LEAF ANATOMY
Dual Jouye (1875) first suggested systematic significance of the leaf anatomy in Gramineae on the basis of differences in the distribution of bulliform cells among species of its different tribes. Schwendener (1890) considered the bundle-sheaths and their variation in different species as a taxonomic character. Other characters which he considered is the distribution of sclerenchyma between the vascular bundle and the upper and lower epidermis. Pee-Laby (1893) used the concentration of chlorophyll in parenchyma sheath cells as a diagnostic feature and recognized five groups in Gramineae splitting natural tribes. This grouping was not valid as the characters used for differentiation were very poor (Brown 1958). Avdulov (1931) used leaf anatomy as a supplementary character and recognized two
basic groups in the leaf structure of grasses. Group I consisted of species having thick walled mestome sheath, connected by sclerenchyma to the upper and lower epidermis, a poorly developed parenchyma sheath and irregularly arranged chlorenchyma. Group II consisted of species having large sized parenchyma sheath cells separating the xylem from the sclerenchyma next to the upper epidermis and radially arranged chlorenchyma cells. Prat (1936) termed these groups as "festucoid" and "panicoid" respectively. Avdulov (1938) found the festucoid type in tribes Festuceae, Agrostideae, Hordeae, Aveneae, and Phalarideae; and the panicoid type in the tribes Andropogoneae, Maydeae, Chlorideae, and Zoysieae. These two types were considered the basic types by authors like Burbridge (1946), Prat (1937), Tateoka (1956 a,b,c,d,e,f) and Hickery (1935). Stebbins (1956) recognized two more types, namely the Bambusoid and the Chlorigoid. Brown (1958) on basis of his studies on 72 grass genera recognized six groups. These groups with the genera included in them are:

I. Bambusoid:

Arundinaria, Phyllostachys, Uniola, Strotochaeta,
Leersia, Zihtiopsis, Danthonia, Stipa, Brachyelytrum,
Oryzopsis.

II. Festucoid.

Agrostis, Cinna, Milium, Hordeum, Elymus, Poa, Festuca, Melica, Bromus, Glyceria, Phalaris.
III. Arundoid;

**Arundo, Phragmites, Cortaderia.**

IV. Panicoid;

*Cenchurus, Panicum, Paspalum, Pennisetum, Echinochloa, Setaria, Brachiaria, Digitaria, Eriochloa, Stenotaphrum, Andropogon, Sorghum, Sorghastrum, Eremochloa, Manisuris, Elyonurus, Trachypogon, Friianthus, Zea, Hyparrhenia, Heteropogon, Tripsacum, Arundinella, Danthoniopsis.**

V. Aristidoid:

**Aristida.**

VI. Chloridoid:

*Chloris, Trichloris, Leptochloa, Elusine, Bouteloua, Cynodon, Tripogon, Buchloe, Schedonardus, Eragrostis, Distichlis, Jouvea, Monanthochloa, Tridens, Vaseyochloa, Calamovilfa, Blepharoneuron, Lycerus, Blepharidachne, Pappophorum, Muhlenbergia, Hilaria, Sporobolus.*

Brown's classification seems to be natural as it nearly corresponds with the groupings in grasses on the basis of other morphological characters. After Brown, MetCalfe (1960) made the most detailed anatomical studies of 206 grass genera. For the present study the classification of grass leaf types is after Metcalf (1960) supplemented by the classification given by Brown (1953). Different groups created on the basis of leaf anatomy in the Gramineae by Brown (1953) are briefly described.
I. Bambusoid, characterized by an endodermis, some specializations of the thick walled parenchyma sheath cells, containing typical chloroplasts and modified chlorenchyma tissue.

II. Festucoid, well developed thick walled endodermis surrounded by a very/distinct parenchyma sheath, the cells of which are very small and very thin walled and contain chloroplasts similar to those of the loose, irregularly arranged spongy mesophyll cells; vascular bundle of basic type; chlorenchyma not radiate around vascular bundles; bundle sheaths double.

III. Arundinoid, parenchyma sheath cells not containing any chloroplasts. Endodermis poorly developed and chlorenchyma compactly packed.

IV. Panicoid, excepting in a few genera, generally the endodermis is absent, chlorenchyma radially arranged around the bundles. Mesophyll loosely arranged with large air spaces.

V. Aristidoid, mestome sheath lacking, parenchyma double layered and its cells containing specialized plastids.

VI. Chloridoid, presence of endodermis in the form of a single parenchyma sheath, restricted only around the larger bundles. Cells of parenchymatous layer containing specialized plastids.
Fig. 66. Transverse sections of the leaf blades of *Agrostis canina* and *Agrostis munroana.*
For the present study the following diagnostic characters were considered:

1. outline of the lamina
2. micro and macro hairs, prickle hairs
3. vascular bundles
4. ribs and furrows on the adaxial and abaxial surfaces
5. sclerenchyma
6. midrib, keel and keel bundles
7. mesophyll
8. bulliform and colourless cells
9. bundle sheaths

A detailed anatomical description of various taxa follows:

**Agrostis**

*Agrostis canina.*

The lamina flopped inward from the margins. Both adaxial as well as abaxial surface divided into furrows and ribs. Adaxial epidermis bears simple, single celled prickles. The vascular bundles conspicuously rounded in outline and of basic type; at least one and sometimes two metaxylem vessels are present to the right and left of the protoxylem; keel or midrib not conspicuous, with a single vascular bundle. Mesophyll chlorenchymatous, not radiating around the vascular bundles. Sclerenchyma present in form of strands on both upper and lower sides of the large and small vascular bundles. Bulliform cells small, not much inflated, present in furrows on the adaxial surface. Bundle sheath double; in small vascular bundles the inner sheath sometimes inconspicuous. (Fig. 66)
Fig. 67. Transverse section of the leaf of
A. Agrostis gigantea, B. A. subaristata,
Agrostis gigantea.

Lamina flat in outline. Both surfaces divided into furrows and ribs; abaxial epidermis protruded into a flat surface beneath the vascular bundles. The flattened abaxial epidermis beneath the vascular bundles with one small papillae on each side gives the surface an angular look. Microhairs and prickles absent. All vascular bundles equal in size, basic type and rounded in outline. Keel or midrib inconspicuous with a single vascular bundle. Mesophyll consisting of chlorenchyma, distributed irregularly between the two surfaces; not radiate. Very well defined strands of sclerenchyma present on both sides of the vascular bundles. Bulliform cells regular; furrows on the adaxial surface accommodate identical groups of bulliform cells. Bundle sheath double, with outer sheath more prominent.

(Fig. 67)

Agrostis stolonifera.

Lamina flat in outline; margins not folded inward. Both surfaces devoid of hairs, prickles; divided into ribs and furrows. Furrows are shallow on the abaxial surface and deep on the adaxial. Vascular bundles of basic type; large bundles interrupted by two smaller ones. Phloem occupying more than half of the space in the bundles. Keel very conspicuous having three vascular bundles, one large and two small. Chlorenchyma not radiate. Girders of sclerenchymatous strands present on both
upper and lower sides of the bundles. Vascular bundle of the keel exhibits a prominent sclerenchymatous patch in its middle. Bulliform cells almost rounded, not arranged in groups; situated parallel to the epidermis. Bundle sheath double. (Fig. 67)

*Agrostis munroana.*

The lamina folded inward from the margins. Both surfaces divided into deep furrows and high ribs. Adaxial surface bears very small, single celled prickle, swollen at the base. Vascular bundles oval in outline, basic type; large bundles interrupted by the smaller ones. Keel conspicuous with a single vascular bundle. Chlorenchyma not radiate; distributed in form of thin and long strands between the vascular bundles. Girders of sclerenchymatous strands present on both adaxial and abaxial sides of the vascular bundles; the girders being smaller on the adaxial side. Bulliform cells rounded and irregularly outlined; not arranged in groups. Bundle sheath double. (Fig. 66)

*Agrostis subaristata.*

Lamina flat; margins not folded. Adaxial and abaxial surfaces divided into furrows and ribs; devoid of hairs and prickles. Vascular bundles of basic type. Keel conspicuous with three bundles, one large and two small. Chlorenchyma not radiate. Large vascular bundles have well defined patches of sclerenchymatous strands on both adaxial and abaxial sides while small vascular bundles have irregular distribution of sclerenchyma; some are
devoid of it while others have very small girders on the abaxial surface only. Well defined groups of triangular bulliform cells present in the furrows on the adaxial side. Bundle sheath double, both inner as well as outer are well developed. 

(Fig. 67)

**Agrostis tenuis.**

Lamina flat in outline; adaxial surface divided into furrows and ribs, abaxial surface almost smooth. Vascular bundles of basic type, circular in outline. Keel not conspicuous. Chlorenchyma not radiate. Sclerenchyma poorly developed only around large vascular bundles. Bulliform cells not very well developed, oval or elliptic in outline. Bundle sheath double, outer sheath is obscure. (Fig. 67)

**Alopecurus aequalis.**

Lamina flat in outline. Adaxial surface divided into furrows and ribs; the ribs are triangular and acutely angled. Both surfaces bear simple, unicellular prickles. Vascular bundles of basic type, circular in outline. Keel conspicuous with a single vascular bundle. Mesophyll consisting of chlorenchyma, not radiate. Sclerenchyma not well developed; small, poorly differentiated strands present, sometimes, on the adaxial side of large vascular bundles only. Well defined bulliform cells
ALOPECURUS AQUALIS

ALOPECURUS HIMALAICUS

Fig. 68. Transverse sections of the leaf blades of Aloeocurus aequalis and A. himalaicus.
Fig. 69. Transverse section of the leaf of:
A. Alopecurus arundinaceus,
B. A. myosuroides, C. Calamagrostis epigejos, D. C. turkestanica X1800.
present on the adaxial side; some colourless cells identical with the bulliform cells are present on the abaxial epidermis. Bundle sheath double, both sheaths well developed. (Fig. 68)

*Alopecurus arundinaceus.*

Lamina folded inward from the margins. Adaxial surface divided into furrows and ribs; furrows very deep, ribs conical. Abaxial surface only wavy; both surfaces devoid of hairs, prickles etc. Vascular bundles of basic type with large metaxylem vessels; circular in outline. Keel inconspicuous. Chlorenchyma not radiate and distributed irregularly around the vascular bundles. Sclerenchyma very prominently developed; linear patches of strands present on both adaxial and abaxial sides of the bundles. Bulliform cells large, conical or rectangular, organised in groups, which are situated in the furrows on adaxial side. Bundle sheath double. (Fig. 69)

*Alopecurus himalaicus.*

Margins of the lamina folded inward. Both epidermis divided into furrows and ribs; these being more prominent on the adaxial surface. Vascular bundles of basic type, oval in outline; phloem occupies more space than xylem. Keel not conspicuous. Chlorenchyma distributed irregularly, not radiate. Well organised groups of conical, bulliform cells present in the furrows on the adaxial surface. Bundle sheath double, outer sheath obscure. (Fig. 63)
Alopecurus myosuroides.

Lamina folded inward from the margins. Both surfaces divided into ribs and furrows; these being more prominent on the adaxial surface. Both surfaces devoid of hairs and prickles. Vascular bundles of basic type, circular in outline. Keel not conspicuous. Chlorenchyma not radiate. Well defined linear girders of sclerenchymatous strands present on both sides of the vascular bundles. Well organised groups of conical bulliform cells present in the furrows on the adaxial surface only. Bundle sheath double. *(Fig. 69)*

**CALAMAGROSTIS**

Calamagrostis emodensis.

Lamina folded inward from the margins. Adaxial surface divided into furrows and ribs; furrows are quite deep but the presence of large groups of bulliform cells makes the whole surface even. Abaxial surface is only wavy. Vascular bundles oval in outline, basic type. Large bundles are interrupted by three smaller ones. Keel not conspicuous. Mesophyll consisting of chlorenchyma is not radiately arranged around the bundles; distributed in the form of thin and flat strips between the vascular bundles. Sclerenchymatous girders present on both adaxial and abaxial sides of the vascular bundles. Bulliform cells tall and conical. Bundle sheath double. *(Fig. 70)*
Calamagrostis epigeios.

Lamina folded inward from the margins. Adaxial surface divided into deep furrows and high dome shaped ribs. The abaxial surface is only wavy and not dissected into furrows and ribs. Adaxial surface bears simple, unicellular prickles. Vascular bundles of basic type; large and small arranged alternately. Keel not conspicuous, with a single vascular bundle. Chlorenchyma not radiate. Large vascular bundles have well defined patches of sclerenchymatous strands on both adaxial and abaxial sides; small bundles have these strands present only on the adaxial side. Well organised groups of conical bulliform cells present in the furrows on adaxial side of the lamina. Some colourless cells, identical to the bulliform cells but different in outline are present on the abaxial side. Bundle sheath double, both sheaths are well developed. (Fig. 69)

Calamagrostis kashmiriana.

Lamina folded inward from the margins. Both adaxial and abaxial surfaces are cut into furrows and ribs; devoid of hairs and prickles. Vascular bundles of basic type, oval in outline; large bundles interrupted by three smaller ones. Keel or midrib inconspicuous. Chlorenchyma not radiate. Moderately large girders of sclerenchyma present on both upper and lower sides of large vascular bundles; small bundles devoid of these strands. Dwarf and blunt bulliform cells, grouped conspicuously, are
Fig. 70. Transverse section of the leaf of:
A. Calamagrostis emodensis,
B. C. pulchella, C. C. scabrescens,
D. Lagurus ovatus. X1800.
present in the furrows on adaxial side. Bundle sheath double, outer sheath not well developed. (Fig. 71)

**Calamagrostis pulchella.**

Lamina folded inward from the margins. Both adaxial and abaxial surfaces divided into furrows and ribs, the divisions being more deep on the adaxial surface. Both surfaces devoid of hairs and prickles. Vascular bundles of basic type, circular in outline. Keel conspicuous with only one vascular bundle. Chlorenchyma not radiate; some chlorenchymatous girders are irregularly distributed in the chlorenchyma. Large girders of sclerenchyma present on both upper and lower side of both small and large vascular bundles. Groups of blunt and dwarf bulliform cells present in the furrows on adaxial surface. Bundle sheath double; in large bundles both sheaths are clearly visible while in small bundles the outer sheath is obscure. (Fig. 70)

**Calamagrostis scabrescens.**

Lamina flat; margins not folded inward. Both surfaces divided into furrows and ribs. Simple, unicellular prickles present on both surfaces. Vascular bundles of basic type, circular in outline. Keel or midrib inconspicuous. Chlorenchyma not radiate, distributed in the form of thin, flat strips between the bundles. Well defined and moderately large girders of sclerenchymatous strands present on both sides of the bundles. Groups of dwarf and conical bulliform cells present in some of
Fig. 7f. Transverse sections of the leaf blades of *Calamagrostis kashmiriana* and *Muhlenbergia huscelli*.
Fig. 71. Transverse section of the leaf of:
  A. Calamagrostis kashmiriana,
  B. Muhlenbergia hugelii.
  X 2250.
the furrows on the adaxial surface. Bundle sheath double; both sheaths well developed. (Fig. 70)

Calamagrostis turkestanica

Margins of the lamina folded inward, from the margins are given out simple, single celled prickles. Adaxial surface deeply cut into furrows and ribs, ribs dome shaped. Abaxial surface only wavy. Adaxial surface also bears simple, single celled prickles. Vascular bundles of basic type; large and small bundles alternate each other in their arrangement. Keel not conspicuous. Chlorenchyma not radiate, arranged compactly and in the ribs. Large girders of sclerenchymatous strands present on both upper and lower side of the bundles. Small bundles have smaller girders around them. Well defined groups of conical, moderately large bulliform cells present in the furrows on the adaxial surface. Some colourless cells different from the bulliform cells present on the abaxial surface. Bundle sheath double, both sheaths distinctly visible. (Fig. 69)

LAGURUS

Lagurus ovatus.

Lamina flat and very thin. Adaxial and abaxial surfaces protruded out only at the places where vascular bundles are present. Both surfaces bear a dense growth of unicellular, simple and very long hairs. Vascular bundles of basic type, oval in
outline, separated from each other by large, thin strips of mesophyll. Keel inconspicuous, having a single vascular bundle. Chlorenchyma not radiate. Sclerenchyma present in form of moderately large strands on abaxial and adaxial sides of vascular bundles only. Bulliform cells irregularly outlined, present in conspicuous furrows between the ribs. Bundle sheath double, both sheaths distinct. (Fig. 70)

**Muhlenbergia**

*Muhlenbergia himalayensis.*

Lamina flat, both surfaces divided into ribs and furrows of almost equal size giving the lamina a shape of beaded necklace. Small, simple and unicellular prickle hairs present on adaxial surface. Vascular bundles of basic type, conspicuously angular with large metaxylem vessels. Keel or midrib conspicuous with a single, large vascular bundle. Chlorenchyma very regularly distributed, conspicuously in a radiate fashion around the vascular bundles. Girders of sclerenchymatous strands present on both upper and lower side of vascular bundles. Bulliform cells not clearly visible. Bundle sheath double, outer sheath is not distinctly visible. (Fig. 72)

*Muhlenbergia huegelii.*

Lamina flat, both surfaces divided into furrows and ribs. Simple, unicellular prickle hairs present on adaxial
surface. Vascular bundles of basic type, typically angular. Keel conspicuous with a single large vascular bundle, which has a sclerenchymatous girder in its middle also. Chlorenchyma distributed conspicuously in a radiate fashion around the vascular bundles. Bulliform cells not seen. Bundle sheath double. (Fig. 71)

**Phleum**

*Phleum alpinum.*

Lamina flat, margins not folded. Adaxial surface divided into deep furrows and ribs; abaxial surface wavy in outline. Small prickle hairs very scarcely present on the adaxial surface. Vascular bundles of basic type, circular in outline. Keel or midrib conspicuous with a single large vascular bundle. Chlorenchyma not radiate, irregularly distributed. Girders of sclerenchymatous strands present on both adaxial and abaxial side of vascular bundles. Well defined groups of conical bulliform cells present in furrows on adaxial side. Bundle sheath double, both sheaths distinctly visible. (Fig. 72)

*Phleum graceum.*

Lamina flat; margins not folded inward. Both surfaces divided into furrows and ribs. Adaxial surface exhibits typical single celled prickle hairs at the top of vascular bundles only. Vascular bundles of basic type, oval in outline. Keel inconspicuous.
Fig. 72. Transverse section of the leaf of:
A. Phleum alpinum, B. Polypogon-
semiverticillatus, C. P. monspeliensis,
D. P. fugax, E. Muhlenbergia himalayensis.
X1800.
Chlorenchyma not radiate. Large girders of sclerenchymatous strands present on both sides of the vascular bundles. Well organised groups of conical bulliform cells present in the furrows on adaxial surface. Bundle sheath double, both sheaths distinctly visible. (Fig. 73)

*Phleum paniculatum.*

Lamina flat, margins not folded inward. Both surfaces divided into furrows and ribs; devoid of hairs and prickles. Vascular bundles of basic type, oval in outline. Keel or midrib inconspicuous. Chlorenchyma distributed irregularly in patches; not radiate. Girders of sclerenchymatous strands present on both upper and lower side of the vascular bundles. Bulliform cells present in large numbers in the furrows of adaxial surface; identical cells present on the abaxial side also. Bundle sheath double. (Fig. 73)

**POLYPOGON**

*Polypogon fugax.*

Margins of the lamina not folded inward. Adaxial surface divided into deep furrows and ribs; at the peak of each rib there is present one or occasionally two simple prickle hairs. The abaxial surface is only wavy. Vascular bundles are of basic type. Keel conspicuous with a single, large vascular bundle. Chlorenchyma not radiate, distributed irregularly.
Fig. 73. Transverse sections of the leaf blades of *Phleum gramineum* and *Phleum paniculatum*.
Fig. 73. Transverse section of the leaf of:

A. Phleum graceum,
B. P. paniculatum X2250.
Sclerenchymatous strands present on both sides of vascular bundles. Well organised groups of conical bulliform cells present in furrows on adaxial surface. Bundle sheath double, occasionally the outer sheath is not clearly visible. (Fig. 72)

**Polypogon monspeliensis.**

Margins of the lamina folded inward; both surfaces divided into furrows and ribs. Occasionally single celled, simple prickle hairs present on the peak of ribs on adaxial side. Vascular bundles of basic type, circular in outline. Keel not conspicuous, with a single vascular bundle. Chlorenchyma not radiate, distributed irregularly. Sclerenchyma present on both sides of the vascular bundles. Bulliform cells moderately tall, arranged in groups which are present in furrows on adaxial side. Bundle sheath double. (Fig. 72)

**Polypogon semiverticillatus.**

Margins of the lamina folded inward; both surfaces deeply cut into furrows and ribs and are devoid of hairs, prickles etc. Vascular bundles are of basic type, circular in outline; large and small bundles alternate with each other in their arrangement in the leaf. Keel or midrib conspicuous with a single vascular bundle. Chlorenchyma not radiate, forms very thin strips between the vascular bundles. Large sclerenchymatous girders are present on both adaxial and abaxial surface of the vascular-
bundles. Bulliform cells conical, grouped into well defined bodies located in furrows on adaxial surface; some rounded, colourless cells are present on abaxial surface also. Bundle-sheath double. (Fig. 72)

CONCLUSIONS:

The anatomical characters of the Agrostidean leaf, in transverse section, are summarized in Table 27.

Broadly speaking, the leaf in all the Agrostidean taxa excepting genus Muhlenbergia is of festucoid type. The structure is apparently the same in all the species but the presence or absence of one or the other character is of taxonomic significance. Thus in Agrostis where structure of the leaf is almost similar in all the six species studied, but a close observation reveals that in Agrostis canina the large vascular bundles are interrupted by two smaller ones, whereas in Agrostis munroana they are interrupted by three smaller ones. Similarly the keel of Agrostis gigantea has one vascular bundle but in case of Agrostis stolonifera three bundles are found; in Agrostis subaristata both outer as well as the inner sheath around the vascular bundle are well defined and clearly visible but in Agrostis tenuis the outer sheath is too obscure. Likewise all the taxa differ from each other in one or the other respect, as described individually. The variation and the static nature of these anatomical characters can be helpful as a supplementary
character in the taxonomy of grasses but a key based exclusively on anatomical characters is difficult to form.

Table 27. Diagnostic anatomical features of Agrostidean leaf.

<table>
<thead>
<tr>
<th>Name of species</th>
<th>Vascular bundles</th>
<th>Keel</th>
<th>Chlorenchyma Bundle sheaths</th>
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<tbody>
<tr>
<td></td>
<td>Angulo-</td>
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<td></td>
<td>Not</td>
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<tr>
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<td>Conspicuous</td>
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<td>Inco-</td>
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<td>Radial</td>
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<td>Not-</td>
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<td>Singule</td>
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</tr>
<tr>
<td></td>
<td>Double</td>
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</tbody>
</table>

| Agrostis canina | - | - | - | - |
| A. gigantea     | - | - | - | - |
| A. munroana     | - | - | - | - |
| A. stolonifera  | - | - | - | - |
| A. subaristata  | - | - | - | - |
| A. tenuis       | - | - | - | - |
| Alopecurus aequalis | - | - | - | - |
| A. arundinaceus | - | - | - | - |
| A. himalaicus  | - | - | - | - |
| A. myosuroides | - | - | - | - |
| Calamagrostis emodensis | - | - | - | - |
| C. epigejos    | - | - | - | - |
| C. kashmiriana | - | - | - | - |
| C. pulchella   | - | - | - | - |
| C. scabrescens | - | - | - | - |
| C. turkestanica | - | - | - | - |
| Lagurus ovatus | - | - | - | - |
| Muhlenbergia himalayensis | - | - | - | - |
| M. huegelli    | - | - | - | - |
| Phleum alpinum | - | - | - | - |
| P. graceum     | - | - | - | - |
Table 27 contd.

<table>
<thead>
<tr>
<th>Species</th>
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<tr>
<td><em>P.paniculatum</em></td>
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<td><em>Polypogon fugax</em></td>
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<td><em>P.monspalensis</em></td>
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<td><em>P.semdiverticillatus</em></td>
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</table>

The only anatomical anomaly found in the tribe Agrostideae is genus *Muhlenbergia*. Both *M.himalayensis* and *M.huegelii* (worked out here) exhibit conspicuously angular vascular bundles with the chlorenchyma radiately arranged around them. The outline of the lamina is also different from other members of the tribe in being like a bead necklace. This leaf is of Chloridoid type. Thus inclusion of *Muhlenbergia* in Agrostideae is unnatural. Brown (1953) also supports this view and advocated its removal from this tribe. Other morphological characters further support this.