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Grass Phylogeny and Classification: Conflict of Morphology and Molecules

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ABSTRACT

The grass family (Poaceae) has been recognized as a unique lineage for more than 200 years, based initially on characters of inflorescence and spikelet morphology and corroborated by anatomical and other features in the latter half of the twentieth century. There have been a number of attempts to derive a phylogeny of sections of the family from structural (morphological and anatomical) characters. However, more recently the Grass Phylogeny Working Group (2001) applied cladistic principles to the whole family using molecular and structural characters. This study produced a single most-parsimonious tree from six molecular sequence data sets, chloroplast restriction site data, and structural data from a representative set of 62 grasses and four outgroup taxa. However, the cladogram reveals a weak correlation with structural characters. Only three out of 12 subfamilies have unequivocal anatomical synapomorphies and there is no unequivocal morphological synapomorphy in any subfamily. Homoplasious character states outnumber synapomorphic states to a large degree. Cladistic analyses of grass genera in recent studies, based on both micromorphological, anatomical, and molecular data, have often produced clades that are difficult or impossible to define by readily observable features. Examples are shown in this paper for some genera of Danthonioideae, the panicoid tribe Andropogoneae, and the chloridoid tribe Triodieae. A recommendation is made that formal taxonomic and nomenclatural changes should only be applied, particularly at the species level, when the lineages within a phylogeny correlate with marker morphological characters.

Key words: Andropogoneae, cladistics, Danthonioideae, Grass Phylogeny Working Group, Poaceae, Triodieae.

INTRODUCTION

Until relatively recently the classification of grasses, as with most other plant groups, was based on traditional characters and principles that were theory-neutral from a phylogenetic perspective. Classifications were based entirely on overall similarity. Early classifications of grasses until the end of the nineteenth century were based entirely on spikelet and inflorescence characters (Scheuchzer 1708; Linnaeus 1753; Brown 1810; Palisot de Beauvois 1812; Kunth 1833; Bentham 1881; Hackel 1887). A significant revolution of grass classification occurred from the end of the nineteenth century to the mid-twentieth century, with the great advance in the design and power of microscopes in a phase that has been termed The New Systematics (enumerated in Bor 1960). Cryptic characters from cytology, leaf anatomy, and embryology were examined in detail for the first time. These characters are well illustrated and discussed in classic papers by Duval-Jouve (1875), Avdulov (1931), Prat (1931, 1936), Hubbard (1948), Stebbins (1956), Brown and Emery (1957), Clark Row and Reeder (1957), Reeder (1957), Brown (1958), Bor (1960), and Jacques-Félix (1962). Their work impacted grass classification in a major way and resulted in changes to the constitution of the main subfamilies (Stebbins 1956; Tateoka 1957; Prat 1960; Jacques-Félix 1962; Roshevitz and Sendulsky 1969; Caro 1982; Clayton and Renvoize 1986; Tzvelev 1989; Watson and Dallwitz 1992). The classifications were mostly implied to have a phylogenetic basis, with the exception of the phenetic classification of Watson and Dallwitz (1992), but the application of phylogenetic framework was applied mostly in an ad hoc, subjective manner.

In the 1970s and 1980s considerable advances were made in the understanding of the ultrastructure of leaf anatomy of grasses and its relationship to the variations in photosynthetic pathway. Early work in this field (Carolin et al. 1973; Hattersley and Watson 1975, 1976) was followed by the significant investigations of Brown (1977) and Hattersley and co-workers (Hattersley 1987; Prendergast and Hattersley 1987; Hattersley and Watson 1992), although the place of the photosynthetic subtype as a definitive character in grass taxonomy (Chapman 1996) and phylogeny (Kellogg 1999*a*) is far from clear-cut.

The impact of the writings and methods of Hennig (1950, 1966) has resulted in a paradigm shift in the classification of all biological groups. Grasses have been subjected to more cladistic analyses, using both morphological and molecular data, than many other groups. Classical early morphological studies for the whole family (Kellogg and Campbell 1987) and for subfamilies (Kellogg and Watson 1993) using data collected by Watson and Dallwitz (1992) for exemplar genera were followed by a few for smaller groups using species (Linder and Verboom [1996] for the Australian danthonioids; Snow [1997] for the genus *Leptochloa* P. Beauv.). With the refinement of techniques in genomic analyses many cladistic analyses based on molecular data followed in the 1990s. Some of the best known and most frequently cited papers are Hamby and Zimmer (1988) using ribosomal RNA sequences, Doebley et al. (1990) using plastid *rbc*L sequence data, Davis and Soreng (1993) using plas-

tid DNA restriction site variation, Nadot et al. (1994) using plastid *rps*4 sequences, Clark et al. (1995) using plastid *ndh*F sequence data, Duvall and Morton (1996) using plastid *rbc*L sequences, Soreng and Davis (1998) using plastid DNA restriction site data, Barker et al. (1999) using plastid *rpo*C2 sequences, Hilu et al. (1999) using *ma*tK sequences, Hsiao et al. (1999) using nuclear ribosomal ITS, Zhang (2000) using plastid *rpl*16 intron sequences, and Mathews et al. (1996, 2000) using the nuclear phytochrome gene family.

The rationale for this paper is to address two important topics in systematics. The first is the apparent conflict between morphology and molecules often seen in phylogenetic analyses. The second is the extent to which traditional classifications should be changed, based on the results of these phylogenetic analyses. There is a relatively greater amount of information for the grass family compared to other plant families or groups, so it is a logical choice to examine these questions. The contents have been divided into two sections: the first examining in some depth the phylogeny and subfamilial classification of the Grass Phylogeny Working Group (GPWG) 2001, and the second looking at three studies of the phylogenies and classifications of particular subfamilies and tribes of grasses, specifically, the subfamily Danthonioideae and tribes Andropogoneae and Triodieae.

GRASS PHYLOGENY WORKING GROUP

The Grass Phylogeny Working Group was set up in 1995 to amalgamate multiple data sets on grass phylogeny with the aim of producing a new classification of the family. The group consisted of the following 13 people: Nigel P. Barker, Lynn G. Clark, Jerrold I Davis, Melvin R. Duvall, Gerald F. Guala, Catherine Hsiao, Elizabeth A. Kellogg, H. Peter Linder, Roberta J. Mason-Gamer, Sarah Y. Mathews, Mark P. Simmons, Robert J. Soreng, and Russell E. Spangler.

The results from a combined analysis of six molecular sequence data sets (*ndh*F, *rbc*L, *rpo*C2, *PHY*B, ITS-2, and GBSSI or *waxy*), chloroplast restriction site data, and structural (morphological and anatomical) data from a representative set of 62 grasses plus four outgroup taxa were published (GPWG 2001).

The main results from this collaborative study may be summarized in a number of points:

(1) The analysis resulted in a single most-parsimonious tree.
(2) Some relationships were strongly supported by the combined analysis:
    (a) The family Joinvilleaceae was sister to a monophyletic Poaceae.
    (b) Earliest-diverging lineages were the subfamilies Anomochlooideae, Pharoideae, and Puelioideae.
    (c) All remaining grasses formed a clade, consisting of two main clades, the BEP clade (Bambusoideae, Ehrhartoideae, Pooideae) and the PACCAD clade (Panicoideae, Aristidoideae, Centothecoideae, Chloridoideae, Arundinoideae, Danthonioideae).
(3) Four genera (*Streptogyna* P. Beauv., *Micraira* F. Muell., *Gynerium* Willd. ex P. Beauv., *Eriachne* R. Br.) did not readily group with other genera and were treated as incertae sedis.

(4) Based on the phylogeny, a classification of 11 previously published subfamilies and one new one (Danthonioideae) was proposed.

In my opinion, the GPWG (2001) classification presents a number of problems:

(1) Only 62 grasses were included in the analysis. This represents 0.56% of all grass species and 8.46% of genera from a total of 11,024 species and 741 genera (current totals of grass species and genera in the Grass World Database maintained at BRI).
(2) There is a rather weak support for structural characters, i.e., there is high homoplasy for morphological and anatomical characters.
(3) Only three of the 12 subfamilies (Panicoideae, Aristidoideae, Danthonioideae) have unequivocal structural synapomorphies, all of which are anatomical.
(4) Other structural synapomorphies are basal in the cladogram, with none linked to a subfamily but only to clades. Homoplasious structural character states far outnumber the synapomorphies.
(5) Subfamilies Anomochlooideae, Pharoideae, Puelioideae, the BEP clade, all subfamilies within the BEP clade, and three subfamilies within the PACCAD clade have no structural synapomorphies. The PACCAD clade itself has a synapomorphy of an elongated embryo mesocotyl internode.
(6) Although seven molecular data sets were used, this is a minute fraction of the DNA sequences potentially available.

The premise of basing a classification on a phylogeny derived mainly from molecular data appears sound from a theoretical perspective. The GPWG (2001) findings appear overwhelmingly convincing in that most of the data came from six molecular sequence data sets and from these data a single most-parsimonious tree resulted. However, if the subfamilies cannot be recognized in practice, using unique morphological characters, by the clients of our classifications, should we be using mainly molecular-based phylogenies as a basis for classification?

There is an alternative current view (N. Snow pers. comm., 2003) that the recognition of higher groups such as tribes and subfamilies by means of obvious structural synapomorphies may not now be as desired an objective as it once was. However, the present basic desire to understand the nature of morphological characters in phylogeny is apparent, with two recent international conferences on the subject (Stuessy et al. 2001; MacLeod and Forey 2002). A fundamental issue is that molecular phylogenetic studies depend in the first place on morphological data, in that exemplar taxa are from a classification that is primarily morphologically based.

The lack of morphological support for most subfamilies of Poaceae does not appear to be of concern to some grass phylogeneticists. When this issue was raised with E. A. Kellogg, she replied (pers. comm., 2001), ''It is true that many of the subfamilies as defined by the GPWG do not have any morphological synapomorphies. I think it's probably an inevitable consequence of a cladistic classification, since there is not any particular reason why evolution should always

produce a handy macroscopic character at every speciation event. A major argument against a cladistic classification is that it is not always practical.'' A total of 46 structural characters were assessed by the GPWG (2001) as those that could be interpreted to be of use as measures of phylogenetic signal in the grasses. These characters can be grouped as follows: culm (2 characters), leaf (5), spikelet (10), floret (14), fruit and embryo (9), seedling (6). In most cases they are two-state characters indicating absence or presence.

These characters and their states were optimized on the overall phylogeny, but the results suggest that some of them ''may be useful for delimiting groups within tribes or subfamilies, but are too variable to be useful in delimiting subfamilies'' (GPWG 2001). A further problem in the assessment of structural characters is whether they are homologous. An example is the presence of paired spikelets in both Andropogoneae and Pharoideae. If the spikelet pairing character state can be considered to be equivalent from a developmental point of view, this character is homoplasious, but if spikelet pairing is due to a different developmental pathway, it is synapomorphic. In other words, if development of the paired condition in these lineages is not equivalent, the paired spikelet character has to be split into two characters, with appropriate wording to define the nature of the pairing. Knowledge of the assessment of homology in structural characters in grasses is very restricted and until much more is known about this subject, the use of morphological characters in grass phylogeny will probably have a limited application. In this regard, it is interesting that the concept of homoplasy was treated at some length as far back as the 1920s by Vavilov, when discussing his ''law of homologous series in variation'' (Vavilov 1922).

Of the 46 characters only 17 can be said to be of an easily observable macroscopic nature. The other 29 are more difficult to detect in that they require microscopic examination or careful dissection. Nevertheless, they can be detected for one major clade (PACCAD) and three subfamilies (Panicoideae, Aristidoideae, and Danthonioideae) and thus are diagnosable. The PACCAD clade has a synapomorphy of an elongated embryo mesocotyl internode and within the PACCAD clade there are three anatomical synapomorphies as markers for subfamilies: NADP-ME anatomy for Panicoideae, a special type of NADP-ME leaf anatomy for Aristidoideae, and the presence of haustorial synergids for Danthonioideae. However, the majority of the clades and subfamilies do not have any diagnosable structural characters. It is unlikely many more structural characters with phylogenetic application in the grass family will be detected, due to the great depth in which the grass family has been researched.

Since GPWG (2001), further work has been conducted by researchers, particularly with regards to some of the genera treated as incertae sedis by GPWG. For example, it appears that the genus *Micraira* has affinities with the genus *Isachne* R. Br. (tribe Isachneae) (Sánchez-Ken and Clark 2007), traditionally regarded as part of Paniceae but not included in the GPWG (2001) study. In fact, they constitute a separate clade, based on two plastid markers (*ndh*F gene and *rpl*16 intron) and a morphological synapomorphy of the lemmas being similar (as opposed to the sterile lemma being glumelike). There is also a trend towards two bisexual florets, although this character is not unique, in that a few species do have only one bisexual floret. Furthermore, other work undertaken on grass phylogeny since GPWG (2001) reveals that the genus *Eriachne* may also belong in the same clade as *Micraira* and *Isachne (*Duvall et al. 2007).

EXAMPLES FROM STUDIES OF SUBFAMILIES AND TRIBES

Thus far, this paper has assessed the GPWG (2001) phylogeny and subsequent work whereby the grass family has been classified into 12 or more subfamilies based on phylogenetic principles using cladistic methodology from a combined analysis of molecular sequence data sets, chloroplast restriction site data, and structural data. More detailed phylogenetic work has also been undertaken on individual grass subfamilies, tribes, and genera using micromorphological, anatomical, and molecular data. Sometimes, the clades resulting from these studies have been extrapolated into classifications where the taxa are difficult to recognize by readily observable features. Examples are shown for some genera of the subfamily Danthonioideae, the panicoid tribe Andropogoneae, and the chloridoid tribe Triodieae.

Subfamily Danthonioideae

A cladistic analysis of 70 mainly Australasian species of danthonioid genera using morphological data (49 characters) by Linder and Verboom (1996) was the basis for a new classification of this group. Linder and Verboom proposed a division of the Australasian representatives of *Rytidosperma* Steud. s.l. into three smaller genera, *Austrodanthonia* H. P. Linder, *Notodanthonia* Zotov, and *Rytidosperma* s.s., on rather weak morphological evidence. There is no unique synapomorphy for *Notodanthonia* and those for *Austrodanthonia* (long callus) and *Rytidosperma* (small metaxylem vessels) are characters difficult to detect by the general user. Nevertheless, the name changes have now been applied to the Australian taxa in both the AusGrass interactive key and information system (Sharp and Simon 2002) and the introductory *Flora of Australia* grass volume (Mallet and Orchard 2002). In contrast, the *Flora of New Zealand* grass volume (Edgar and Connor 2000) does not take up these generic splits, only recognizing *Rytidosperma* s.l., following a similar view for this danthonioid group as Clayton and Harman (2002 and ongoing) in their world grass database.

More recent work for this group based on three molecular data sets, a morphological data set, and 54 species (Barker et al. 2000) recognizes a *Rytidosperma* clade that comprises Australasian *Rytidosperma, Notodanthonia, Austrodanthonia,* and *Joycea* H. P. Linder, African *Karroochloa* Conert & Türpe*, Schismus* P. Beauv., and *Tribolium* Desv., and some species of *Merxmuellera* Conert. Because of this general uncertainty of the classification and composition of danthonioid genera, there are current plans to undertake a worldwide study of danthonioid grasses to include as many species as possible (H. P. Linder pers. comm., 2003*).* When that stage has been reached, we should be in a better position to discern whether a spitting or lumping solution is the correct one for the danthonioid grasses. To this end, the African clade to which the species of *Pentaschistis* (Nees) Spach belong is already being studied in some depth (Galley and Linder 2003).

It is possible, however, that the genera ultimately recognized still may not have clear morphological characters. A couple of quotes by H. P. Linder (pers. comm., 2002, 2003) in this regard exemplify current thinking by researchers in danthonioid grasses:

> It would be nice to have each genus with a unique morphological character. I am not convinced that this is possible. I would suggest waiting until we have a full molecular phylogeny, then we can start looking for better generic boundaries, if they exist. I suspect they will remain very difficult in the danthonioids.

> I doubt that we will get much out of morphological data and I guess morphological data will get ever more tangled in definitions of when a tuft is a tuft, and when not.

Tribe Andropogoneae

The pantropic tribe Andropogoneae is best represented in the Old World savannas and has ca. 960 species (Clayton and Renvoize 1986). It is one of the two traditionally recognized subtribes of subfamily Panicoideae, representing ca. 32% of the subfamily; the other tribe being Paniceae with ca. 2000 species (Clayton and Renvoize 1986). The two tribes are traditionally separated on the basis of a number of characters. Andropogoneae have paired spikelets, with one sessile and the other pedicelled, arranged in modified racemes known as rames, which terminate in a triad of one sessile and two pedicelled spikelets. Usually the sessile spikelets are bisexual and the pedicelled spikelets are staminate, and a spikelet pair usually disarticulates with a segment of the rachis and the pedicel. Furthermore, most Andropogoneae have firm outer spikelet bracts, possess a geniculate and hairy awn, and are C_4 grasses with a NADP-ME photosynthetic pathway. In contrast, Paniceae have membranous outer spikelet bracts, spikelets that usually are not paired, or if they are, they are generally both pedicelled, sometimes unequally, and similar in sexuality. Spikelets of Paniceae disarticulate without any attached rachis segments and if awns are present they are not geniculate and hairy. Paniceae are C_3 or C_4 grasses with three types of photosynthetic pathways (NADP-ME, PCK, and NAD-ME), as well as C_3/C_4 intermediates (Sage et al. 1999).

Recent cladistic analyses of subfamily Panicoideae using molecular characters (Giussani et al. 2001; Aliscioni et al. 2003) cut across this traditional classification. Paniceae, with a base chromosome number of $x = 10$, forms a sister group to Andropogoneae (also $x = 10$); whereas, Paniceae that have $x = 9$ form a sister group to the first two clades. What bearing this will have on future classifications of the subfamily, which has had such a stable classification based on morphology, is a possible cause for concern.

Although Andropogoneae are monophyletic (Clayton 1987; Kellogg and Watson 1993; Kellogg 2000; Giussani et al. 2001; Aliscioni et al. 2003), the classification of the tribe itself, consisting of 85 genera (Clayton and Renvoize 1986), continues to present problems. The original tribal circumscription of Hackel (1889) based on morphology is largely similar to that of Clayton and Renvoize (1986), although many subgenera of *Andropogon* L. have since been elevated to generic rank. Both Hackel (1889) and Clayton and Renvoize (1986) present diagrams depicting the evolutionary development of selected genera where trends are indicated by progressive levels of morphological complexity. In three accounts of the tribe, Clayton formerly assigned andropogonoid genera to subtribes; one account dealing with the awned genera (Clayton 1972; subtribes Dimeriinae, Saccharinae, Germainiinae, Sorghinae [as Arthraxoninae], Andropogoninae, Anthistiriinae, and Ischaeminae), and the other accounts dealing with the awnless genera (Clayton 1973, 1981; subtribes Rottboelliinae, Tripsacinae, Coicinae, and Chionachninae); summarized by Clayton and Renvoize (1986). However, phylogenetic studies based on morphological (Kellogg and Watson 1993) and molecular (Spangler et al. 1999; Kellogg 2000; Spangler 2000; Skendzic et al. 2007) data have demonstrated that none of Clayton's (1972, 1973, 1981) subtribes of Andropogoneae is truly monophyletic, although there is partial support for some.

The studies using the plastid *ndh*F gene (Spangler et al. 1999; Spangler 2000) have Andropogoninae, Sorghinae, and Coicinae grouping as a clade, and two other clades that follow traditional groupings to some degree. One comprises mostly other components of Sorghinae (including three clades of *Sorghum* Moench s.l. elevated to generic rank as *Sorghum, Sarga* Ewart, and *Vacoparis* Spangler [Spangler 2003], respectively), and the other consists mostly of Tripsacinae (*Tripsacum* L., *Zea* L.), Chionachninae (*Chionachne* R. Br.), and *Elionurus* Kunth ex Willd.

A study using nuclear ribosomal (ITS) and plastid (*trn*L–F) sequences, Skendzic et al. (2007) has the major groups identified but only weakly supported. The "core" Andropogoneae (defined as Andropogoninae, Anthistiriinae, and the *Bothriochloa* Kuntze clade of Sorghinae) are well supported, as is a clade comprising Tripsacinae and the genus *Imperata* Cirillo, as well as another clade including two members of Rottboelliinae.

In general, the sampling of species for cladistic studies in Andropogoneae has been rather sparse and many more genera will have to be sampled before it will be possible to accept as valid any classificatory changes from the traditional groupings presently in use. This applies particularly to Germainiinae, Ischaeminae, and Dimeriinae.

Arundinella Raddi is sister to Andropogoneae in all recent molecular studies mentioned, and on this basis, it has been proposed that this genus be included in the tribe (Kellogg 2000). However, its paired spikelets are not of the sessile-pedicelled type as met within true andropogonoids, so it may be better to consider it as intermediate between the true Andropogoneae and the true Paniceae.

Tribe Triodieae

The Australian endemic chloridoid tribe Triodieae (the spinifex grasses) was originally classified into two large genera, *Triodia* R. Br. and *Plectrachne* Henrard, on the basis of spikelet differences: three-awned lemmas and glumes longer than the florets (*Plectrachne*) or three-toothed or three-lobed lemmas and glumes shorter than florets (*Triodia*) (Jacobs 1971). Two additional genera, *Symplectrodia* Lazarides (Lazarides 1985) and *Monodia* S. W. L. Jacobs (Jacobs 1985), were described based on morphological characters. *Symplectrodia* differs from the other genera by the rachilla elongating with maturity, having a single bisexual floret below with

several sterile florets above, and the basal lemma entire to aristulate (Jacobs 1992). *Monodia* differs from the other genera by having only a single bisexual floret per spikelet and in the solitary terminal lemma awn (Jacobs 1985). All spinifex grasses are thought to comprise one uniform group in an ecological sense (Jacobs 1982, 1984, 1992). A recent revision (Lazarides 1997) does not uphold the *Triodia–Plectrachne* division, on the basis that the traditional spikelet characters formerly used to distinguish the genera cannot be upheld. Leaf anatomical characters (Burbidge 1946) also cut across the traditional *Triodia–Plectrachne* classification, with the recognition of ''soft'' and ''hard'' spinifex types depending on whether stomatal grooves are located on one or both leaf surfaces. The ''soft'' species have stomatal grooves mostly on the upper surface of the leaves and the ''hard'' species have the stomatal grooves equally arranged on both leaf surfaces. In addition, the ''soft'' species commonly produce noticeable amounts of resin, whereas the ''hard'' species produce very little or no resin (Jacobs 1992). Other characters noted by Mant et al. (2000) were the softer-appearing foliage, weakly pungent leaf apices, strongly curled senescent leaves, and a less hummocked habit of the ''soft'' species. Furthermore, *Monodia* was noted by Mant et al. (2000) to have a ''soft'' anatomy, whereas *Symplectrodia* is ''hard.''

A molecular analysis based on the ITS region was undertaken on 27 representative taxa of Triodieae and three outgroups of species of *Eragrostis* Wolf, *Muhlenbergia* Schreb., and *Chloris* Sw. (Mant et al. 2000). Representatives of Triodieae included 17 species of *Triodia* s.s., seven species of *Triodia* formerly placed in *Plectrachne,* two species of *Symplectrodia,* and the monospecific *Monodia*. The strict consensus of 22 most-parsimonious trees shows strong support for monophyly of the tribe, corroborating previous morphological support for recognition of the tribe (Van Den Borre and Watson 1997).

Within the ingroup, however, the clades produced appear to support the divisions based on anatomy better than on spikelet morphology. For example, all the taxa with a ''soft'' anatomy (other than *Monodia stipoides* S. W. L. Jacobs) are in a well-supported clade, nested within some of the ''hard'' species. The ''hard'' species are paraphyletic in four separate clades and the genus *Symplectrodia* is nested within one of them. *Monodia,* although a ''soft'' species, is sister to the clade of ''hard'' species within which the other ''soft'' species are nested.

It is clear that complete sampling across the whole range of spinifex grasses is necessary before any new classification is proposed for Triodieae. From the preliminary cladistic studies there is a serious conflict between the morphological and molecular characters, with more support between anatomical and molecular characters.

Although only three grass groups have been focused on to show the conflict existing between traditional classifications and those resulting from contemporary molecular cladistic studies, there are many other examples from the literature, including those reported in the Proceedings of Monocots II in Sydney (Jacobs and Everett 2000) and that appear elsewhere in this volume.

CONCLUSION

The view has been expressed in this paper by two researchers who feel it is not absolutely necessary to have taxonomic groups based on phylogenies (clades) supported by morphological synapomorphies. However, I am of the opinion that this trend should be discouraged from becoming too established by systematic practitioners, otherwise confusion is transmitted to the users of our classifications, and we lose a degree of credibility in their eyes. Formal taxonomic and nomenclatural changes should surely only be applied, particularly at the species level, when the lineages within a phylogeny correlate with marker morphological characters, i.e., when genotypic differences are reflected through the phenotype. Much more thought and research though needs to be directed toward establishing the exact nature of morphological characters and their interpretation in reflecting phylogeny. Furthermore, the homologous and developmental nature of these characters needs much more attention.

If new classifications are inflicted on the agrostological community without adequate comprehension of the underlying characters, there is a real threat that these changes to classifications will not be implemented, and that the traditional classifications that have stood the test of time and based more on phenetics may be more comprehensible to users. Perhaps the real question to be asked is this. As systematists, is our prime responsibility to the users of our classifications or is it to attempt to discover the correct evolutionary history of a group? In the past, these two aims have been regarded as compatible, but maybe we now have to recognize that we are dealing with two mutually exclusive outcomes; classification (based on characters we can see, defining groups we can communicate about) and phylogeny (based on clades derived mainly from molecular data, and about which it may be difficult to communicate). Another view is that we should have two classifications; one based on morphological phenetics (with the consequent recognition of paraphyletic groups), and the other based on molecular cladistics. However we produce a classification, its value will depend to some extent on its predictability and the reliability it has as a sampling guide.

Cladograms based on molecular data provide powerful tools in contemporary systematic research. Results that are both ''exciting but exasperating'' (Watson and Dallwitz 1992) are produced and caution is advised before extrapolating them into classifications. A good example of the situation where classification of the family has purportedly become more stabilized through molecular approaches is the work of Clark and co-workers (Clark et al. 1995, 2000; Clark and Judziewicz 1996), whereby the discovery of basal groups in Poaceae has resulted in the establishment of separate subfamilies for those lineages. However, none of these subfamilies has unequivocal structural support from the GPWG (2001) analyses. An interesting observation in both the PACCAD and BEP clades is that traditional ''phenetic'' subfamilies are produced on the cladogram, although the data from which it is derived are mainly molecular.

In the majority of the traditional subfamilies of the PACCAD and BEP clades, sample size, particularly at the species level, has been too thin for the lineages produced from these

studies to be used as extrapolations into new classifications, had they been radically different from the traditional groupings. Many more grass species need to be sampled over the whole range of the family in order to confirm whether the GPWG (2001) classification, on the basis of an extremely small sample size, reflects the actual situation in the family.

The three examples at lower taxonomic levels (Danthonioideae, Andropogoneae, Triodieae) reflect the same kinds of issues that the GPWG (2001) had to deal with at the subfamily level. Recommending conservatism in making nomenclatural changes is probably advisable, until it is possible to demonstrate some diagnosable features that can be observed fairly readily and simply.

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