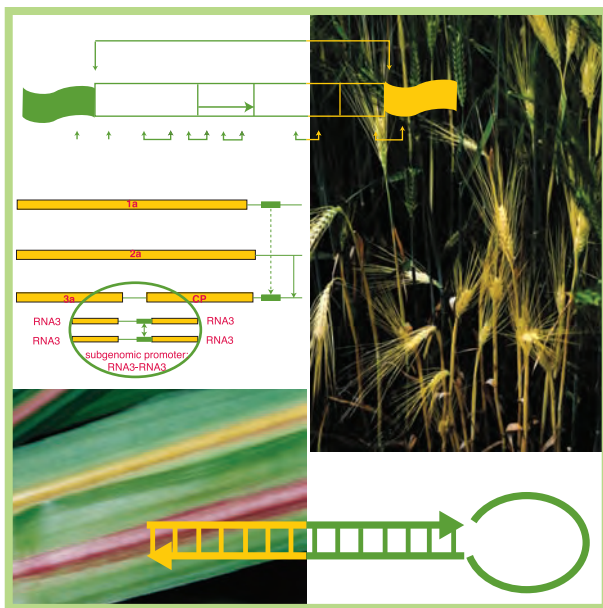




Viruses and virus diseases of *Poaceae* (*Gramineae*)

H. Lapierre, P.-A. Signoret, editors



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Hervé Lapierre
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Foreword

Marc H.V. Van Regenmortel

This volume is devoted to the viruses that infect graminaceous hosts, i.e. the plants that represent the most important food source on our planet. In view of the economic importance of plants like wheat, rice, maize and sugarcane, this compendium is an important and welcome addition to the literature on plant virus diseases.

The editors have enlisted contributions from nearly two hundred virologists and agronomists world-wide and have succeeded in assembling a truly encyclopaedic volume that covers all aspects of the virus diseases of the *Poaceae*. Plants belonging to this family are infected by a very large number of viruses, causing considerable economic losses in both developing and developed countries. Descriptions of virus species that belong to 15 of the virus families and 36 of the virus genera currently recognized by the International Committee on Taxonomy of Viruses (ICTV) are included in this volume. In addition, viruses and subviral agents that infect the *Poaceae* but for which the taxonomic status has not yet been clarified by the ICTV are also included.

The authors have been careful to follow the current official taxonomy and classification of viruses published in 2000 in the 7th ICTV Report. In particular, they have followed the typographic convention of writing in italics the names of officially recognized virus families, genera and species.

Latinized names of virus genera and families ending in the suffix *-virus* for genera and *-viridae* for families have been in use for many years and have always been written in italics with a capital initial letter. The ICTV extended this typography to the names of virus species in spite of the fact that the species names are not Latinized but are English names. The use of English instead of Latin names for species is in line with the fact that English has replaced Latin as the language of communication used by scientists. The use of italics provides a clear sign that species are viral taxa i.e. abstract classes like genera and families. Italics also make it possible to differentiate between official virus species and other viral entities such as viral strains and isolates or viruses for which the taxonomic position is not yet clear.

It should be stressed that the use of italics is necessary only when the author is referring to the species as a taxonomy entity in the classification scheme, for instance in the

Materials and Methods section of a scientific paper. When the author is referring to the virus as a concrete physical entity that causes a disease or to virus particles that can be purified or seen in an electron microscope, the name of the virus should be written in lower-case Roman script. The name then refers to a general term designated by the vernacular virus name corresponding to a physical entity and not to an abstract taxonomic class. It is, indeed, impossible to centrifuge, purify or visualize an abstract species or a family since only physical entities are amenable to experimentation.

In addition to using the italicized, official species names, the authors have also, at various places, made use of the unofficial, non-latinized virus binomial (NLVB) system that is popular with plant virologists. In this system, the word *virus* appearing in the species name is replaced by the genus name which also ends in *-virus*. The advantage of the binomial system is that the inclusion of the genus name in the species name indicates relationships with other viruses and provides additional information about the properties of the virus. Many virologists find the NLVB system attractive and it is possible that the ICTV may decide in future to adopt binomial names as the official species names for all viruses.

The authors in this volume, like virologists working in any area of virology, were sometimes confronted with the difficult task of deciding whether a newly described virus is sufficiently different from other similar viruses to be considered a member of a separate virus species. It is not easy to find an answer to the question: how different is different enough to be considered something else! In other words, when is a virus sufficiently different to be considered a member of a new virus species rather than a variant or a strain of a known species. The difficulty lies in the fact that a species is a so-called polythetic class and not a universal class like a genus or a family whose members all share one or more defining properties, both necessary and sufficient for establishing class membership. The existence of a defining property present in all members of a given family and absent in members of other families makes it easy to draw sharp boundaries between families and to allocate any virus to a particular family without any ambiguity. In contrast, a virus species is a polythetic class defined by a replicating lineage and a particular ecological niche. The members of such a class do not have a single defining property in common which could be used for allocating a virus to a particular species because that property is absent in other species.

The concept of polythetic virus species is useful because it allows one to group together replicating entities that show intrinsic variability and undergo continual evolutionary change. Some members of a virus species may lack one or other character considered typical of the species and still be included in that species. This means that a single discriminating character such as a particular host reaction or a certain degree of genome sequence dissimilarity cannot be used, on its own, as a criterion for differentiating between two virus species. There is no single sequence identity percentage that can be taken as an absolute cut-off point to decide if two viruses belong to the same species. In general, a range of identity values are observed for different viruses, and alternative groupings could be considered sensible options, depending on the relative importance given to other structural and biotic properties. It is always a combination of properties that provides the justification for deciding whether a virus should be considered a member of a particular species.

The wealth of nucleic acid sequence data that have become available in recent years has led many virologists to use a given, arbitrary level of sequence identity as the sole basis for identifying the members of a virus species. Although the use of phylogenetic trees for differentiating between species is in line with the definition of a species as a replicating lineage, there are frequently no clear cut boundaries between the phylogenetic branches to indicate when two species diverged. Furthermore, different phylogenies may be constructed when different parts of viral genomes are analysed. Species demarcation only on the basis of genome sequence contradicts the definition of species as a polythetic class and amounts to a classification of genomes instead of a classification of viruses.

The biological properties of a virus which are based on ecological niche occupancy, i.e. host responses, vector tropism, pathogenicity etc represent the phenotypic characters that are of most importance for the study of viruses as infectious agents. The contribution that genome sequences and hypothetical phylogenetic trees can make to virus classification should not overshadow the importance of biotic properties which are the ultimate reason why virologists want to develop a practical virus taxonomy in the first place. The suggestion has been made, for instance, that the two viruses *Soil-borne wheat mosaic virus* and *Oat golden stripe virus* should be considered members of the same species because they have very similar genome sequences. However, these two viruses do not have a single natural host in common and such a clear difference in ecological niche justifies the decision to consider them as distinct species.

Interestingly, the difficulties experienced in demarcating different virus species are mirrored in the taxonomic structure of the *Poaceae*. In this plant family, hybridization between members of different species and different genera is common and this blurs the usual demarcation line between species when they are defined on the basis of reproductive isolation from other species. However, even if they can hybridize in nature, the individual plant species can still be recognized since the frequency of such hybrids is low enough to prevent parental gene pools to merge.

This volume will be extremely valuable for anyone interested in the virus diseases of graminaceous hosts. Each virus is described in detail in terms of the virion and genome properties, the biological properties, as well as disease and agronomical aspects. Plant virologists working in this area will find this volume an invaluable reference work.

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Introduction

Hervé Lapierre

The *Poaceae* family comprises a very high number of genera and species. The links between these species and other families are still the subject of many adjustments (see chapter 1). The rapid and continual evolution of our knowledge of biochemical properties and of genomic sequences of the different taxa in this plant family keeps widening perspectives to breeders, agronomists and, of course, to pathologists. The detailed studies of the genetic potential of these species allows us to diversify our strategies in the framework of a sustainable agriculture, particularly concerning the control of viruses that still remains difficult.

The globalisation of exchanges of cultivated plants started many thousands years ago and was accelerated with the opening of the oceanic spaces in the XVIth century. The four following centuries have seen the diffusion, all over the world, of the main industrial and dietary *Poaceae*. The beginning of our century seems to have initiated the diffusion of ornamental *Poaceae* and parks.

The diffusion of *Poaceae* species in new ecosystems, and, sometimes in very wide areas as well as the rapid modifications of cultivation methods, inevitably brought about modifications of plant/bio-aggressor balances. The methods for fighting viruses as counterparts to other bio-aggressors still often exploit chemical action against the vectors when the natural resistances are low or non-existent. The use of chemical fighting methods against these vectors has become a considerable societal issue as are all the new methods using transgenesis. Many analyses focusing on the challenges linked to transgenesis as a method for fighting the viruses of *Poaceae* are presented in this book.

Almost twenty percent of known viruses infecting plants can be detected in *Poaceae* either as a natural infection or following an experimental inoculation. Some of these viruses are highly polyphagous and can infect many species belonging to a fairly large number of families. This is the case in *Cucumber mosaic cucumovirus* (Brunt *et al.*, 1996), and in *Tobacco rattle tobnavirus* (Huth and Lesemann, 1984) which infect species included in 17 and 24 families respectively. Both these viruses preliminarily described on Eudicots also infect monocots including some *Poaceae* species. Conversely,

two viruses, first identified on *Poaceae*, have a relatively wide range of hosts on Eudicots. Thus *Brome mosaic bromovirus* infects three dicot families including *Fagaceae* (Huth and Lesemann, 1984; and *Oat blue dwarf marafivirus* is present in six species of Eudicot families. Some other viruses such as *Turnip mosaic potyvirus* infect dicot and monocot species but not *Poaceae* species. Lastly, some viruses infect exclusively *Poaceae* species. A few viruses of this category infect many taxa inside this family. For example, part of the species belonging to the *Polerovirus* and the *Luteovirus* genera infect most of the different sub-families of *Poaceae* (D'Arcy and Burnett, 1995; Albouy and Devergne, 1998). On the contrary, *Sugarcane yellow leaf virus*, very close to the viruses of the *Polerovirus* genus, has a very limited host range in the *Andropogoninae* sub-tribe (Scaglusi and Lockhart, 2000). Very few elements can help to provide an explanation of the causes of the seemingly great diversity in the levels of polyphagy of viruses. In some cases, a rupture in the specificity of hosts, linked to the necessity in the nature of bio-vectors, shows the limitations of classical methods of appreciation of host ranges. The development of our knowledge of the genetic material of plants and viruses will allow us to better characterise their interactions and consequently, to define host ranges more precisely. Until now, host ranges were not correctly evaluated because of the limited number of plant species checked using either an inoculum containing a single virus or containing also a potential virus assistant.

Maize has been the most frequently checked, using viruses which did not have this plant species as natural host. The viruses in maize represent about 15% of known plant viruses (figure 1). Few dicot viruses have yet been found on *Poaceae* or experimentally transmitted to species of this family (tab. 1). But it should not altogether be excluded that some viruses apparently subservient to other families could be found in the future on *Poaceae*. The apparition mechanisms of emergent-type viruses currently being

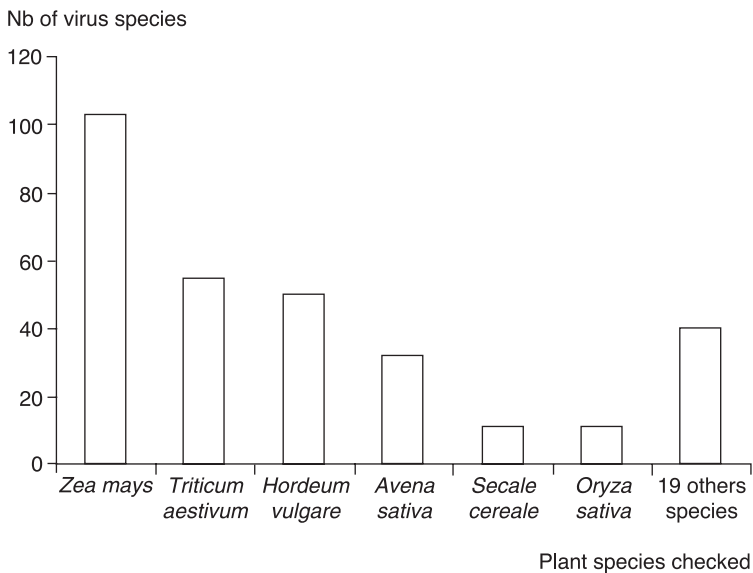


Figure 1. Virus species described in different Eudicot families checked in *Poaceae*.

Table 1. Virus species infecting *Poaceae* firstly described on Eudicots^a.

Natural infection ^b	Experimental infection
<i>Arabidopsis mosaic nepovirus</i> * <i>Carnation ring spot dianthovirus</i> <i>Cucumber mosaic cucumovirus</i> <i>Indian peanut clump pecluvirus</i> ** <i>Peanut clump pecluvirus</i> ** <i>Tobacco mosaic tobamovirus</i> <i>Tobacco rattle tobnavirus</i> * <i>Tomato spotted wilt tospovirus</i>	<i>Abelia latent virus</i> * <i>Alfalfa mosaic alfamovirus</i> <i>Beet mild yellowing polerovirus</i> <i>Beet ringspot virus</i> <i>Beet western yellows polerovirus</i> <i>Cassia mild mosaic carlavirus</i> <i>Cassia yellow blotch bromovirus</i> <i>Cowpea chlorotic mottle bromovirus</i> <i>Cymbidium mosaic potexvirus</i> <i>Cymbidium ring spot tombusvirus</i> <i>Heracleum latent trichovirus</i> <i>Pepper vein (al)mottle potyvirus</i> <i>Physalis mosaic tymovirus</i> <i>Strawberry latent ring spot virus comoviridae</i> <i>Tobacco necrosis necrovirus</i> <i>Tobacco ringspot nepovirus</i> <i>Tobacco streak ilarvirus</i>

a. The very rare viruses of other monocots which experimentally infect *Poaceae* are not given

b. Agronomical importance either on local areas (*) or on wider areas (**).

studied on cultures of dicot viruses have not been tackled much in viruses of large cultures of *Poaceae*. We notice however that, essentially, the natural host range of viruses infecting the species of *Poaceae* of large cultures (straw cereals, maize, sugar cane, various fodder species) is limited to this family. So, on about 85 viruses present in these types of cultures, less than 10 of them use species belonging to other families as reservoir plants or sensitive hosts. Furthermore, the spectral viruses covering many families and infecting *Poaceae* have in most case a limited impact in terms of a diminution of yield and prevalence in the zones of extensive culture. The relative specificity of the *Poaceae* viruses justifies the choice of this family as an anchoring point in the study of these viruses. The European conferences held since the 1970's on the virus diseases of *Poaceae* have constituted a basis in the elaboration of this project for which many contributions have been sought. The first part is focussing on taxonomic data on the *Poaceae* family, and on the plant viruses for which the phylogenetic links are still unclear. The different viral taxa, often provisional, represented in the *Poaceae* are described following the nomenclature established by the ICTV (Van Regenmortel *et al.*, 2000). The viruses in question, as well as the diseases that determine them, and the methods for fighting them are presented for each of the plant species with which we associate viral diseases. The basic biological and molecular elements that could characterize quite a high number of *Poaceae* viruses are still missing, in particular many viruses infecting forages and wild grasses. This situation explains why for these types of viruses, a grouping not favouring the host plant has been proposed, as opposed to the order accepted for *Poaceae* of extensive cultures.

The effects on the host plants of certain viral complexes are very poorly understood (viruses transmitted by *Polymyxa*) although some data are available on the aerial vec-

tors of virus complexes. These data are presented and also the rare information concerning the virus complexes with other bio-aggressors.

The set of shortcomings related here show very well all the distance that still remains to be covered to reach more complete description of the known viruses of *Poaceae* when, at the same time, new viruses regularly come to light in this family of plants.



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Poaceae family

Grass taxonomy

Terry D. Macfarlane

Introduction

The grass family (*Poaceae* or *Gramineae*) is one of the largest plant families, comprising about 700 genera and 10,000 species. Grasses occur on every continent and occupy a wide range of latitudes, altitudes and habitats, from wet and dry tropical to arctic. They are important ecologically frequent components of vegetation, dominating in grasslands and savannas, as well as providing food for grazing animals. Grasses are also of great economic importance, comprising the three most important food crops, wheat, rice and maize (corn), as well as several of the other top 20 food crops. They also contribute other products, including fodder, fibre and construction materials (from bamboos). Some have argued that this concentration of human reliance on a small number of species represents a vulnerability to such threats as diseases of crops.

This review aims to provide current information on grass classification and to summarise recent findings about the position of grasses among the Flowering Plants. It is clearly important to know what plant families are related to the grasses in order to be able to properly investigate such questions as the origin of particular features of grasses, or the limits of susceptibility to particular viruses, which might indicate the antiquity of various plant/virus relationships. Classifications of the grasses themselves can be used to improve the coverage of grass diversity in research designs. As an example, it is clear from current classifications that major groups (*e.g.* subfamilies and tribes) of grasses have geographical biases toward particular regions of the world, especially tropical versus temperate, or concentrations in particular hemispheres or continents. Consequently, when choosing a representative sample of grasses for research projects, a selection of the species native to any one region, even if it is a large selection, is likely to be an inadequate sample of the diversity of the whole grass family. A classification or phylogeny also provides a framework in which to view the results of research.

Family relationships

Currently the *Poaceae* are accepted as a well-defined monophyletic family without any doubtfully included genera. Genera with unusual morphology such as *Anomochloa* and *Streptochaeta* which have in the past been considered doubtful members are now accepted as grasses, although they are atypical in some respects, especially spikelet structure, and occupy an evolutionarily basal position. Morphological features which define the grasses are: flowers arranged in spikelets which have a characteristic set of specialised bracts (glumes, lemma and palea); conventional perianth lacking but with structures called lodicules which may be derived from the perianth; pollen lacking scrobiculi but with intraaxinous channels; fruit a caryopsis, *i.e.* the seed coat fused to the inner ovary wall at maturity; embryo well differentiated, with obvious shoot and root meristems; embryo lateral in position. There are also molecular sequence markers unique to the family (GPWG 2001).

In a recent phylogenetic classification of the Angiosperms based mainly on molecular data (APG 1998) the *Poaceae* were placed in the Order *Poales* along with 14 other families. The two most closely related to the grasses appear to be *Joinvilleaceae*, a small family of two species of the Pacific region (Campbell and Kellogg, 1987; APG, 1998; illustrated in Judziewicz *et al.*, 1999), and *Ecdiocolaceae*, a small family of two species of south western Australia (Briggs *et al.*, 2000) which may together form a sister group to the *Poaceae*. Less closely related is the southern hemisphere *Restionaceae* (Restiads or Southern Rushes; Meney and Pate, 1999) and the related small wind-pollinated and spikeleted Australian families *Anarthriaceae*, *Hopkinsiaceae* and *Lyginiaceae*. The latter two families were recently separated from the *Restionaceae* (Briggs and Johnson, 2000) and increase the *Poales* to 16 families. Their spikelets differ from those of the *Poaceae*. *Flagellariaceae* is somewhat less closely related to the *Poaceae*. All these preceding families were regarded by APG (1998) as forming the graminoid clade of the Order *Poales*.

The remaining families in the *Poales* (in alphabetic order) are *Centrolepidaceae*, *Cyperaceae* (Sedges), *Eriocaulaceae*, *Hydatellaceae*, *Juncaceae* (Rushes), *Sparganiaceae*, *Thurniaceae*, *Typhaceae* (Bullrushes) and *Xyridaceae*.

Classification of the grasses

Two hundred years of research have progressively improved the classification of grasses as understanding has grown and new data have become available. Recently considerable advances have been made as better access and increased research in the tropics and southern hemisphere has allowed poorly known grasses to be studied in detail, especially the bamboos (Soderstrom and Ellis, 1987; Judziewicz *et al.*, 1999) and genera important in the evolutionary structure of the family such as *Streptochaeta* and the formerly mysterious and lost *Anomochloa* (Judziewicz and Soderstrom, 1989). More rigorous data compilation, computer-aided analysis and cladistic analysis has improved the understanding of morphological and anatomical variation and evolutionary trends (Watson and Dallwitz, 1992; 1994; Kellogg and Campbell, 1987; Kellogg and Watson, 1993). Recently molecular data and its analysis have provided an improved understanding of inter-relationships and adjustment of groupings which earlier had been largely

defined using the more traditional data from morphology and anatomy. In the last two decades there have been two major symposia on grass systematics (Soderstrom *et al.*, 1987; Jacobs and Everett, 2000).

- Current classifications

The *Poaceae* are classified into subdivisions at usually 2-3 hierarchical levels, subfamily, tribe and subtribe although other informal levels such as “super tribe” or “clade” may be used. Three recent examples of classifications are as follows. Clayton and Renvoize (1986) published an evolutionary classification which was developed by intuitive assessment of the morphological, anatomical and cytological information and presented informal diagrams of suggested evolutionary relationships. This classification has been widely used, and the identification keys, brief descriptions of genera and attention to nomenclature are useful. Watson and Dallwitz’s (1992) classification (part of a series developed over many years) was based on computer phenetic analyses of an extensive database of non-molecular data, and it has also been widely cited and used, with a revised edition appearing in 1994 and subsequent updates appearing on the Web. The Grass Phylogeny Working Group (GPWG 2000, 2001) conducted computer cladistic analyses on 8 datasets, one morphological and seven molecular (four plastid and three nuclear) and using a sample of 62 carefully selected genera. The cladistic results were discussed in terms of relationships between the major groups which the sample genera represented, evolutionary trends in morphological and other features were examined, and a classification into subfamilies was presented, with component tribes derived from those of Clayton and Renvoize (1986) and other sources listed alphabetically, but with no listing of genera. The morphological data in fact contributed little to the results, the main determinant of the results being chloroplast molecular data.

Although all three classifications are relatively recent and comprehensive, I present here an outline of the most recent one, GPWG (2001). There is a great deal of agreement between the recent classifications in the content of the groups (tribes and subfamilies), as might be expected since the GPWG classification studied the relationships of groups previously defined based on a sample of the constituent genera. Where they mainly differ is in the number of top level groups (subfamilies) recognised, and the subfamily to which certain tribes or genera are assigned. Most of the additional subfamilies recognised by GPWG contain few species, albeit important evolutionarily, so that the changes to previous classifications affect few species. There remain various uncertainties, information deficiencies and subjective aspects in the classification of grasses (see later).

- The Grass Phylogeny Working Group (GPWG 2001) classification

The genera of each tribe are not listed in the original, hence the partial listings given below (full listings can be obtained from Watson and Dallwitz, 1992 or the associated website, see later). All genera are shown for each group except where “e.g.” indicates only a subset of the genera are listed, usually those with many species or which are otherwise noteworthy.

Family Poaceae (or Gramineae): 12 subfamilies (-oideae): two large clades are also shown because they indicate additional structure in the classification.

<p>Anomochloideae (2 tribes, 4 species) Anomochloae <i>Anomochloa</i> Streptochaetaeae <i>Streptochaeta</i> Pharoidae (12 species) e.g. <i>Pharus</i>, <i>Leptaspis</i> Puelioideae (2 tribes, c. 14 species) Guaduelleae <i>Guaduelia</i> Puelieae <i>Puelia</i></p>	<p>PACCAD clade (i.e. Panicoideae-Arundinoideae-Chloridoideae-Centothecoideae-Aristidoideae-Danthonioideae) Aristidoideae (c. 350 species) e.g. <i>Aristida</i> Arundinoideae (c. 38 species) e.g. <i>Arundo</i>, <i>Phragmites</i> Danthonioideae (c. 250 species) e.g. <i>Austroanthonia</i>, <i>Cortaderia</i>, <i>Danthonia</i>, <i>Merxmüllera</i>, <i>Pentaschistis</i> Centothecoideae (2 tribes, c. 45 species) Centothecaeae e.g. <i>Centotheca</i>, <i>Chasmanthium</i>, <i>Zeugites</i> Thysanolaeneae e.g. <i>Thysanolaena</i> Panicoideae (6 tribes, c. 3270 species)</p>
<p>BEP clade (i.e. Bambusoideae-Ehrhartoideae-Pooideae) Bambusoideae (2 tribes, c. 1200 species) Bambuseae e.g. <i>Arundinaria</i>, <i>Bambusa</i>, <i>Chusquea</i>, <i>Guadua</i>, <i>Merostachys</i>, <i>Phyllostachys</i>, <i>Sasa</i>, <i>Sinarundinaria</i> Olyreae e.g. <i>Arberella</i>, <i>Buergersiochloa</i>, <i>Cryptochloa</i>, <i>Olyra</i>, <i>Pariana</i> Ehrhartoideae (formerly Oryzoideae) (3 tribes, c. 120 species) Ehrharteae e.g. <i>Ehrharta</i>, <i>Microlaena</i>, <i>Tetrarrhena</i> Oryzae e.g. <i>Leersia</i>, <i>Oryza</i>, <i>Zizania</i> Phyllorachideae e.g. <i>Phyllorachis</i> Pooideae (13 tribes, c. 3300 species) (tribal sequence re-arranged to provide more structure) Brachyelytreae <i>Brachyelytrum</i> Lygeaeae <i>Lygeum</i> Nardeae <i>Nardus</i> Brylkinieae <i>Brylkinia</i> Diarrheneae <i>Diarrhena</i> Meliceae e.g. <i>Glyceria</i>, <i>Melica</i> Ampelodesmeae <i>Ampelodesmos</i>, <i>Anisopogon</i> Phaenospematideae <i>Phaenosperma</i> Stipeae e.g. <i>Arenatherum</i>, <i>Nassella</i>, <i>Stipa</i></p>	<p><i>Andropogoneae</i> e.g. <i>Andropogon</i>, <i>Bothriochloa</i>, <i>Cymbopogon</i>, <i>Dichanthium</i>, <i>Dimeria</i>, <i>Hyparrhenia</i>, <i>Imperata</i>, <i>Ischaemum</i>, <i>Miscanthus</i>, <i>Saccharum</i>, <i>Schyzachyrium</i>, <i>Sorghum</i>, <i>Themeda</i>, <i>Vetiveria</i> Arundinelleae e.g. <i>Arundinella</i>, <i>Garnotia</i>, <i>Loudetia</i> Hubbardiaceae <i>Hubbardia</i> Isachneae e.g. <i>Isachne</i> Paniceae e.g. <i>Axonopus</i>, <i>Brachiaria</i>, <i>Cenchrus</i>, <i>Dichantherium</i>, <i>Digitaria</i>, <i>Echinochloa</i>, <i>Ichnanthus</i>, <i>Neurachne</i>, <i>Panicum</i>, <i>Paspalidium</i>, <i>Paspalum</i>, <i>Pennisetum</i>, <i>Setaria</i>, <i>Urochloa</i> Steyermarkochloae e.g. <i>Steyermarkochloa</i> Chloridoideae (5 tribes, c. 1400 species) Cynodonteae (formerly Chlorideae) e.g. <i>Bouteloua</i>, <i>Buchloe</i>, <i>Chloris</i>, <i>Cynodon</i>, <i>Enteropogon</i>, <i>Eustachys</i>, <i>Spartina</i>, <i>Tetrapogon</i>, <i>Tragus</i>, <i>Zoysia</i> Eragrostideae e.g. <i>Acrachne</i>, <i>Crypsis</i>, <i>Dactyloctenium</i>, <i>Diplachne</i>, <i>Eleusine</i>, <i>Eragrostis</i>, <i>Lepochloa</i>, <i>Muhlenbergia</i>, <i>Sporobolus</i>, <i>Tridens</i>, <i>Triodia</i>, <i>Tripogon</i>, <i>Uniola</i> Leptureae <i>Lepturus</i> Orcuttieae e.g. <i>Neostapfia</i>, <i>Orcuttia</i> Pappophoreae e.g. <i>Cottea</i>, <i>Enneapogon</i>, <i>Pappophorum</i> Genus of uncertain position in subfamily Chloridoideae: <i>Centropodia</i></p>
<p>“Core Pooideae”: Brachypodiaceae <i>Brachypodium</i> (incl. <i>Trachynia</i>) Bromaceae <i>Bromus</i> (incl. <i>Boissiera</i>) Triticeae e.g. <i>Aegilops</i>, <i>Agropyron</i>, <i>Elymus</i>, <i>Hordeum</i>, <i>Secale</i>, <i>Triticum</i> Poeae (including Agrostideae, Aveneae, Hairdidae, Seslerieae) e.g. <i>Agrostis</i>, <i>Avena</i>, <i>Calamagrostis</i>, <i>Deschampsia</i>, <i>Dactylis</i>, <i>Elymus</i>, <i>Festuca</i>, <i>Helictotrichon</i>, <i>Koeleria</i>, <i>Lolium</i>, <i>Poa</i>, <i>Puccinellia</i>, <i>Trisetum</i></p>	

Tribes or genera of uncertain placement. Bracketed comments are adapted from GPWG (2001).

<p>Eriachneae (position remains uncertain, but not in Panicoideae): includes only <i>Eriachne</i>; c. 40 species. Micraireae (possibly its own subfamily): includes only <i>Micraira</i>; 13 species. Streptogyneae (within Ehrhartoideae, or possibly its own subfamily): includes only <i>Streptogyne</i>; 2 species.</p>	<p><i>Cyperochloa</i> (likely to be included in Centothecoideae tribe Thysanolaeneae on the basis of similarity to <i>Spartochloa</i>): 1 species. <i>Gynerium</i> (possibly as its own tribe in Panicoideae): 1 species.</p>
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