairs toward the base of the lateral margins, 3-nerved, the middle nerve extending into a golden awn from below the tip of the lemma, 6-10 mm. long; callus of lemma short-pilose; palea equal to or a little longer than the lemma, glabrous.

Holotype in the U.S. National Herbarium, no. 1817864, collected on rock on Mt. Ovando, Chiapas, Mexico, at 2,300 meters altitude, November 14-18, 1939, by Eizi Matuda (no. 4003). Isotypes at F, MICH.

**DISTRIBUTION:** Known only from Chiapas, Mexico, from the type and from the following additional collection:

**MEXICO: CHIAPAS:** Between Escuipulas and Cañada Honda, *Hernández & Sharp* X-311 (US).

*Muhlenbergia xanthodas* appears to be most closely related to *M. lehmanniana* which ranges from Costa Rica to Colombia. Both species are like *M. emersleyi* in general habit and both also have long-awned lemmas, pubescence on the margins of the lemma at the base,

and long membranous ligules. In *M. emersleyi* the lemma is pubescent on the midnerve and the margins, the panicles and awns of the lemma are generally purplish. In *M. xanthodas* and *M. lehmanniana* the lemma is short-pilose at the base, but the midnerve of the lemma is glabrous or bears relatively few inconspicuous hairs, and the panicles are golden, the rather straight awns of the lemmas are golden, and the strongly compressed-keeled sheaths are golden. In typical *M. emersleyi* the paleas are pubescent between the keels, but in *M. xanthodas* and *M. lehmanniana* the paleas are glabrous. *Muhlenbergia xanthodas* is distinct from *M. lehmanniana* in its much shorter, closely appressed panicle branches, producing a very dense panicle; in *M. lehmanniana* the branches are longer and spreading. The glumes of *M. xanthodas* are glabrous, shining (almost translucent), and nerveless; the glumes of *M. lehmanniana* are scabrous and 1-nerved.

The specific epithet is from the Greek words *ξανθός*, yellow or golden, and *δάς*, torch, in allusion to the dense golden panicles.

**26. *Muhlenbergia lehmanniana*** Henr. Med. Rijksherb. Leiden 40:59. 1921.

*M. multinodis* Asplund. Bot. Not. 1939: 796. f. 1. 1939.

*M. attenuata* Swallen. Ann. Missouri Bot. Gard. 30:138. 1943.

Caespitose perennial; culms glabrous to scaberulous, 72–167 cm. tall; nodes 3–4, glabrous beneath; basal sheaths compressed-keeled, glabrous, tightly imbricate, flat, golden yellow, not becoming brown and shredded; ligule somewhat firm at the base, becoming long and membranous, conspicuous from side view, slightly decurrent, 1 cm. long, to as long as 2.5 cm., enclosed in the folded blade above, entire below and for the greater part of its length; sheath auricles lacking or rarely rudimentary ones present, no more than 0.1 mm. long; blades of the culm folded, long and narrow, becoming threadlike toward the tip, 1.5–4 mm. wide when flat, the upper surface of the blade slightly scaberulous to scabrous, the lower surface scaberulous to scabrous; upper throat scabrous; collar scaberulous to scabrous.

Panicle erect, usually dense, the branches ascending 19–40 cm. long, 3–6 cm. wide, generally golden, golden brown, or purplish green; axis scaberulous to scabrous; the primary branches 3.5–12 (rarely to 19) cm. long, the secondary branches 1–5 (mostly 1–2) cm. long, tertiary branches usually lacking (rarely to 1.5 cm. long); pedicels of the lateral spikelets 0.7–2 mm. long, those of the terminal spikelets relatively long, 2–4 mm., scaberulous to scabrous, especially just beneath the spikelet; spikelets 2–3.5 (usually about 2.5) mm. long; glumes longer than the floret, the second glume usually a little longer than the first, mostly scabrous, blunt at the tip or slightly dentate (under high power), usually slightly awn-tipped, the awns to 0.3 mm., hyaline, 1-nerved (1 or 2 additional faint nerves sometimes

present); lemmas 1.8–3 (mostly about 2.5) mm. long, glabrous dorsally except at the base of the midvein, the lower part of the margins conspicuously short-pilose, acutish at tip, 3-nerved, the awns straight, or somewhat flexuous, over 1 (to 3.5) cm. long; callus of the lemma short-pilose; palea a little shorter than the lemma, glabrous or at most with a few hairs at the base between the keels.

Holotype in the Rijksherbarium, Leiden, collected near Popayán, Cauca, Colombia, by F. C. Lehmann, no. B. T. 1267 (in Herb. Lugd. Bat. under no. 908. 350–519). Fragments of type ex K in the U.S. National Herbarium, no. 72978, ex L, no. 72977, and ex. Herb. Lugd. Bat. (L), no. 72979. Isotype at NY.

DISTRIBUTION: Hillsides and barrancas at elevations of mostly between 2,500 and 6,000 ft. One label states "from 100 m.," another "10,000 ft.," but I doubt if the species is found at these extremes. Rather common from Costa Rica, south and eastward into Colombia.

COSTA RICA: *Tonduz* 4630 (US). Las Cóncevas, *Lankester* 676 (US) *Oersted* 14065 (F, US), 14171 (US). Bord du chemin de Mano de Tigre, *Pittier* 4630 (US). Buenos Aires, Canton de Osa, *Valerio* 873 (F). PUNTARENAS: Savanes de Cañas Gordas, *Pittier* 7355 (US), 7358 (US), 11019 (US). ALAJUELA: San Pedro de San Ramón (cerca del Río Barranca), *Brenes* 21415 (F, NY). SAN JOSÉ: Tablazo hasta 1800 m., *Valerio* 1052 (F). CARTAGO: Tejar, *Solis* 618 (44) (F). Mount Irazu, *Oersted* 14012 (US).

PANAMA: CHIRIQUÍ: El Boquete, *Hitchcock* 8174 (US holotype of *M. attenuata*). Grassy hillsides, *Hitchcock* 8241 (US). Foothills, *Hitchcock* 8242 (US). Barranca, road toward Dolega, *Hitchcock* 8340 (US). Cerro Vaca, *Pittier* 5360 (US), 5362 (US). COCLÉ: S. of El Valle de Antón, *Allen* 2812 (GH, MO, US). Vicinity of Olá, *Pittier* 5042 (US), *Pittier* 5062 (US).

COLOMBIA: ANTIOQUIA: Medellín, *Bro. Daniel* 246 (US). Barbosa, vicinity of Medellín, *Toro* 697 (US). VALLE: Cordillera Occidental, Hoya del Río Cali, *Cuatrecasas* 18737 (F, US). CAUCA: Popayán, *Lehmann* B.T. 1267 (US fragments of type ex K and L, NY isotype). Loma de Bichiquí near Toribió, *Pittier* 1468 (US). El Tambo, *von Sneider* 1323 (S holotype of *M. multinodis*), A. 231 (A).

*Muhlenbergia lehmanniana* is distinguished by the long ligule, pyramidal panicles of spikelets with scabrous glumes, long-awned lemmas pubescent only at the base, paleas glabrous between the keels, and calluses acute rather than truncate.

This species looks much like *M. emersleyi* and has been confused with it. The panicles of long-awned spikelets resemble some forms of *M. emersleyi*. However, a number of characters differentiate the two species. *Muhlenbergia lehmanniana* occurs in the mountains of Costa Rica through Panama and into the Colombian Andes; *M. emersleyi* is most abundant in southwestern United States and northern Mexico, becoming less frequent southward into Mexico until, beyond the Isthmus of Tehuantepec, it disappears. The basal sheaths of *M. lehmanniana* are distinctly flabellate and golden,

more so than *M. emersleyi*, and the blades are long, narrow, and attenuate, rather threadlike at the ends. The acute callus of the floret distinguishes this species from *M. emersleyi*. The hairs on the callus and lower part of the margins of the lemma and midnerve (where confined) are longer individually than in *M. emersleyi*. In that species the hairs usually extend about two-thirds up the lemma. In most specimens of *M. lehmanniana* the palea is glabrous but pubescent on a half to two-thirds of its length in *M. emersleyi*.

Swallen's *M. attenuata*, although distinctive because of the unusually long panicle branches long-naked at the base, is evidently an extreme form of this species, and the type of *M. multinodis* unquestionably fits within the morphological range of *M. lehmanniana*.

*Muhlenbergia lehmanniana* is closely related to *M. xanthodas* which differs in the nerveless, glabrous, almost translucent glumes, and short, appressed panicle branches. The ranges of both species are well separated, *Muhlenbergia xanthodas* being known only from Chiapas.

#### Species Described as *Epicampes* but Excluded from Section *Epicampes*

- Epicampes argentea* (Vasey) Jones. Contr. West. Bot. 14:7. 1912. = **Muhlenbergia argentea** Vasey. Bull. Torrey Club. 13:232. 1886. A weak, somewhat decumbent perennial with rounded basal sheaths [SW. Chihuahua, Mexico].
- Epicampes arundinacea* (Trin. [error for Griseb.]) Hack. Anal. Mus. Nac. Buenos Aires 11:107. 1904. = **Sporobolus rigens** (Trin.) Desv. in C. Gay. Fl. Chile 6:295. 1853. [Chile.]
- Epicampes buchingeri* Fourn. Mex. Pl. 2:88. 1886. = An annual **Muhlenbergia** (from description; type not seen). [Mexico.]
- Epicampes clomena* (Trin. [error for Kunth]) Jones. Contr. West. Bot. 14:7. 1912. = **Muhlenbergia peruviana** (Beauv.) Steud. Nom. Bot. ed. 2. 1:41. 1840. An annual [Peru].
- Epicampes coerulea* Griseb. Abh. Ges. Wiss. Göttingen 19:256. 1874. = ?**Muhlenbergia angustata** (Presl) Kunth. Rev. Gram. I. (Supp.): xvi. 1830. [Colombia to Argentina.]
- Epicampes coerulea* var. *submutica* Hack. ex Stuck. Ann. Mus. Nac. Buenos Aires 13:471. 1906. = ?**Muhlenbergia angustata** (Presl) Kunth. 1830. Rev. Gram. I (Supp.): xvi. [Colombia to Argentina.]
- Epicampes crassiculmis* Piper. Proc. Biol. Soc. Wash. 18:144. 1905. = **Sporobolus wrightii** Munro ex Scribn. Bull. Torrey Club 9:103. 1882. [USA, Mexico.]
- Epicampes kunthiana* Griseb. Abh. Ges. Wiss. Göttingen 19:256. 1874. = **Muhlenbergia angustata** (Presl) Kunth. Rev. Gram. I (Supp.): xvi. 1830. [Colombia to Argentina.]
- Epicampes macroura* (H.B.K.) Benth. Journ. Linn. Soc. Bot. 87. 1881. = **Muhlenbergia macroura** (H.B.K.) Hitchc. A member of section *Podosemum*. [Mexico and Guatemala.]
- Epicampes mexicana* (Scribn.) Jones. Contr. West. Bot. 14:7. 1912. = **Muhlenbergia biloba** Hitchc. Contr. U.S. Nat. Herb. 17:294. 1913. An annual [Mexico].

- Epicampes phleoides* (H.B.K.) Griseb. Abh. Ges. Wiss. Göttingen 19:256. 1874. = *Muhlenbergia angustata* (Presl) Kunth. 1830. Rev. Gram. I (Supp.): xvi. [Colombia to Argentina.]
- Epicampes rigens* Benth. in Journ. Linn. Soc. Bot. 19:87. 1881. = *Muhlenbergia rigens* (Benth.) Hitchc. A member of section *Podosemum*. [SW. USA and Mexico.]
- Epicampes rigens* (Trin.) Phil. Anal. Mus. Nac. Chile sect. II(8):82. 1891. Based on *Vilfa rigens* Trin. which = *Sporobolus rigens* (Trin.) Desv. in C. Gay. Pl. Chile 6:295. 1853. [Chile.] Not *Epicampes rigens* Benth. Journ. Linn. Soc. 19:87. 1881. [USA, Mexico.]

### New Species and New Combination

- Muhlenbergia gooddingii* Soderstrom, sp. nov.  
*Muhlenbergia inaequalis* Soderstrom, sp. nov.  
*Muhlenbergia iridifolia* Soderstrom, sp. nov.  
*Muhlenbergia reederorum* Soderstrom, sp. nov.  
*Muhlenbergia virletii* (Fourn.) Soderstrom, comb. nov.  
*Muhlenbergia xanthodas* Soderstrom, sp. nov.

### Voucher Specimens Examined

Specimens used in the study of leaf anatomy, embryos, and lodicules are listed below. The letters in the herbarium citation indicate the study for which the specimen was used (A=leaf anatomy: cross section and/or epidermis, E=embryo, and L=lodicule). The author was fortunate to have access to the John R. Reeder collection, indicated by (R), of slides and drawings of many grasses.

### MUHLENBERGIA

- M. andina* (Nutt.) Hitchc. USA: ARIZONA: Grand Canyon Natl. Park, North Rim, along Point Sublime Road, *Reeder* 1808 (YU): L.
- M. angustata* (Presl) Kunth. ECUADOR: Cañar, near the village of San Marcos, *Camp* E-2519 (NY): A, L.
- M. arenicola* Buckl. MEXICO: CHIHUAHUA: Plains near Chihuahua, *Pringle* 479 (NY): A, L.
- M. argentea* Vasey. MEXICO: CHIHUAHUA, *Palmer* 160, in 1885 (US holotype): A.
- M. arizonica* Scribn. MEXICO: DURANGO: N. of Cd. Durango, *Reeder* 2602 (YU): A(R).
- M. articulata* Scribn. MEXICO: SAN LUIS POTOSÍ: Cárdenas, *Pringle* 3913 (NY): A, L.
- M. asperifolia* (Nees & Mey.) Parodi. USA: NEW MEXICO: Albuquerque, *Hardies* M-103 (YU): A(R).
- M. biloba* Hitchc. MEXICO: CHIHUAHUA: Near Chihuahua, *Pringle* 819 (NY): L.
- M. breviligula* Hitchc. GUATEMALA: JALAPA: Vicinity of Jalapa, *Standley* 76731 (F): A.
- M. brevis* C. O. Goodding. MEXICO: CHIHUAHUA: 12 miles W. of Cuauhtémoc, *Reeder* 2620 (YU): L(R).

- M. brevivaginata* Swallen. MEXICO: JALISCO: 6 mi. NW. of Cuautla, *McVaugh* 13671 (US holotype): A.
- M. capillaris* (Lam.) Trin. USA: FLORIDA: Near Highland View, *Kral & Godfrey* 54211 (NY): L. TEXAS: Bastrop State Park, *Silveus* 2396 (YU): A(R).
- M. confusa* (Fourn) Swallen. MEXICO: CHIHUAHUA: 10 miles N. of Largo, *Reeder* 2684 (YU): A(R).
- M. crispiseta* Hitchc. MEXICO: DURANGO: 23 miles W. of Cd. Durango, *Reeder* 2545 (YU): A(R).
- M. curvula* Swallen. MEXICO: GUANAJUATO: 12 mi. from Guanajuato on road to Santa Rosa, *Moore* 1353 (US holotype): A.
- M. depauperata* Scribn. MEXICO: GUANAJUATO: 11 miles S. of San Miguel Allende, *Reeder* 2279 (YU): L(R).
- M. distans* Swallen. MEXICO: DISTRITO FEDERAL: Lomas, *Lyonnet* 55 (NY): A. OAXACA: Las Sedas, *Pringle* 5574 (NY): A, L.
- M. distichophylla* (Presl) Kunth. MEXICO: JALISCO: Near Guadalajara, *Pringle* 2346 (NY): A, L. GUERRERO: Vallceitos, Montes de Oca, *Hinton* 11635 (NY): A.
- M. dubia* Fourn. MEXICO: MEXICO: 12 miles E. of Ixtlahuaca, *Soderstrom* 509 (YU): A, L.
- M. dubioides* C. O. Goodding. MEXICO: CHIHUAHUA: 12 miles N. of Chihuahua, *Soderstrom* 931 (YU): A.
- M. elongata* Scribn. MEXICO: CHIHUAHUA: Near Chihuahua, *Pringle* 938 (NY): A.
- M. emersleyi* Vasey. MEXICO: ZACATECAS: 13 miles W. of Sombrerete, *Soderstrom* 746 (YU): A, L.
- M. erectifolia* Swallen. COLOMBIA: SANTANDER: Páramo de Santurbán, near Vetas, *Killip & Smith* 17470 (US holotype): A.
- M. eriophylla* Swallen. MEXICO: MEXICO: Luvianos, Temascaltepec, *Hinton* 5307 (US holotype): A.
- M. expansa* (DC.) Trin. USA: SOUTH CAROLINA: 5 miles S. of Georgetown, *Godfrey* 8151 (NY): A, L. NORTH CAROLINA: Wilmington, *Amer. Gr. Nat. Herb.* 1374 (NY): A, E.
- M. filiculmis* Vasey. USA: COLORADO: Green Mountain Falls, *Sheldon* 321 (US holotype): A.
- M. firma* Beal. MEXICO: HIDALGO: Pachuca, *Amer. Gr. Nat. Herb.* 1351 (NY): A, L.
- M. flexuosa* Hitchc. PERU: Huacachi, estación near Muna, *Macbride* 3874 (US holotype): A.
- M. frondosa* (Poir.) Fernald. USA: CONNECTICUT: New Haven (no voucher): L.
- M. gigantea* (Fourn.) Hitchc. MEXICO: DURANGO: 22 miles E. of Santa Lucía, *Reeder* 2488 (YU): A, L. JALISCO: Near Guadalajara, *Pringle* 3335 (NY): A, E; 8 miles W. of Guadalajara, *Soderstrom* 607 (YU): A.
- M. glabrata* (H. B. K.) Kunth. MEXICO: PUEBLA: San Marcos, *Amer. Gr. Nat. Herb.* 1356 (NY): A, L.
- M. glomerata* (Willd.) Trin. USA: CONNECTICUT: 6 miles W. of Tolland, *Reeder* 944 (YU): L.
- M. grandis* Vasey. MEXICO: JALISCO: Near Guadalajara, *Pringle* 2765 (NY): A, E, L.
- M. hintonii* Swallen. MEXICO: MEXICO: Crucero, Temascaltepec, *Hinton* 3059 (US holotype): A.
- M. holwayorum* Hitchc. BOLIVIA: Sorata, *Rusby* 201 (NY): A.
- M. involuta* Swallen. USA: TEXAS: Boerne-Bandera Road, N. of San Antonio, *Silveus* 780 (NY): A(R), L.

- M. jaliscana* Swallen. MEXICO: JALISCO: Sierra de Manantlán (15–20 mi. SE. of Autlán), *McVaugh* 13991 (US holotype): A.
- M. lindheimeri* Hitchc. USA: TEXAS: 15 miles S. of San Antonio, *Burr* 513 (NY): A, L.
- M. longiglumis* Vasey. MEXICO: JALISCO: *Pringle* 2365 (NY): A, L.
- M. longiligula* Hitchc. USA: ARIZONA: Chiricahua Mts., Barfoot Park, *Blumer* 1424 (NY): A. MEXICO: CHIHUAHUA: 38 miles S. of Casas Grandes, *Reeder* 2699 (YU): A, E; 31 miles W. of Colonia Juárez, *Reeder* 3222 (YU): L.
- M. lucida* Swallen. MEXICO: CHIHUAHUA: Sierra Gazachic 35 km. SW. of Miñaca, *Pennell* 18955 (US holotype): A.
- M. macrotis* (Piper) Hitchc. MEXICO: JALISCO: *Pringle* 2360 (NY): E. GUERRERO: Petlacala, S. of Reyes, *Mexia* 9098 (NY): A, L.
- M. macroura* (H. B. K.) Hitchc. MEXICO: MICHOACÁN: Quinceo, near Morelia, *Arsène*, Nov. 11, 1909 (F): E; 14 miles E. of Morelia, *Soderstrom* 551 (US): L. CHIAPAS: Chiquihuite, Vol. Tacana, *Matuda* 2829 (NY): A.
- M. matudae* Sohns. MEXICO: MORELOS: Lago de Zempoala, *Matuda* 25601 (US holotype): A.
- M. metcalfei* Jones. USA: NEW MEXICO: Grant County, Santa Rita Mountains, *Metcalf* 1485; (US holotype): A.
- M. mexicana* forma *ambigua* (Torr.) Fernald. USA: CONNECTICUT: New Haven (no voucher): L.
- M. montana* (Nutt.) Hitchc. MEXICO: SONORA: Trail from El Tigre to El Rancho de Robles, *Santos* 1924 (NY): A. MICHOACÁN: Morelia, *Arsène* 5811 (NY): L.
- M. aff. montana* (Nutt.) Hitchc. MEXICO: DURANGO: 7 miles E. of El Salto, *Reeder* 2572 (YU): A(R).
- M. nigra* Hitchc. MEXICO: DISTRITO FEDERAL: Serranía de Ajusco, *Pringle* 6676 (NY): A. Near Cima, *Pringle* 11739 (NY): L. GUATEMALA: Volcán de Agua, *Cook*, May 12, 1905 (NY): E.
- M. orophila* Swallen. GUATEMALA: HUEHUETENANGO: Cerro Chemal, summit of Sierra de los Cuchumatanes, *Steyermark* 50309 (US, holotype): A.
- M. palmeri* Vasey. MEXICO: CHIHUAHUA: Sierra Madre, *Pringle* 1417 (NY): A, L.
- M. peruviana* (Beauv.) Steud. PERU: AREQUIPA: July 11, 1946, *Pearson* 1: (YU): A(R).
- M. plumbea* Scribn. in Beal. MEXICO: MEXICO: 17 miles E. of Toluca, *Reeder* 2218 (YU): A(R).
- M. pubescens* (H. B. K.) Hitchc. MEXICO: JALISCO: 15 miles SE. of Encarnación de Díaz, *Soderstrom* 692 (YU): A, 693 (YU): E. TLAXCALA: Sta. Ana Chiautempan, *Arsène*, 10–11–1908 (NY): E. PUEBLA: 5 miles NE. of Zacatepec, *Soderstrom* 483 (YU): L.
- M. pulcherrima* Scribn. in Beal. MEXICO: DURANGO: 15 miles E. of Ciudad, *Reeder* 2535 (YU): A(R).
- M. purpusii* Mez. MEXICO: SAN LUIS POTOSÍ: Near km. 549, 36 mi. S. of Matehuala, *McVaugh* 18204 (US): A.
- M. quadridentata* (H. B. K.) Kunth. MEXICO: MEXICO: Temascaltepec, Las Cruces, *Hinton* 4389 (NY): A, L.
- M. racemosa* (Michx.) B. S. P. USA: En route from Fort Duchesne to Dakotah, *Cornman*, in 1888 (NY): L.
- M. reverchonii* Vasey & Scribn. USA: TEXAS: S. of Austin, *Silveus* 2478 (YU): A(R), L.
- M. richardsonis* (Trin.) Rydb. USA: COLORADO: Leadville, *Goodding* M-3272 (YU): A(R).

- M. rigens* (Benth.) Hitchc. USA: ARIZONA: Chiricahua Mts., Riggs' Ranch, Blumer 1491 (NY): E. MEXICO: Chihuahua, 27 miles NW. of Madera, Reeder 2662 (YU): A. ZACATECAS: 25 miles NW. of Fresnillo, Soderstrom 731 (YU): A, L.
- M. rigida* (H. B. K.) Kunth. MEXICO: JALISCO: 2 miles W. of Guadalajara, Soderstrom 640 (YU): L. ZACATECAS: 2 miles W. of Sombrerete, Soderstrom 743 (YU): A, L.
- M. robusta* (Fourn.) Hitchc. MEXICO: JALISCO: Near Guadalajara, Pringle 2321 (NY): E. MICHOACÁN: Punguato, near Morelia, Arsène (NY): L. MEXICO: Temascaltepec, Carboneras, Hinton 1853 (NY): A. 3 miles NW. of Tlamanaco, Soderstrom 382 (YU): L. CHIAPAS: 20 miles E. of Chiapa de Corzo, Reeder 2128 (YU): A. GUATEMALA: CHIMALTENANGO: Near Chimaltenango, Standley 59136 (F): E.
- M. schreberi* Gmel. USA: CONNECTICUT: New Haven (no voucher): A(R), L.
- M. scoparia* Vasey. MEXICO: SINALOA: Mesa Malqueson, Cerro Colorado, Gentry 5178 (NY): L; 10 miles E. of Santa Lucía, Reeder 2451 (YU): E.
- M. setifolia* Vasey. USA: TEXAS: Guadalupe Mountains, Havard 9 (US, holotype): A.
- M. aff. speciosa* Vasey. MEXICO: DURANGO: 21 miles E. of Santa Lucía, Reeder 2476 (YU): A, L.
- M. stricta* (Presl) Kunth. MEXICO: JALISCO: La Granja, near Guadalajara, Soderstrom 642 (YU): A, L.
- M. subaristata* Swallen. MEXICO: DURANGO: El Salto (Aserraderos), Sierra Madre Occidental, Pennell 18572 (US holotype): A.
- M. sylvatica* (Torr.) Torr. ex Gray. USA: CONNECTICUT: New Haven (no voucher): L(R).
- M. torreyana* (Schult.) Hitchc. USA: NEW JERSEY: Egg Harbor, Bissell (NY): A(R), L.
- M. torreyi* (Kunth) Hitchc. USA: NEW MEXICO: Capitan, Goodding M-189 (YU): L.
- M. uniflora* (Muhl.) Fernald. USA: NEW YORK: Wading River, Miller 130 (NY): L. NEW HAMPSHIRE: Chatham, Johnson, August 7, 1927: A(R).
- M. versicolor* Swallen. MEXICO: OAXACA: Sierra de San Felipe, Smith 927 (NY): L.
- M. virletii* (Fourn.) Soderstr. MEXICO: MEXICO: Sultepec, Hinton 3219 (NY): A, L.
- M. wrightii* Vasey. USA: NEW MEXICO: Soil Conservation Service Nursery, Albuquerque (seed from Flagstaff, Arizona), Goodding and Hardies A-6498 (YU): L.
- M. xerophila* C. O. Goodding. USA: ARIZONA: Forest Cabin Canyon, Baboquivari Mountains, Goodding A-9493 (YU): L; Moristo Canyon, Baboquivari Mts., Goodding 443-45 (NY): A.

#### GENERA OTHER THAN MUHLENBERGIA

- Agrostis alba* L. USA: CONNECTICUT: Guilford, Dudley, July 17, 1904 (YU): L.
- Agrostis scabra* Willd. USA: Continental Divide, near Beardshead, Goodding, July 25, 1939 (YU): E(R).
- Blepharoneuron tricholepis* (Torr.) Nash. USA: ARIZONA: Tiyo Plateau, Grand Canyon, Reeder 1807 (YU): L(R).
- Cinna arundinacea* L. USA: CONNECTICUT: New Haven (no voucher): L. NEW JERSEY: Plainfield, Tweedy, September 1881 (YU): E(R).
- Lycurus phleoides* H. B. K. MEXICO: JALISCO: 11 miles N. of Ciudad Guzmán, Reeder 2352 (YU): L(R).

- Polypogon monspeliensis* (L.) Desf. USA: MASSACHUSETTS: Lowell, Swan, July 14, 1880 (YU): L. BELGIUM: Ripe fruits received from Hortus Botanicus Bruxellensis in 1955: E(R).
- Sporobolus asper* (Michx.) Kunth. USA: CONNECTICUT: East Haven, Nichols, Aug. 31, 1912 (YU): L(R).
- Sporobolus heterolepis* (A. Gray) A. Gray. USA: CONNECTICUT: West Rock, Nichols, Sept. 5, 1911 (YU): L(R).
- Sporobolus wrightii* Munro ex Scribn. USA: ARIZONA: San Pedro, Toumey, July 25, 1894 (YU): L; ripe fruits collected by L. N. Goodding, October 1955: E(R).
- Stipa avenacea* L. USA: MASSACHUSETTS: Boston, Blue Hills Reservation, Reeder 233 (YU): E(R), L(R).

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Muhlenbergias, *Podosemum* section: FIG. 1.—*Muhlenbergia rigens* among rocks in a dry streambed, 12 mi. W. of Chihuahua, Chihuahua, Mexico, alt. 4,800 ft. (Soderstrom 927-929). FIG. 2. *M. rigens*, closeup of Soderstrom 927. FIG. 3.—*M. macroura*, pine-zone area with volcanic soil, La Joya, Veracruz, Mexico, alt. 7,000 ft. (Soderstrom 478). FIG. 4.—*M. macroura* on eroded bank at edge of pine-oak hillside, 14 mi. E. of Morelia, Michoacán, Mexico, alt. 6,700 ft. (Soderstrom 551).



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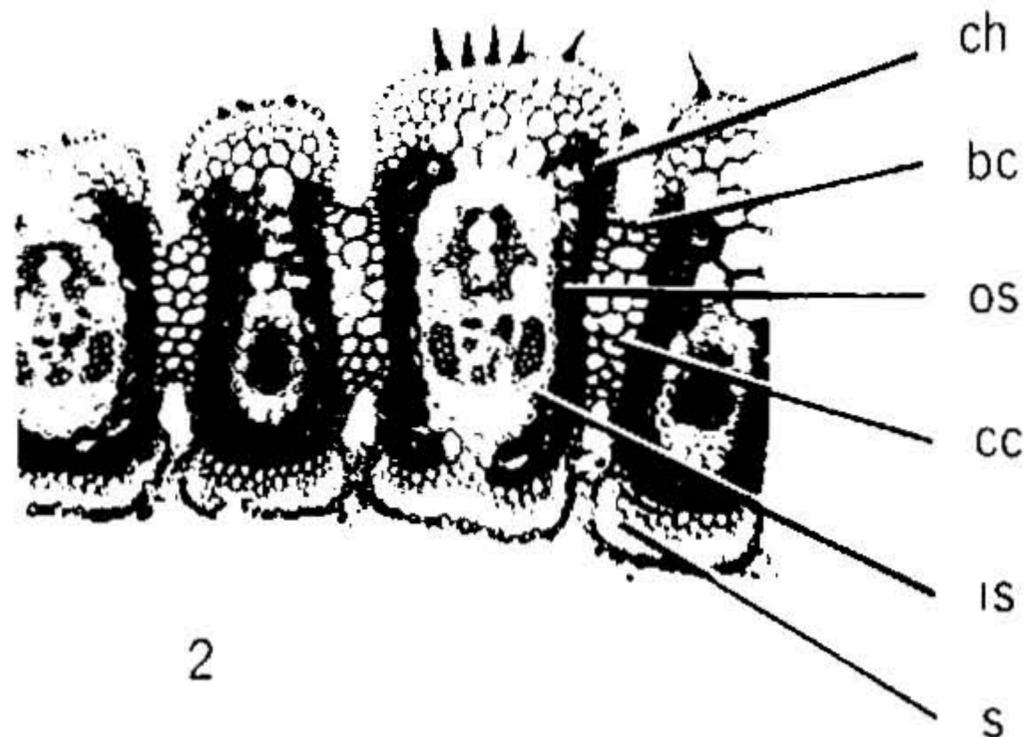
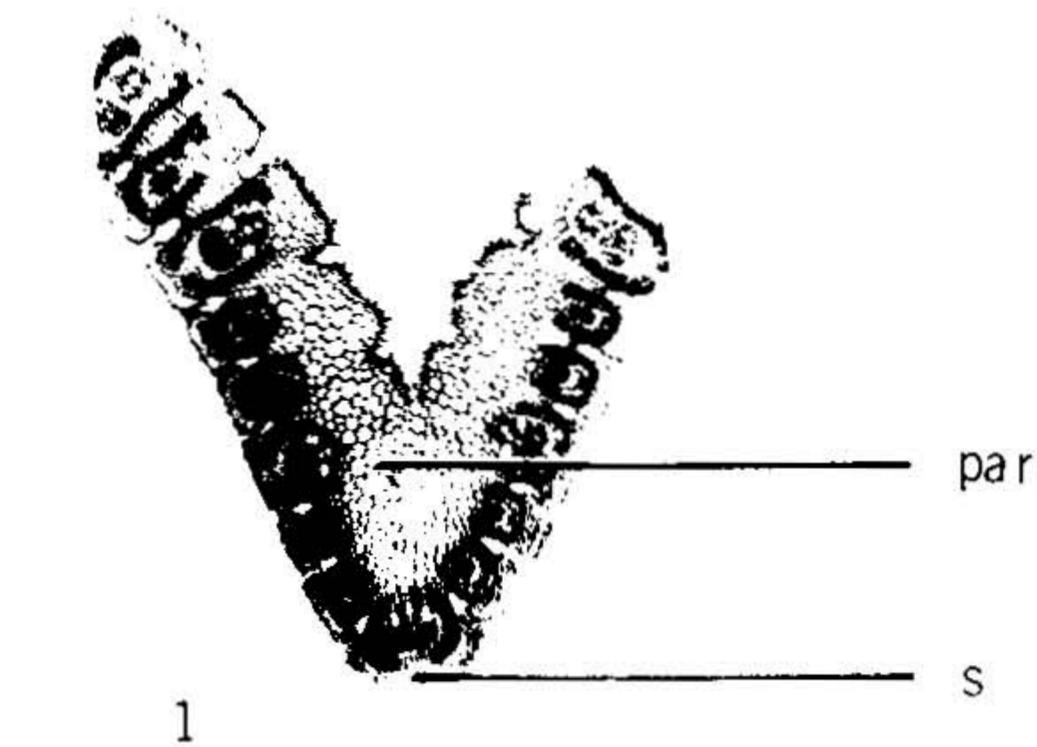
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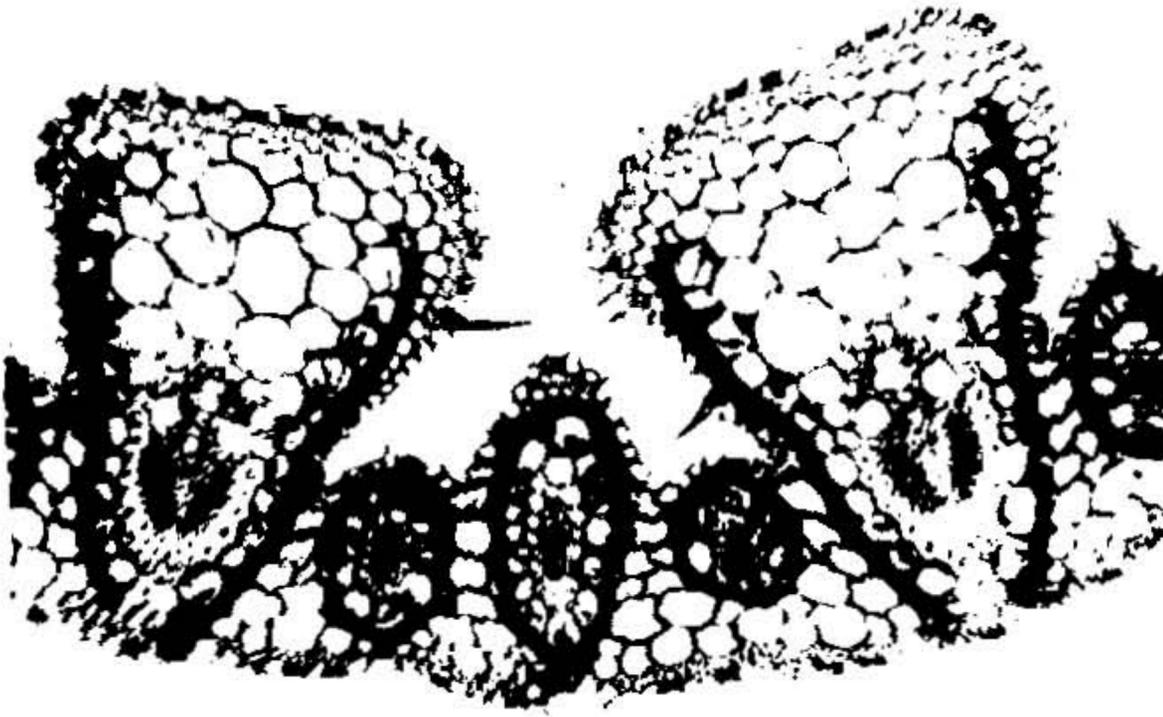
Muhlenbergias, *Epicampes* section: FIG. 1. *Muhlenbergia emerleyi* (awnless) near ledge of arroyo, 15 mi. SE. of Encarnación de Díaz, Jalisco, Mexico, alt. 7,000 ft. (Soderstrom 697). FIG. 2. Clump of *M. emerleyi* (long awned) growing in protection of "maguey silvestre" (*Agave* sp.), plateau near San Francisco de Oro, Chihuahua, Mexico, alt. 7,000 ft. (Soderstrom 870). FIG. 3. *M. robusta*, upper ledge of arroyo, 6 mi. E. of Santa Cruz, Jalisco, Mexico, alt. 5,500 ft. (Soderstrom 566). FIG. 4. *M. distans*, rocky ledge of arroyo, 15 mi. W. of Zacatecas, Zacatecas, Mexico, alt. 7,200 ft. (Soderstrom 724).



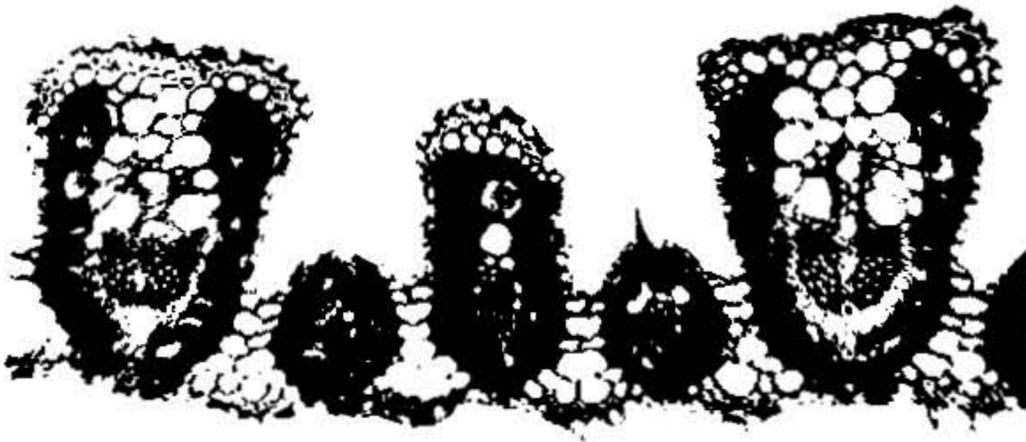
Habitats of Muhlenbergias, subgenus *Podosemum*: FIG. 1: Clumps of *M. pubescens* are common on the rocky desert hillside near Durango, Durango, Mexico, alt. 6,200 ft. FIG. 2: Barranca de Oblatos near Guadalajara, Jalisco, Mexico. Many early C. G. Pringle collections of *Muhlenbergia* came from this and nearby barrancas; an area of Mexico that appears to be the center of distribution of the genus. FIG. 3: *M. rigens* is found at the base and *M. emersleyi* higher on the ledges of a dry arroyo, 25 mi. NW. of Fresnillo, Zacatecas, Mexico, alt. 7,300 ft. FIG. 4: Large clumps of *M. robusta* not yet in bloom, 3 mi. NW. of Tlamanalco, Mexico, Mexico, alt. 7,000 ft. (Soderstrom 580 collected here).



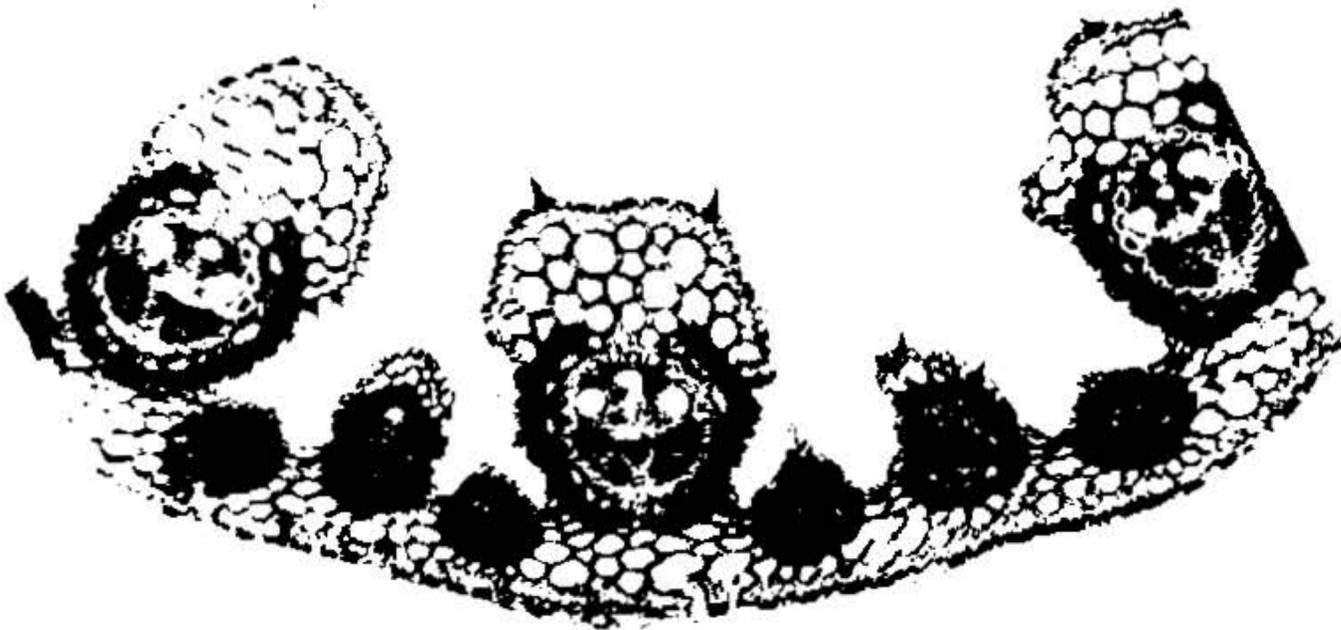
Anatomical structures of the leaves of Muhlenbergias, subgenus *Podosemum*: FIG. 1.—*Muhlenbergia lindheimeri*, cross section through central part of leaf, showing heavily sclerified central unit and mass of thick-walled parenchyma of keel (*Burr 513*),  $\times 50$ . FIG. 2.—*M. lindheimeri*, cross section through lateral part of leaf, showing two  $1^\circ$  and two  $2^\circ$  units (*Burr 513*),  $\times 134$ . FIG. 3.—*M. palmeri*, cross section through central part of leaf, including two  $1^\circ$  units and, between them, one  $2^\circ$  and two  $3^\circ$  units (*Pringle 1417*),  $\times 134$ . Abbreviations: par—parenchyma (thick-walled); s—sclerenchyma; ch—chlorenchyma sheath (mesophyll); bc—bulliform cells; os—outer sheath; cc—colorless cells; is—inner sheath; x—xylem; ph—phloem (line points to darkstained, active, nonsclerosed portion).



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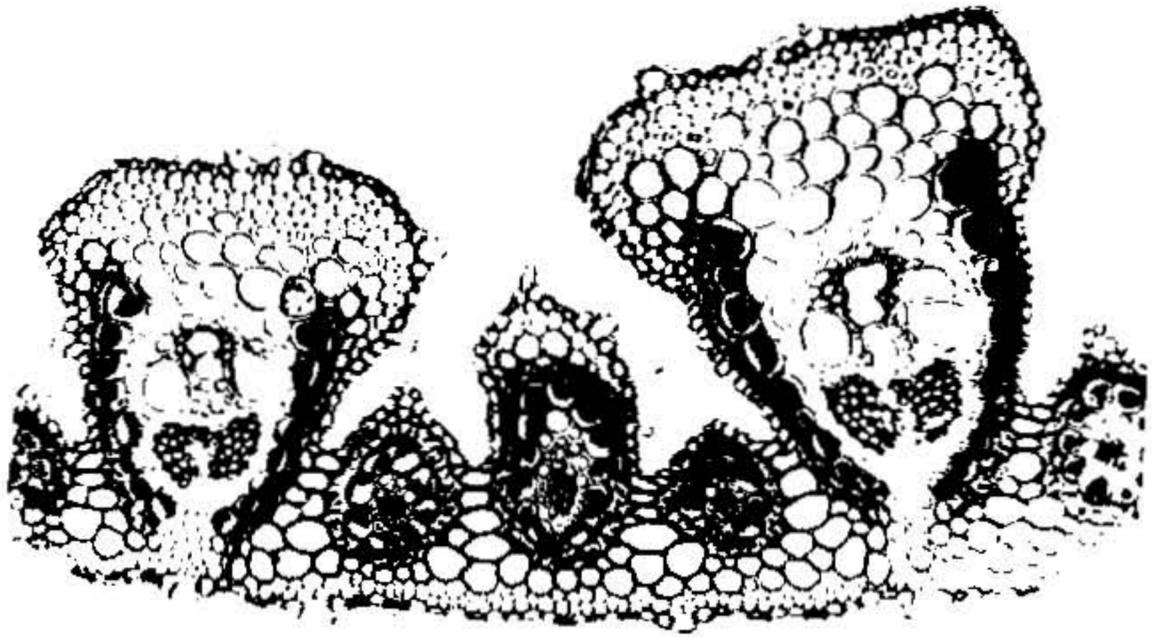


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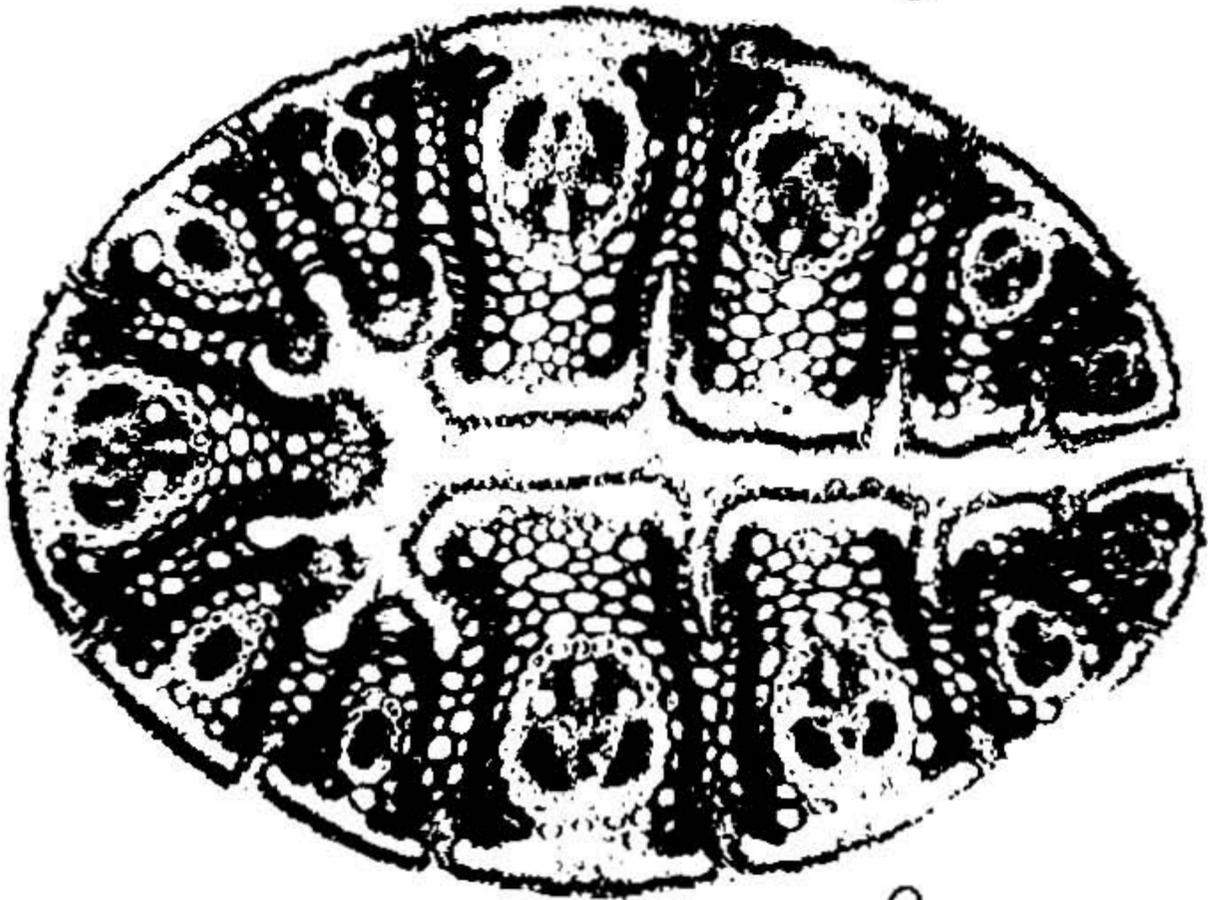


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Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia rigens*, young innovation leaf, between ligule and point 2.5 cm. from ligule on blade (Soderstrom 731),  $\times 187$ . FIG. 2.—*M. rigens*, culm leaf, between ligule and point 1 cm. from ligule on blade (Reeder & Reeder 2662),  $\times 150$ . FIG. 3.—*M. dubia* (Soderstrom 509),  $\times 150$ .



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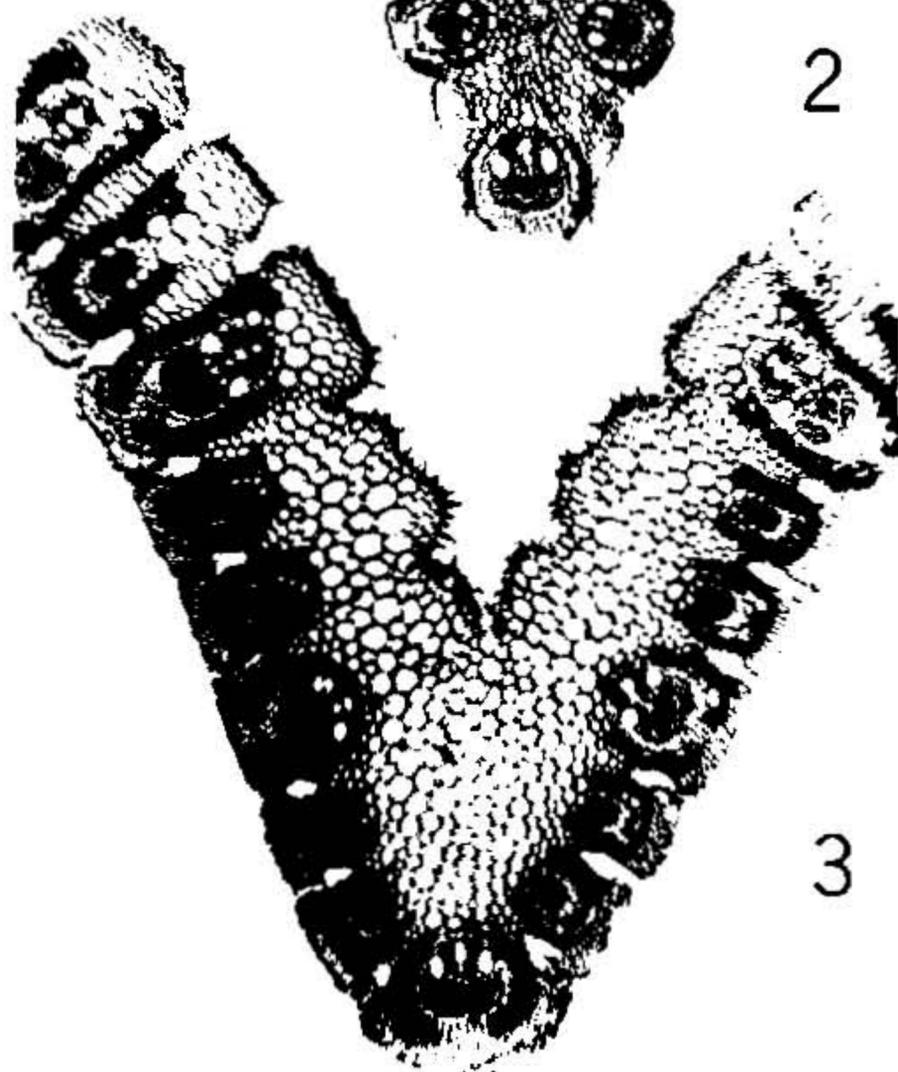
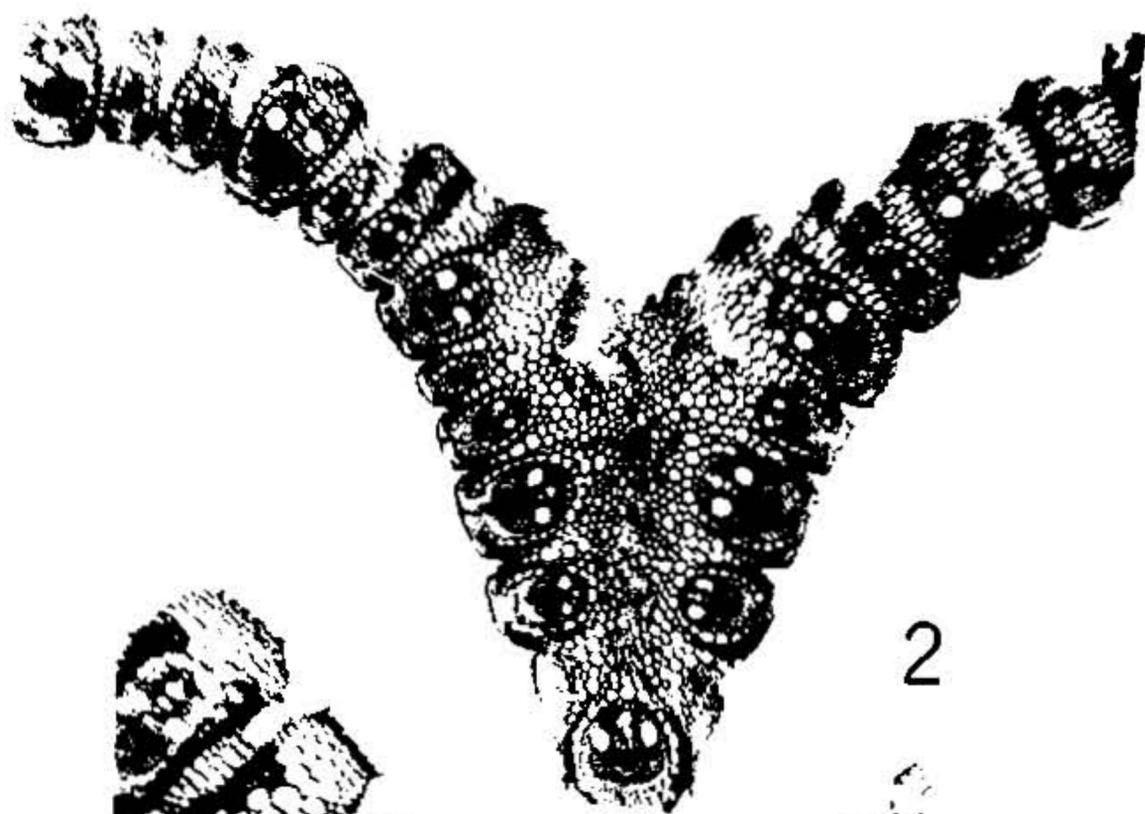
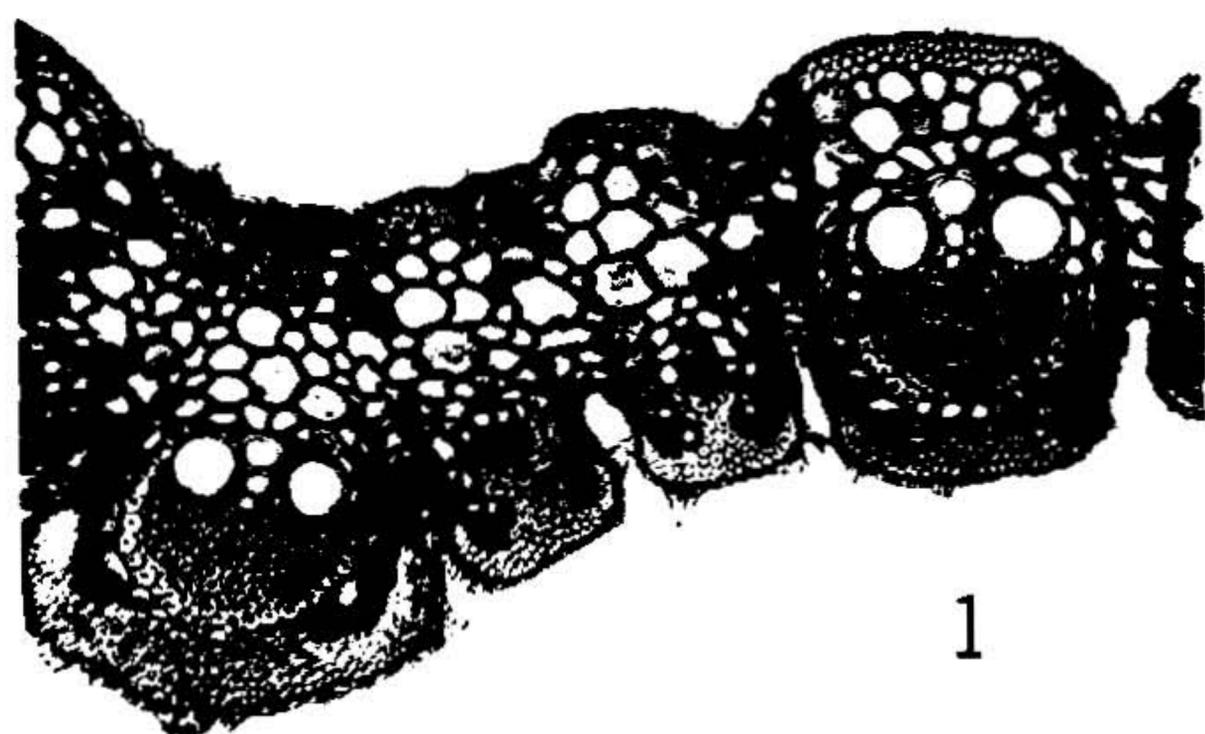


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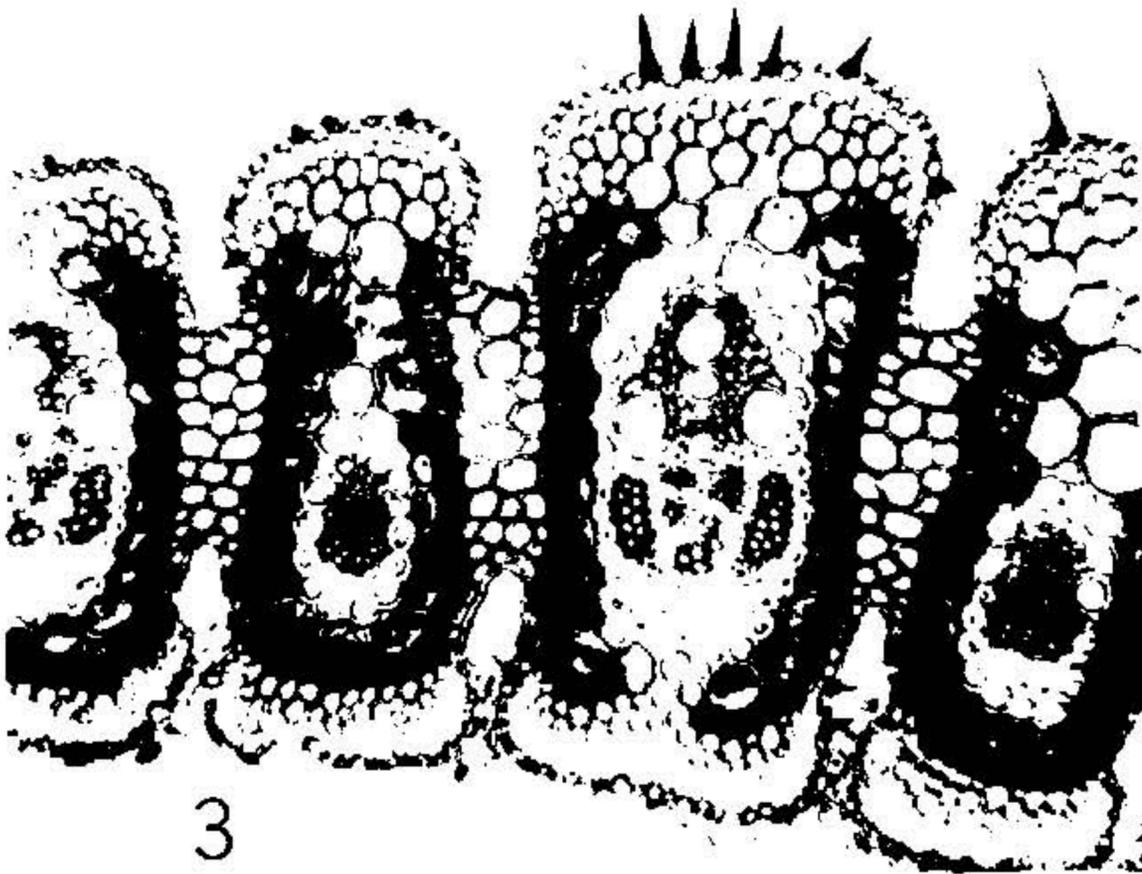
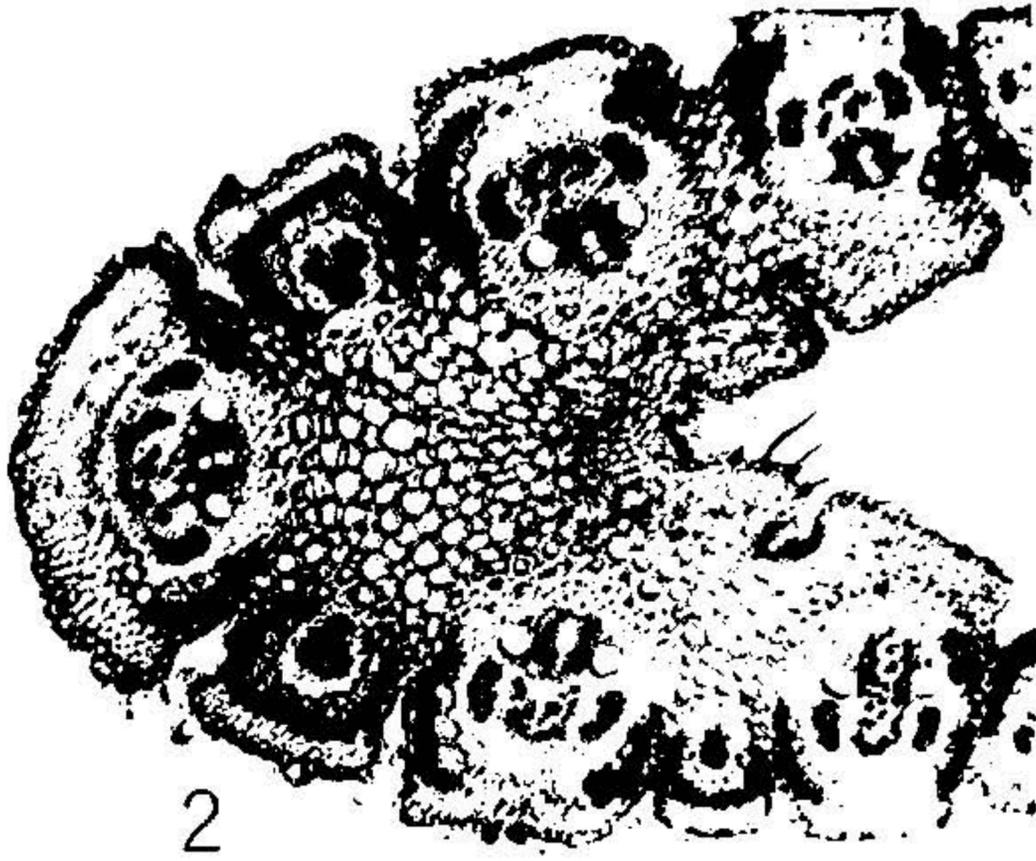
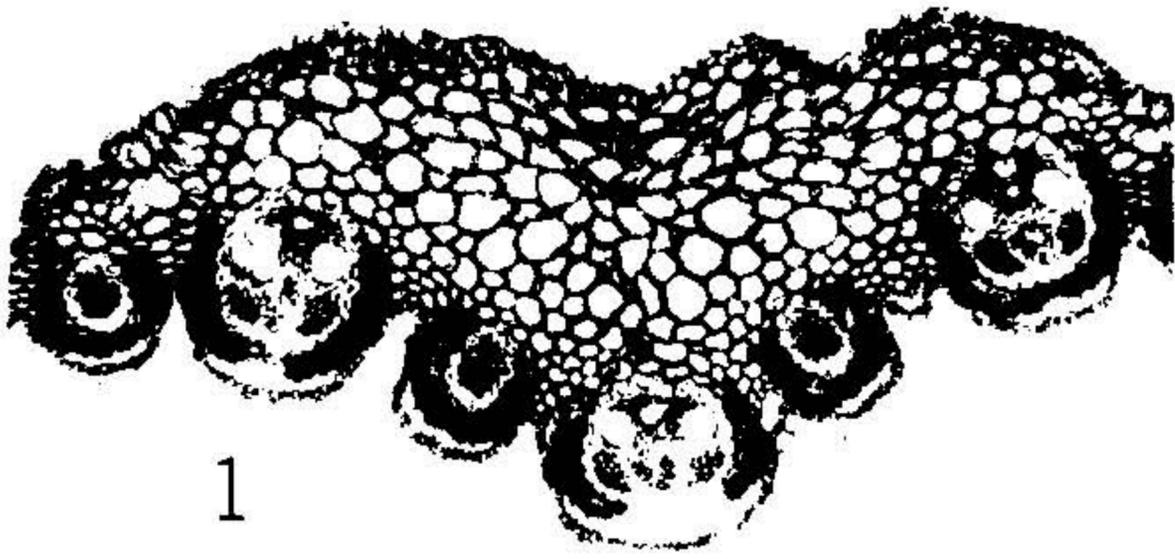


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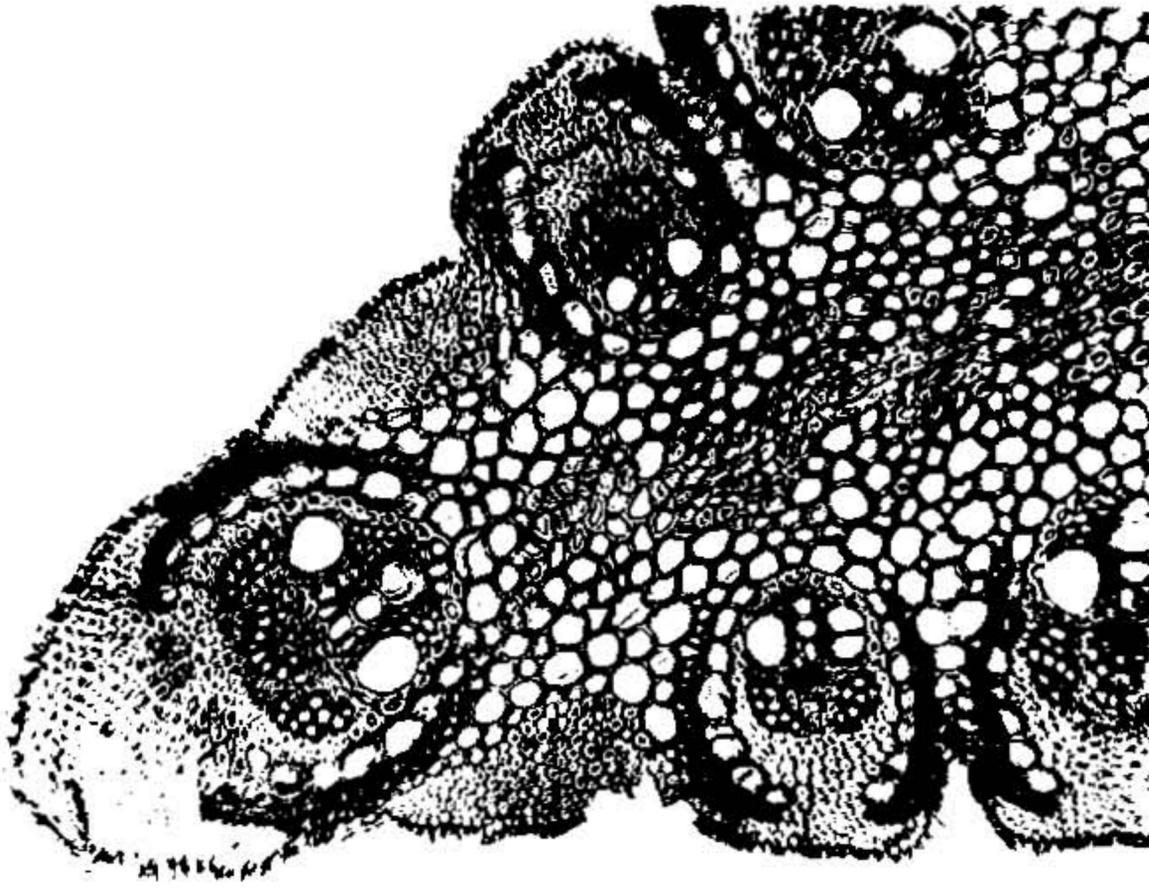
Photomicrographs of leaf cross sections: FIG. 1. *Muhlenbergia palmeri* (Pringle 1417),  $\times 194$ . FIG. 2. *M. expansa* (Amer. Gr. Nat. Herb. 1374),  $\times 156$ . FIG. 3. *M. holwayorum* (Rusby 201),  $\times 156$ .



Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia macrotis* (Mexia 9098),  $\times 165$ . FIG. 2.—*M. gigantea* (Soderstrom 607),  $\times 58$ . FIG. 3.—*M. lindheimeri* (Burr 513),  $\times 77$  (cf. pl. 8, fig. 3).



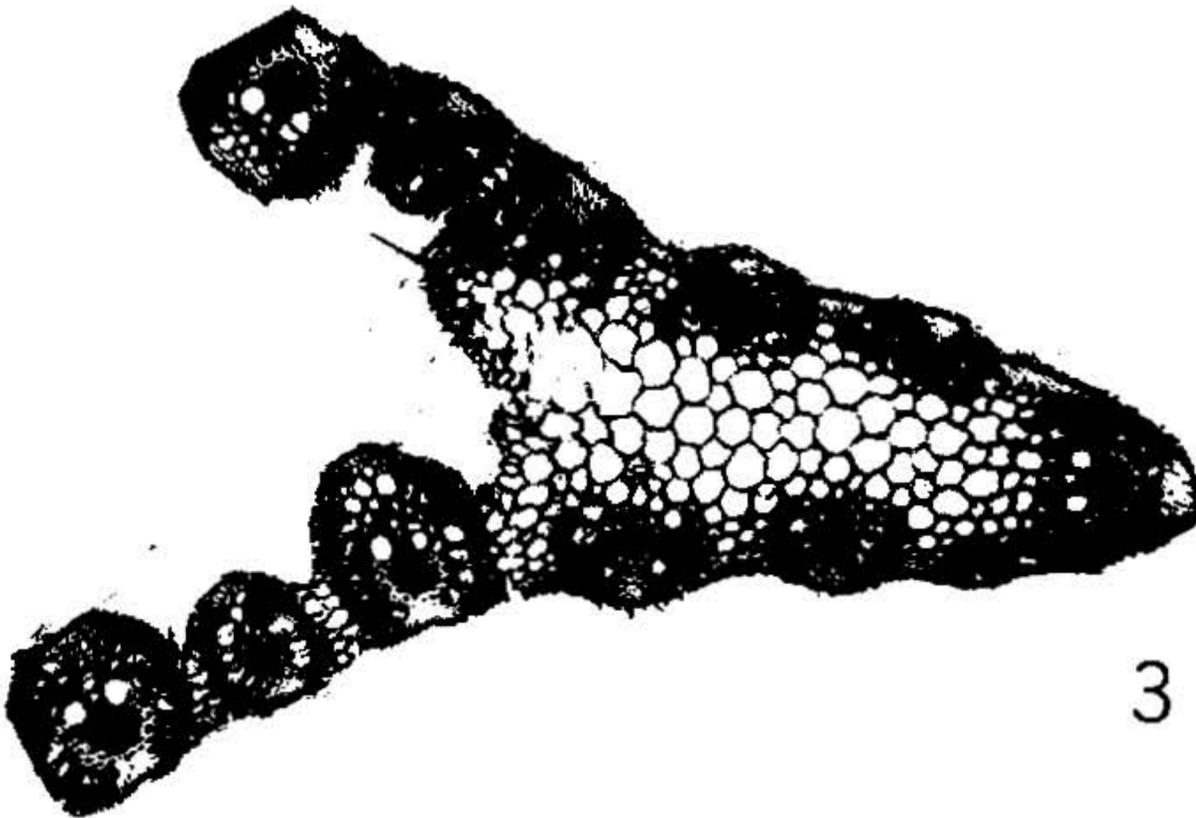
Photomicrographs of leaf cross sections: FIG. 1. *Muhlenbergia breviligula* (Standley 76731),  $\times 165$ . FIG. 2. *M. incoluta* (Silecus 780),  $\times 165$ . FIG. 3. *M. lindheimeri* (Burr 513),  $\times 206$  (cf. pl. 7, fig. 3).



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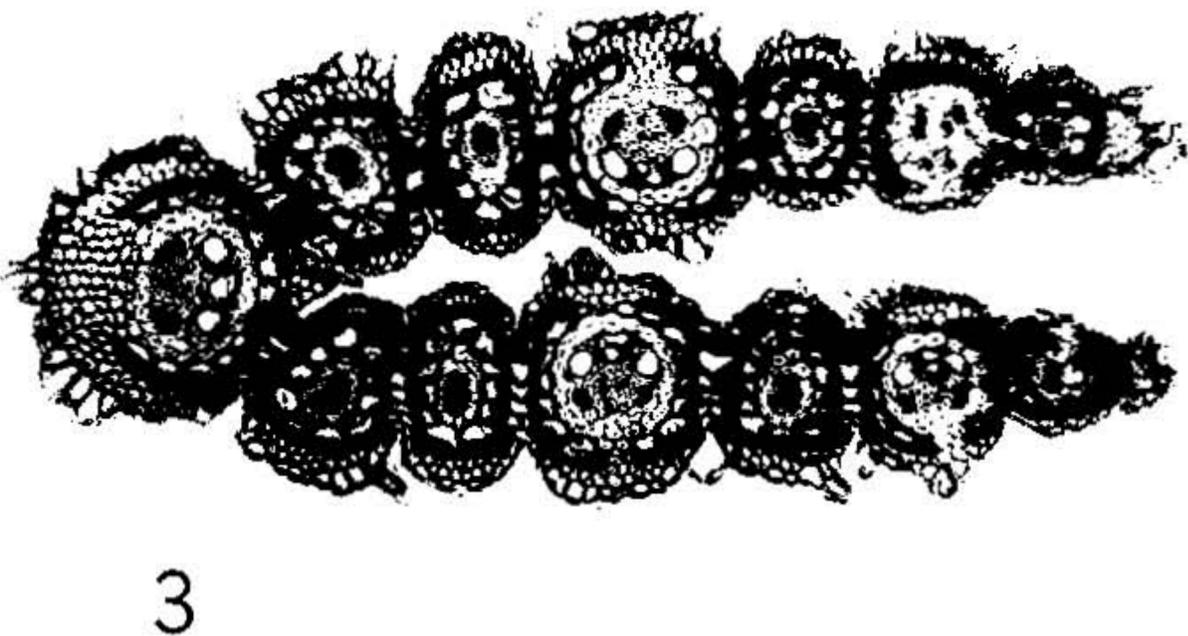
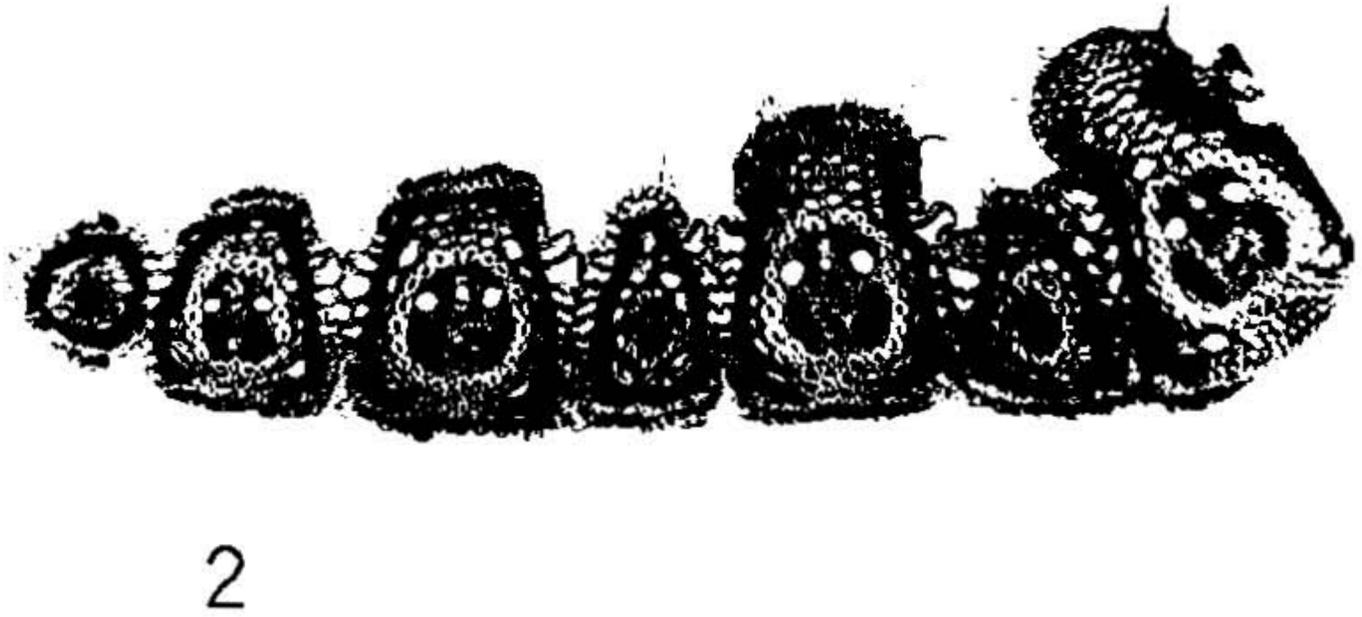
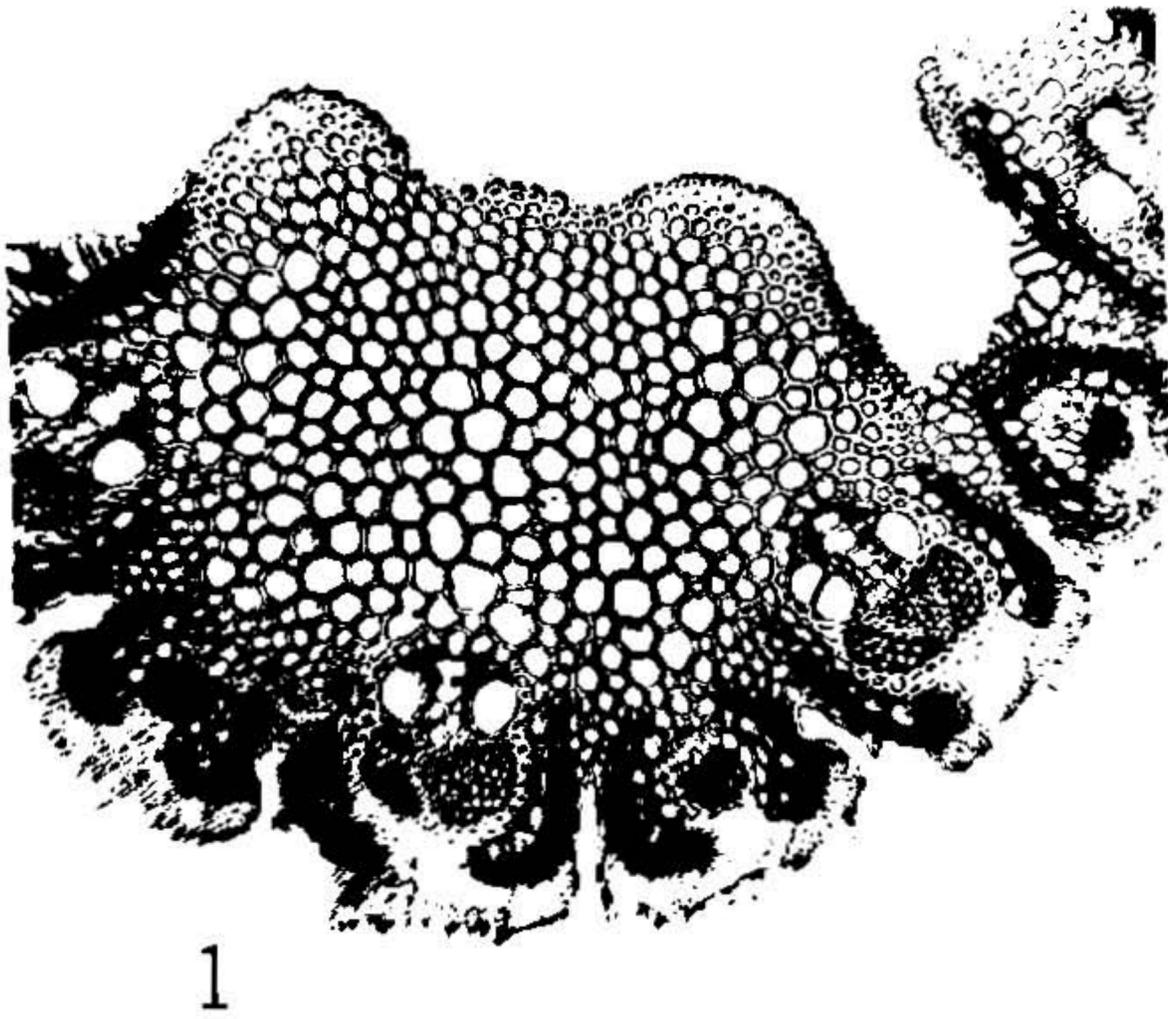


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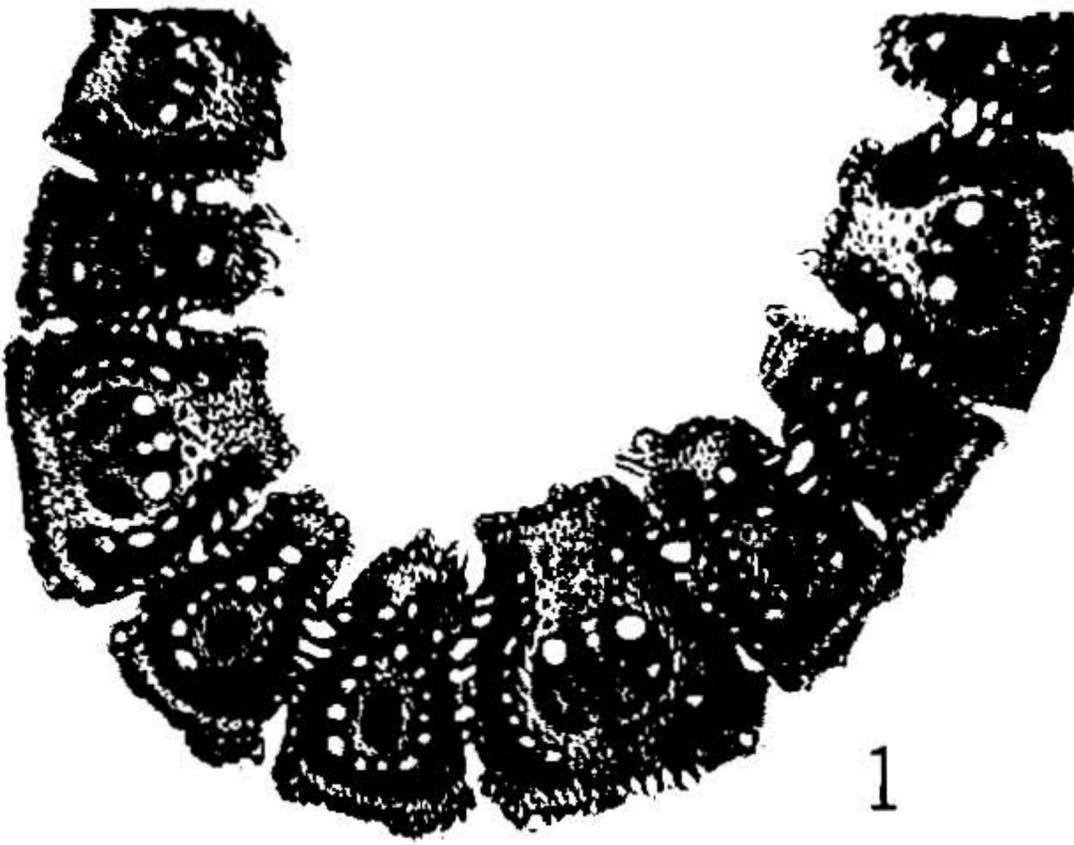


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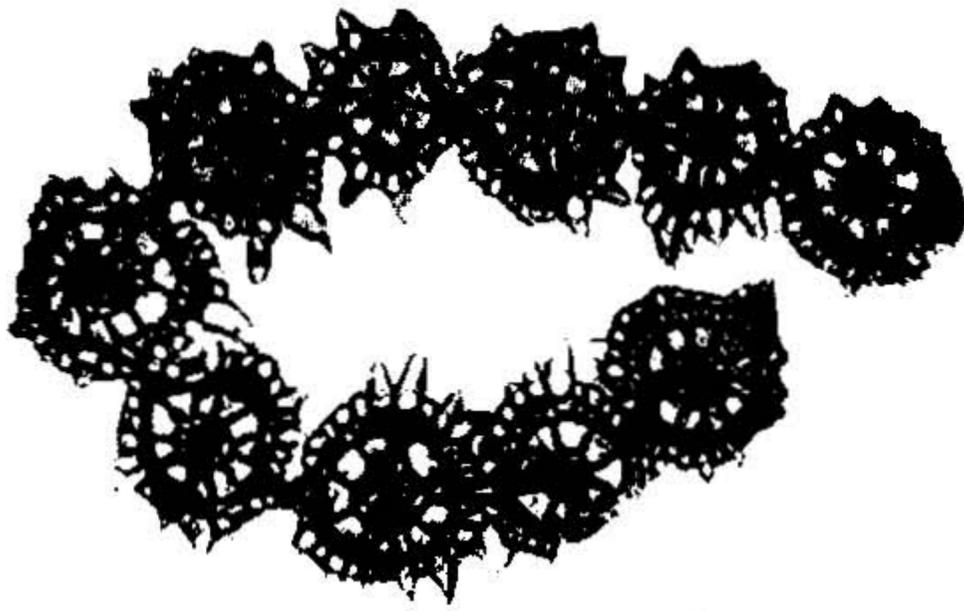
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia gigantea*, showing keel (Soderstrom 607),  $\times 165$ . FIG. 2.—*M. robusta* (Reeder & Reeder 2128),  $\times 165$ . FIG. 3.—*M. torreyana* (Bissell),  $\times 165$ .



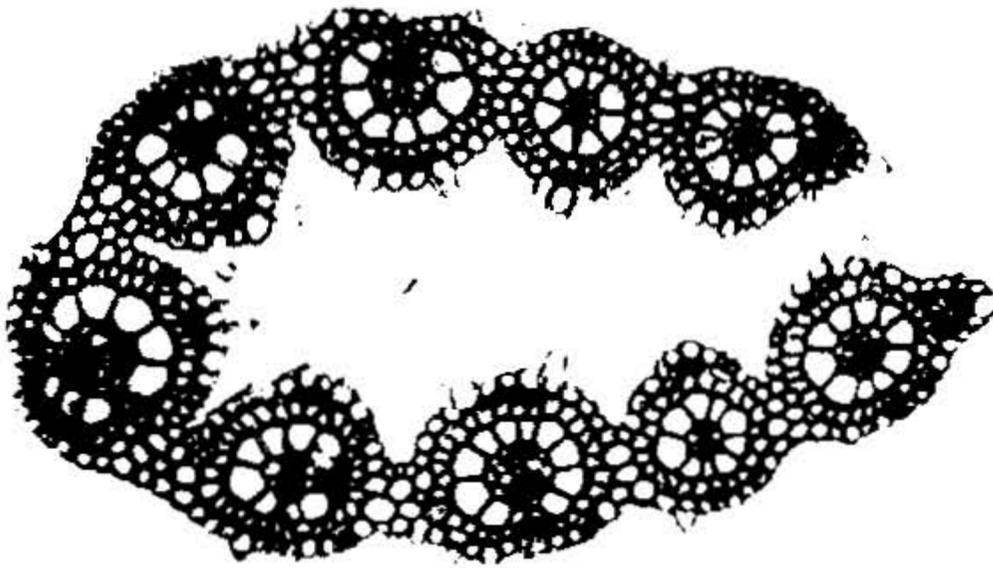
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia longiligula* (Blumer 1424),  $\times$  165. FIG. 2. *M. capillaris* (Sileucus 2396),  $\times$  165. FIG. 3.—*M. longiglumis* (Pringle 2365),  $\times$  165.



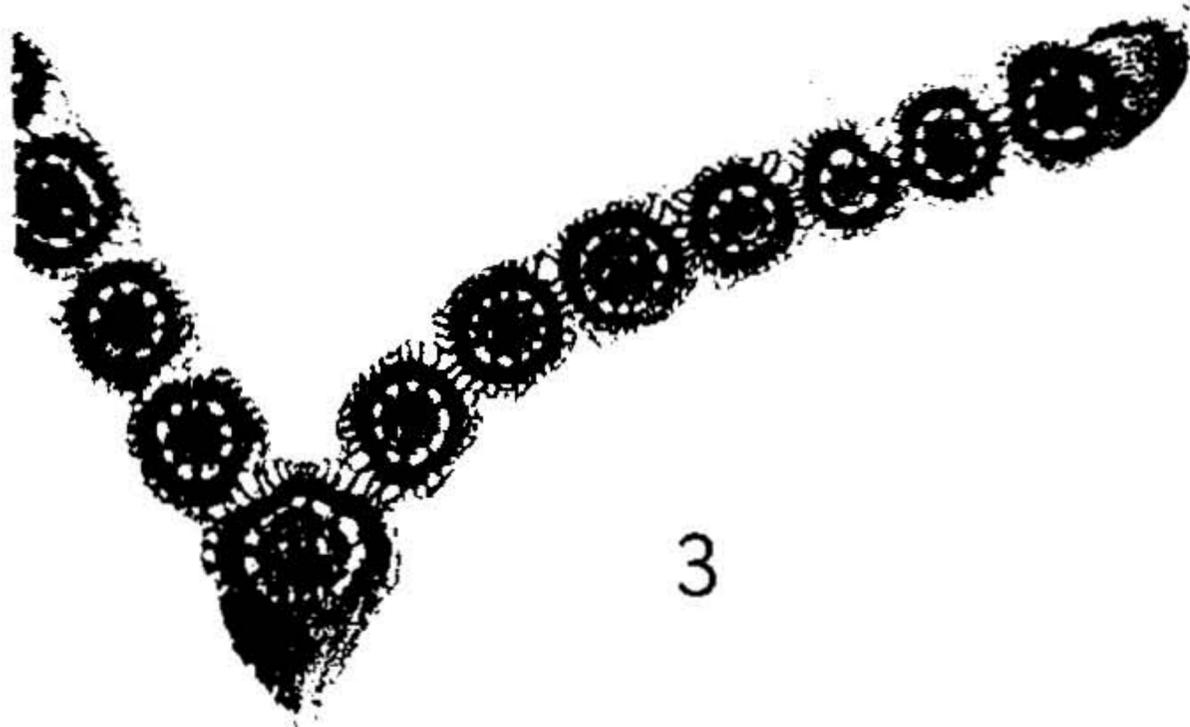
Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia reverchonii* (Silveus 2478),  $\times 165$ . FIG. 2.—*M. elongata* (Pringle 938),  $\times 165$ . FIG. 3.—*Muhlenbergia* aff. *montana* (Reeder & Reeder 2572),  $\times 165$ .



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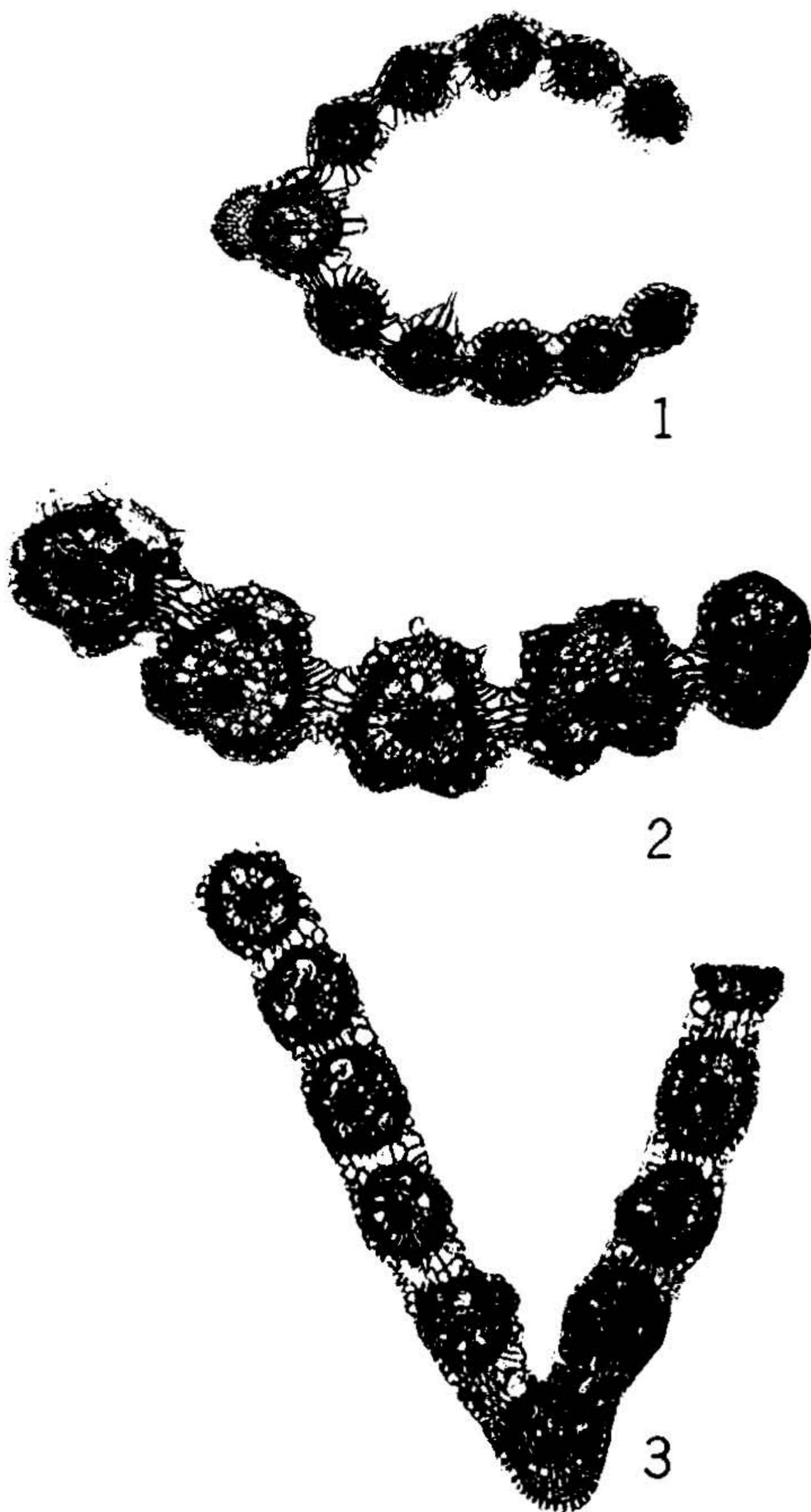


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Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia peruviana* (Pearson 1),  $\times 165$ . FIG. 2.—*M. pulcherrima* (Reeder & Reeder 2535),  $\times 165$ . FIG. 3.—*M. arizonica* (Reeder & Reeder 2602),  $\times 165$ .



Photomicrographs of leaf cross sections: FIG. 1.—*Muhlenbergia confusa* (Reeder & Reeder 2684),  $\times 165$ . FIG. 2.—*M. richardsonis* (Gooding M-3272),  $\times 206$ . FIG. 3.—*M. plumbea* (Reeder & Reeder 2218),  $\times 165$ .



Photomicrographs of leaf cross sections: FIG. 1. *Muhlenbergia crispiveta* (Reeder & Reeder 2545),  $\times 165$ . FIG. 2. *M. asperifolia* (Hardies M 103),  $\times 165$ . FIG. 3. *M. uniflora* (Johnson),  $\times 206$ .