Discussion.

Hubbard (1948) derived tribes Phalarideae, Aveneae and Agrostideae from a single line which on one hand gave rise to Phalarideae and on other to Aveneae and Agrostideae. This line itself had a common origin with Monocotyledones-Festuceae. The group of tribes Festuceae and Agrostideae share amongst themselves, with a few exceptions, festucoid type of epidermis and leaf anatomy, first leaf blade in the seedling erect, narrow; usually 7 as basic chromosome number; 1-many floreted spikelets; mostly laterally compressed and typically articulated above the glumes so that they break up at maturity; 5-many nerved lemma. They show an increasing degree of modification or reduction of their spikelets and/or inflorescence as one proceeds from more
primitive Festuceae to the Hordeae and Agrostideae. Of this group, he considered Aveneae awf very closely related to Festuceae. But in general structure, distribution, the greater development of glumes wholly or partially enclosing glumes to provide additional protection to florets and frequent presence of a geniculate, twisted awn on the lemma assisting in wider distribution and ultimate burial of seed, the tribe shows advance over Festuceae; Phalarideae is akin to Aveneae in many features but has its own distinctions. Some of its members such as Ehrharta, Microlaena and Tetrarrhena are now transferred to Oryzaeae and one of its genera Anthoxanthum has x=5. Agrostideae is stated to reach climax of evolution in festucoid group of tribes with respect to spikelets which are 1-floreted.

Tateoka (1957) in his discussion on phylogeny of Poaceae considers four tribes: Festuceae, Monermeae, Triticeae and Agrostideae under subfamily Pooidea. Tribe Agrostideae is sensu Nees(Pilger, 1954). In Pooidea as in the whole family, he stress on chromosomes and leaf structure in systematics and arranged the tribes following results of such a sequence though the tribes are polyphyletic from a single line "which has arisen between tribes Lygeeae and Danthoniaeae of Arundoideae. The origin of subfamily Eragrostideae is shown between tribes Arundineae and Phenospermoae. The genera included by him in tribe Agrostideae, vide agreement with Ohwi (1942) include most of the genera from tribe Aveneae. He also merges both Aveneae and Agrostideae but retains the name Agrostideae.
In recent classifications of Gramineae six subfamilies are recognized (Table 32) but most of them do not recognize the tribe Agrostideae.

Table 32. Comparative chart of the grass subfamily groupings of various workers.

<table>
<thead>
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<tbody>
<tr>
<td><strong>POATAE</strong></td>
<td><strong>Festucoideae</strong></td>
<td><strong>Festucoideae</strong></td>
<td><strong>Festucoideae</strong></td>
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<td><strong>Fesucifor</strong></td>
<td><strong>Festucoideae</strong></td>
<td><strong>Festucoideae</strong></td>
<td><strong>Festucoideae</strong></td>
<td><strong>Festucoideae</strong></td>
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<tr>
<td><strong>mes</strong></td>
<td><strong>Bambusoideae</strong></td>
<td><strong>Bambusoideae</strong></td>
<td><strong>Bambusoideae</strong></td>
<td><strong>Bambusoideae</strong></td>
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<tr>
<td><strong>Phragmiti</strong></td>
<td><strong>Panicoideae</strong></td>
<td><strong>Oryzoideae</strong></td>
<td><strong>Oryzoideae</strong></td>
<td><strong>Oryzoideae</strong></td>
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<tr>
<td><strong>formas</strong></td>
<td><strong>Panicoideae</strong></td>
<td><strong>Oryzoideae</strong></td>
<td><strong>Oryzoideae</strong></td>
<td><strong>Oryzoideae</strong></td>
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<tr>
<td><strong>Sacchariferae</strong></td>
<td><strong>Eupanicoideae</strong></td>
<td><strong>Phragmitoideae</strong></td>
<td><strong>Arundinoideae</strong></td>
<td><strong>Eragrostoideae</strong></td>
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<td></td>
<td><strong>Phragmititiformes</strong></td>
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<tr>
<td><strong>Chloridoideae</strong></td>
<td><strong>Panicoideae</strong></td>
<td><strong>Panicoideae</strong></td>
<td><strong>Eragrostoideae</strong></td>
<td><strong>Eragrostoideae</strong></td>
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<tr>
<td><strong>formas</strong></td>
<td><strong>Chloridoideae</strong></td>
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<td></td>
<td><strong>Chloridoideae</strong></td>
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</table>

Gould (1963) also followed Stebbins and Crompton (1961) and transferred Agrostideae into Aveneae. In the tribe Agrostideae it is still agreed that:

1. Genera with firm terminally awned lemmas exerted from the glume resemble Festuceae; and
2. Genera with shorter, dorsally awned and more delicate lemmas and relatively longer, firmer glumes resemble Aveneae.

Thus on the whole the tribe shows two important tendencies. However, with the anatomical considerations we find four tendencies as follows:

1. Festucoid, the rule.

2. Aristidoid, *Aristida* (close to chlorodoid group)

3. Chloridoid, *Biepharoneuron, Calamvilia, Muhlenbergia*, *Sporo- Brachyelytrum* has often been included in Agrostideae but Pilger (1954) removed it to Festuceae and *Muhlenbergia* to Eragrostaeae. Reeder (1957) supported transfer of *Muhlenbergia* but doubted if *Brachyelytrum* belongs to Festuceae. Its embryo suggests relationship to *Oryza* or perhaps *Stipa*. The chromosome No. is 11

*Milium, Oryzopsis, Piptochaetium and Stipa* are often grouped in a tribe Stipeae (Pilger, 1954). But leaf anatomy is of two types, and chromosome number in *Milium* is 4, 9, 14 while in other genera multiples of 11 or 12, though basic type of embryo is the same.

Reed (1957) recognized the following types of embryo in Gramineae and gave illustrations of the various types in a number of genera. He proposed the formula F+FF for the festucoid and P-PP for the panicoid embryo. The four features selected by him are enumerated below (cf. Gould, 1968)

F Vascular trace to scutellum and coleoptile diverging at approximately the same point.
* Epiblast present.
* F Coleorhiza and scutellum not separated by cleft.
* F Embryonic leaf margins overlapping.

P Vascular traces to scutellum and coleoptile separated by an internode.
* Epiblast absent.
* P Coleorhiza and scutellum separated by a cleft.
* P Embryonic leaf margins overlapping.

Reed (1957) recognized the following types of embryo:

1. True festucoid. F+FF *(X***=7, small chromosomes, temperate, epi+)*
   
2. Panicoid. P-PP *(X=5, 9, 10, predominantly tropical)*

3. Chloridoid-Eragrostoid
   
4. Bambusoid
   
5. Oryzoid-Olyroid F-PP, F+PP, F+FP *(X=12, festucoid, vascularization, embryonic leaf panicoid, epi+ in most; mostly tropical, shows affinities with bamboooids)*

According to description given by Tateoka (1956)

Exceptional numbers of X=4, 6, 8, 11, 13, 17, 19, 23 are also reported in various subfamilies. Typical basic numbers alone are given here.
6. Arundinoid-Danthonoid. \( P-PF \ (X=6,12 \text{, basically panicoid, tropical}) \)

The following types of embryo occur in Agrostideae according to Reeder* (1957)

\[ F+FF: \text{Agrostis, Alopecurus, Ammophila, Agropyron, Calamagrostis,} \]
\[ \text{Cicuta, Colocanthes, Limnodea, Milium, Crysopsia, Phippsia,} \]
\[ \text{Phleum, Piptochaetium, Polygona, Stipa.} \]

\[ F+PF: \text{Brachyelytrum.} \]

\[ P+PF: \text{Blepharoneuron, Calamovilfa, Cypsila, Helocloa, Lycurus,} \]
\[ \text{Muhlenbergia, Peralena, Sporobolus.} \]

\[ F+PP: \text{Phaenosperma.} \]

\[ P-PF: \text{Aristida.} \]

Avdulov (1931) divided grasses on basis of leaf anatomy in two groups. Later Prat (1936) also recognized two groups, namely Festucoid and Panicoid, including panicoid subtype, chloridoid subtype and Bambusoid subtype. Tateoka (1957) has summarized differences between these two types and remarked that his own work on leaf anatomy and that of subsequent workers, notwithstanding valuable data which has established significance of this character, yet anatomy of many species has remained unknown.

On basis of anatomy, Brown (1958) considered Festuca of today as primitive ancestral grass group due to presence of endodermal sheath of cells with thick walls surrounding the vascular tissue; no distinct parenchyma sheath, arrangement of chlorenchyma cells irregular and large intercellular spaces, typical unspecialized spongy tissue.

In Festucoid grasses we also find absence of two celled hairs and presence of silica cells quite significant. Specialization of Festucoideae by reduction in leaf epidermis, caryopsis, embryo and seedling; and this reduction has lead to complexity (Brown, 1958).

* Reeder followed Hitchcock's (1950) classification.
On a comparative study of the embryo it is tempting to prepare lineological chart, assuming that the two great groups Festucoid and Panicoid had a common ancestor, and both have contributed in part to "formation of the various groups". Considering Agrostidaceae and nearest relatives we find that even these may have followed parallel paths in evolution. Thus whereas Festuceae shows true festucoid and Chloridoid-Eragrostoid features, it also shows traces of Bambusoid and Arundinoid-Danthonoid features. The Aveneae share Festucoid and Arundinoid-Danthonoid features alone. But Agrostidaceae shares embryo features with all the classes excepting truly Panicoid and Bambusoid. In this respect, it represents an offshoot parallel to Festucoid series, rather than having evolved through it.

Awdulov (1931) considered Bambusoideae, Oryzeae and Phragmitites primitive on basis of morphological and anatomical characters. He considered $x=12$ as the base number of the family Gramineae. Flovik (1948) regarded 5 as the primary basic number. Wanscher (1934) considered 7 as the basic chromosome number of the family, which he thought to have been derived from 8, which itself is a multiple of 4 (considered by him to be basic number for Angiospermeae). Brown (1948) also regarded 7 as base number for grasses which on reduction gave rise to 6 and 5 and then through hybridization 12 and 10. deWet (1954) regarded 6 as the original base number.

Mehra et al (1963) gave an evolutionary chart depicting their generalisations. It is interesting to find that their scheme embraces the embryo and leaf types shown in the family to a large extent.

Thus considering the various characteristics, the following phylogenetic chart (Fig. 160) emerges, though it is presented with much reservations since a thorough investigations into a number of species is yet to be available. However, considering ensemble of characters; lemma, awn, chromosome number
Figure 10. Phylogeny in Tribe Agrostideae.
the relationship amongst genera (Fig 101) are not drastically altered, e.g., *Muhlenbergia*, *Blepharoneuron*, *Brachyelytrum*, and *Calamovilfa* have same ancestors; *Cinna*, *Limnodea*, *Alopecurus* and *Polypogon* again share same ancestry but *Agrostis* behaves differently.

The results of the studies on the floristics, distribution, morphology, morphological variations, leaf anatomy, leaf epidermis, embryo, root hair development, starch grain of endosperm and chromosomes of various taxa belonging to tribe *Agrostideae* agree that this tribe (Excluding genus *Muhlenbergia*) is one of the most stable and natural assemblages in the family Gramineae. But the present disagreement amongst various workers on the systematic arrangement of Gramineae has made this tribe also a prey to sub-divisions, mergers and dissolutions. Where some of the workers like Brown (1950) etc., were worried about the unnatural assemblage of this tribe at the same time others like Pilger (1954) and Stebbins and Crompton (1961) left no time in dissolving the tribe as a whole and merging its members with *Aveneae* and *Eragrostideae*. Their main argument for this merger is that reduction in the number of spikelets in *Agrostideae* has taken place more than once, and the *Agrostidean* genera resemble more closely the genera with spikelets having two florets.

The morphology of various taxa show the tribe to be highly advanced. The spikelet is 1-floreted, glumes are small, lemma conspicuously different from glumes in texture and form, palea small, in some cases altogether absent, lodicules too absent in some cases. These characters in various taxa show close
relationships with each other, excepting genus *Muhlenbergia* which has exceptionally long awns, projecting from glumes.

The statistical analysis of the variations of morphological characters in natural populations of various taxa shows that most of the characters are not subject to significant variations. Only a few characters in some populations are of statistical significance but the significance is not of that magnitude as to create isolation for new species, sub-species or varieties. This shows a high degree of natural stability of this tribe. This stability may be because of the fact that the altitudes at which the species of this tribe are found in Kashmir have not been subject to heavy environmental changes. The lower altitudes of the valley have, of course, been subject to considerable climatic and geological fluctuations which in turn have added a lot of exotic element to the flora of valley. Sexual reproduction, interspecific and intergeneric crosses also seem to have contributed nothing towards the variation in this tribe. Intergeneric as well as interspecific crosses are known in this tribe but none was found in Kashmir. Thus presumably the static nature of this tribe is due to well established habitats which are not subject to environmental fluctuations and adaptability of the various species to them; as well as the incompatibility of the species to give rise to interspecific and inter-generic crosses or various cytological races. The chromosomes, of course, have contributed various ploidy levels in various taxa but phenotypically none of the levels have expressed themselves significantly.
The study of anatomical characters of leaf in the 
tribe reveals festucoid structure in all the genera except 
*Muhlenbergia*. The leaf epidermis is also panicoid in *Muhlenbe-
gia*, whereas it is festucoid in rest of the genera of the tribe. 
The embryo structure is also festucoid in all the genera except 
*Muhlenbergia* in which it is chloridoid-eragrostoid type. Root 
hair development is again festucoid in all the genera except 
*Muhlenbergia* in which it is of intermediate type. Similarly 
the study of starch grains in endosperm and chromosomes reveal 
that *Muhlenbergia* is the only unnatural assemblage in Agrostideae.

It may be concluded that Agrostidean taxa are truly 
festucoid as far as various morphological characters are conc­
erned. Genus *Muhlenbergia* is the only anomalous inclusion in 
the tribe being showing panicoid-chloridoid characters. Hence 
it is suggested that instead of dissolving the whole tribe 
*Muhlenbergia* may be segregated from it and included in tribe 
Eragrostieae as suggested by Stebbins and Crompton (1961). It 
is further suggested that sub-tribe *Muhlenbergiinae* Pilger may 
be recognized under Eragrostieae to accommodate *Muhlenbergia*. 
As far as the merger of Agrostideae and Aveneae are concerned 
the present study reveals that due to a natural assemblage and 
distinct morphological characters Agrostideae deserves a sepe-
rate place. Besides, it will not be appropriate to merge it with 
Aveneae which itself seems to be an unnatural assemblage as 
suggested by Hartley (1950) who feels that even after the segg-
regation of Danthonieae from it (Hubbard, 1948) the tribe Aveneae
still shows unnatural grouping. The reduction of the number of florets in spikelet may have taken place more than once but now the tribe Agrostideae after living a great geological age has attained approximate equilibrium with the environment (Hartley, 1950).