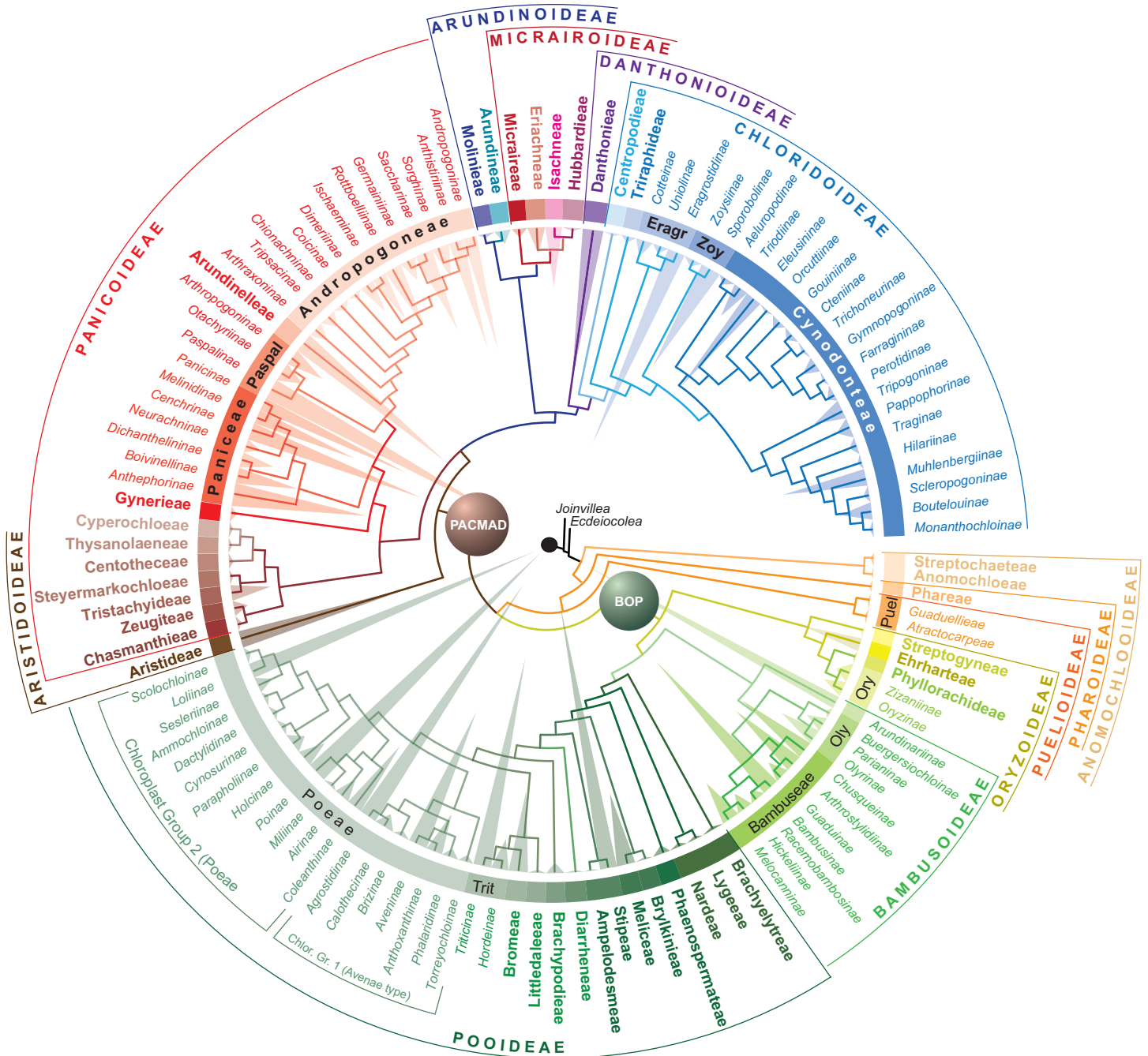


# JSE

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## Invited Review

# A worldwide phylogenetic classification of the Poaceae (Gramineae)

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**Abstract** Based on recent molecular and morphological studies we present a modern worldwide phylogenetic classification of the ±12074 grasses and place the 771 grass genera into 12 subfamilies (Anomochlooideae, Aristidoideae, Arundinoideae, Bambusoideae, Chloridoideae, Danthonioideae, Micraioideae, Oryzoideae, Panicoideae, Pharoideae, Puelioideae, and Pooideae), 6 supertribes (Andropogonodae, Arundinarodae, Bambusodae, Panicodae, Poodae, Triticodae), 51 tribes (Ampelodesmeae, Andropogoneae, Anomochloae, Aristideae, Arundinarieae, Arundineae, Arundinelleae, Atractocarpeae, Bambuseae, Brachyelytreae, Brachypodiaceae, Bromeae, Brylkinieae, Centothecaeae, Centropodieae, Chasmanthieae, Cynodonteae, Cyperochloaeae, Danthonieae, Diarrheneae, Ehrharteae, Eragrostideae, Eriachneae, Guaduellieae, Gynerieae, Hubbardieae, Isachneae, Littledaleeae, Lygeae, Meliceae, Micraireae, Molinieae, Nardeae, Olyreae, Oryzae, Paniceae, Paspaleae, Phaenospermateae, Phareae, Phylloachloaeae, Poeae, Steyermarkochloaeae, Stipeae, Streptochaeteae, Streptogyneae, Thysanolaeneae, Tripharideae, Tristachyideae, Triticeae, Zeugiteae, and Zoysiaceae), and 80 subtribes (Aeluropodinae, Agrostidinae, Airinae, Ammochloinae, Andropogoninae, Anthephorinae, Anthistiriinae, Anthoxanthinae, Arthraxoninae, Arthropogoninae, Arthrostylidiinae, Arundinariinae, Aveninae, Bambusinae, Boivinellinae, Boutelouinae, Brizinae, Buergersiochloinae, Calothecinae, Cenchrinae, Chionachninae, Chusqueinae, Coicinae, Coleanthinae, Cotteinae, Cteniinae, Cynosurinae, Dactylidinae, Dichantheinae, Dimeriinae, Duthieinae, Eleusininae, Eragrostidinae, Farragininae, Germainiinae, Gouiniinae, Guaduinae, Gymnopogoninae, Hickeliinae, Hilariinae, Holcinae, Hordeinae, Ischaeminae, Loliinae, Melinidinae, Melocanninae, Miliinae, Monanthochloinae, Muhlenbergiinae, Neurachninae, Olyrinae, Orcuttiinae, Oryzinae, Otachyriinae, Panicinae, Pappophorinae, Parapholiinae, Parianinae, Paspalinae, Perotidinae, Phalaridinae, Poinae, Racemobambosinae, Rottboelliinae, Saccharinae, Scleropogoninae, Scolochloinae, Sesleriinae, Sorghinae, Sporobolinae, Torreyochloinae, Traginae, Trichoneurinae, Triodiinae, Tripogoninae, Tripsacinae, Triticinae, Unioliinae, Zizaniinae, and Zoysiinae). In addition, we include a radial tree illustrating the hierarchical relationships among the subtribes, tribes, and subfamilies. We use the subfamilial name, Oryzoideae, over Ehrhartoideae because the latter was initially published as a misplaced rank, and we circumscribe Molinieae to include 13 Arundinoideae genera. The subtribe Calothecinae is newly described and the tribe Littledaleeae is new at that rank.

**Key words:** classification, DNA, Gramineae, grasses, morphology, phylogeny, Poaceae, subfamily, subtribe, tribe.

In 1991, most of the authors of this paper attended the 42nd American Institute of Biological Sciences Annual Meeting in San Antonio, Texas to discuss the possibility of creating a large digital database that would include nomenclature, taxonomy, synonymy, original publications, type collections, secondary references using accepted names, and distribution by country of all New World grasses. Nine years later the first hard copy treatment of subfamilies Anomochlooideae, Bambusoideae,

Ehrhartoideae, and Pharoideae was published (Judziewicz et al., 2000). Subsequently, the Chloridoideae (Peterson et al., 2001), Pooideae (Soreng et al., 2003), and the Panicoideae, Aristidoideae, Arundinoideae, and Danthonioideae (Zuloaga et al., 2003) were printed. Within each of these, provisional but now woefully out of date treatments, we included our best estimate of the generic classification of the tribes and subtribes for each subfamily. The online database for the

classification of New World grasses was first posted as a separate file in Tropicicos in 2005. Since that time it has been updated and revised continuously and was expanded in 2011 to account for all grass genera and supragenera worldwide <http://www.tropicicos.org/projectwebportal.aspx?pagename=ClassificationNWG&projectid=10> (Soreng et al., 2014).

The grass family was probably characterized as a distinct entity in most cultures. There are many words for herbaceous grasses around the world, including *cǎo* (草), *capim*, *çayır*, *çimen*, *darbha*, *ghaas*, *ghas*, *gish*, *gramas*, *graminius*, *gräser*, *grasses*, *gyokh*, *he-ben-ke*, *hullu*, *kasa*, *kusa* (草), *nyasi*, *o'tlar*, *pastos*, *pillu*, *pullu*, *rumpu*t, *zlaki* (злаки), etc. Three hundred years before the Christian era, Theophrastus, a Greek scholar, recognized the grass family. The first scientific subdivision of the family was made by Brown (1814) who recognized two different spikelet types between Panicoideae and Pooideae (Festucoideae) subfamilies. Bentham (1881) recognized 13 tribes in two major subfamilies. Hitchcock (1935) and Hitchcock and Chase (1951) in their treatments of the grasses of the United States, recognized 14 tribes in these two major subfamilies. The two-subfamily classification was used by most agrostologists for almost 150 years until more modern syntheses. With the infusion of molecular data, our present concept and classification of the grasses is changing at a rapid rate. The crown age for the grasses has been estimated to be  $71 \pm 9$  million years old (Ma) based on fossil pollen and spikelet calibration (Vicentini et al., 2008) while the estimated crown age using only macrofossils is 51–55 Ma (Christin et al., 2014). Our current classification builds on earlier work (Brown, 1814; Bentham, 1881; Hitchcock, 1935; Hitchcock & Chase, 1951; Tzvelev, 1976 1989; Clayton & Renvoize, 1986; Soderstrom & Ellis, 1987; Watson & Dallwitz, 1992; Judziewicz et al., 2000; Grass Phylogeny Working Group (GPWG), 2001; Peterson et al., 2001; Soreng et al., 2003; Zuloaga et al., 2003). Over the last 25 years, molecular studies have greatly improved our understanding of the relationships of the genera and suprageneric taxa, leading towards a new classification that is phylogenetically informative using four hierarchical ranks of subfamily, supertribe, tribe, and subtribe, while attempting to disrupt the older classification as little as possible (Linder, 2005; Grass Phylogeny Working Group (GPWG II), 2012; Bouchenak-Khelladi et al., 2008, 2014). In addition to our generic classification, we provide a hierarchical tree with detail of relationships that a linear classification cannot reflect without additional ranks or notations. For extended bibliographic references relating to DNA studies and classification in Poaceae, see Tropicicos available at: <http://www.tropicicos.org/ReferenceSearch.aspx> (use the Advanced Search option and Key Words: "Poaceae; DNA").

## Material and Methods

### Phylogenetic data

We conducted a maximum likelihood analysis (GARLI 0.951; Zwickl, 2006) on a large dataset of 448 grass species using *matK* and *ndhF* plastid DNA markers (available upon request). DNA sequences were primarily gathered from GenBank with secondary sources taken from Hilu & Alice (2001), Davis & Soreng (2007), Romaschenko et al. (2008, 2012), Davis & Soreng (2010), GPWG II (2012), Morrone et al. (2012), and

Peterson et al. (2010a, 2014c). A radial phylogenetic tree produced in FigTree version 1.4.2 (Fig. 1) was derived from this large dataset, incorporating the genera into tribes and subtribes (Rambaut, 2006–2014). Proportional area shading inside the spiral tree is based on the number of species per tribe and/or subtribe. The number of species per genus, leading to the total number per subtribe, tribe, etc., was calculated by consulting GrassWorld (Simon, 2014). *Joinvillea* Gaudich. ex Brongn. & Gris and *Ecdeiocolea* F. Muell. were used as outgroups based on previous studies (Michelangeli et al., 2003).

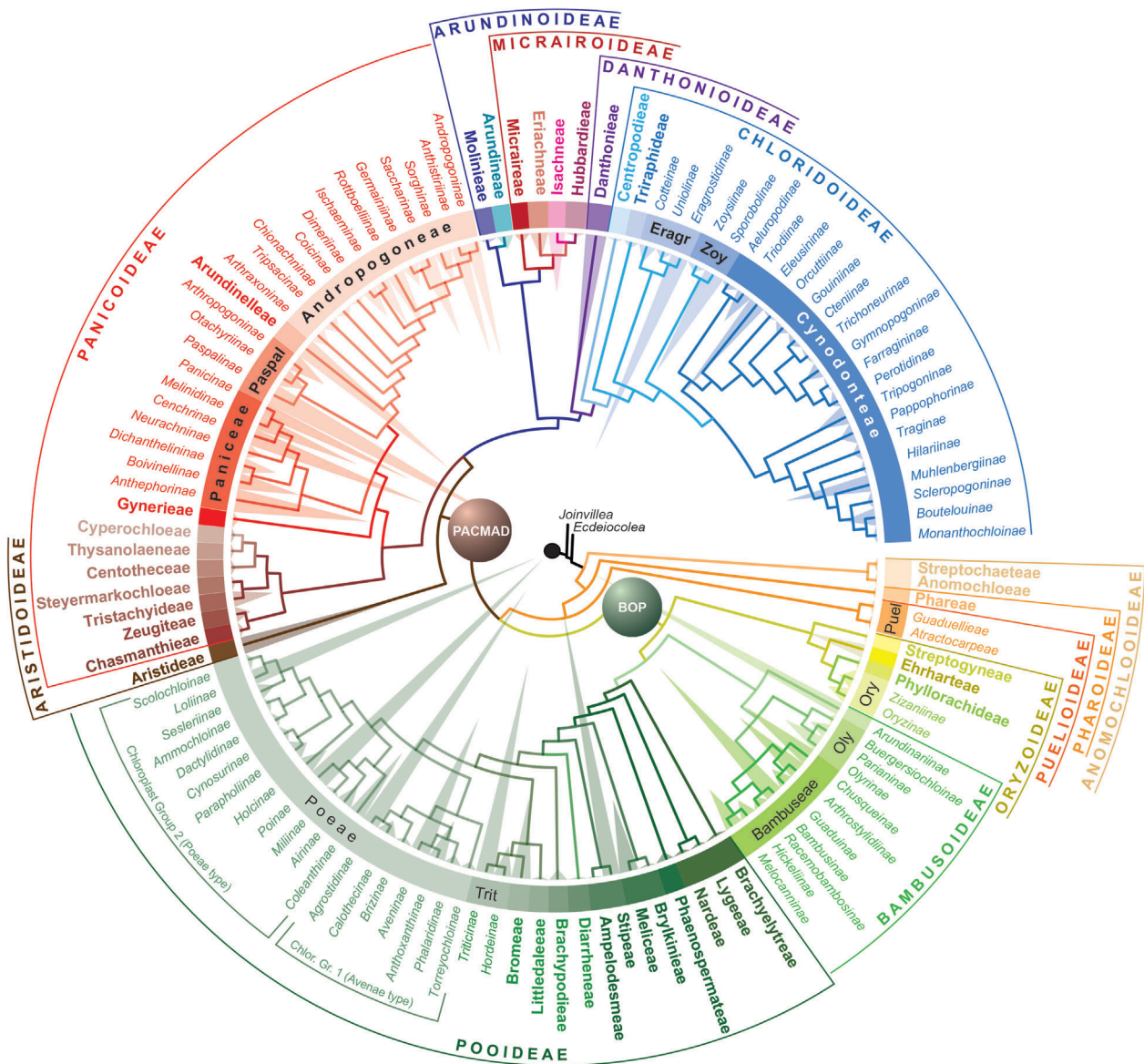
### Nomenclature and classification

All suprageneric taxa and genera are recorded in the Missouri Botanical Garden's taxonomic database, Tropicicos (<http://www.tropicicos.org/Home.aspx>), with their original place of publication and authorship. Suprageneric taxa lists can be generated in Tropicicos using the Advanced Search options under <http://www.tropicicos.org/NameSearch.aspx>. A number of older legitimate names and invalid, illegitimate, and unranked names have been detected since the publication of *Genera Graminum* (Clayton & Renvoize, 1986). We have consulted Index Nominum Supragenericorum Plantarum Vascularium (Reveal, 2015) in the preparation of our revised classification (see Table 1). At the International Botanical Congress in 2011, an emendation to the Code of Botanical Nomenclature was accepted to allow terminations of *oideae*, *eae*, and *inae* for subfamily, tribe and subtribe to determine rank, even if rank was not stated, to extend back to 1887; previously, the cutoff was 1 Jan 1908 (Art. 35.2). Although Reveal suggested this would not impact many names (mostly only dates of publication and authors), we have not evaluated the impact of this change for Poaceae. In Table 1 we list recent generic synonyms and nothogenera are excluded.

## Results

### Classification

We currently recognize 12 subfamilies: Anomochlooideae, Aristidoideae, Arundinoideae, Bambusoideae, Chloridoideae, Danthonioideae, Micraioideae, Oryzoideae, Panicoideae, Pharoideae, Puelioideae, and Pooideae, and in these subfamilies we recognize 51 tribes, 80 subtribes, and 771 genera in approximately 12074 species (Table 1; Soreng et al., 2014). Each genus in Table 1 is color coded to indicate the predominant indigenous distribution of its species. A radial tree illustrating the hierarchical relationships among the subtribes, tribes, and subfamilies is provided (Fig. 1), and the number of species in each tribe or subtribe is shown as a shaded triangle. Using *Joinvillea* and *Ecdeiocolea* to polarize the grasses, our tree (Fig. 1) depicts Poaceae as monophyletic with 12 monophyletic subfamilies followed by, in order of divergence: Anomochlooideae, Pharoideae, and Puelioideae forming the basal lineages; Oryzoideae, Bambusoideae, and Pooideae forming the BOP clade (Clark et al., 1995); and Aristidoideae + Panicoideae as sister to the remaining set of Arundinoideae + Micraioideae, and Danthonioideae + Chloridoideae, forming the PACMAD clade (Sánchez-Ken & Clark, 2010). We tally at least 4978 species with known C<sub>4</sub> metabolism occurring in Aristidoideae, Chloridoideae,



**Fig. 1.** A phylogenetic classification of the Poaceae, includes 12 subfamilies, 51 tribes, and 80 subtribes evolving clockwise from *Joinvillea* and *Ectdeiocolea* (outgroups). Triangles are proportional in height to the size of the taxon where the *Poinae* is the largest with 697 species; BOP = Bambusoideae, Oryzoideae, and Pooideae; PACMAD = Panicoideae, Aristidoideae, Chloridoideae, Micraioideae, Arundinoideae, and Danthonioideae.

Micraioideae, and Panicoideae or approximately 41% of the grasses.

### Suprageneric names

There are still problems with the application of some of the earliest proposed suprageneric names. As already indicated by Clayton (1981), those proposed by Link (1827) are especially problematical. Link used (pp. 1–254) the rank of *ordo* for Gramineae, the rank of *Sectio* for 10 taxa (these are all descriptive names under misplaced rank and, therefore, invalid) below Gramineae, and below that, the ranks of *familia*, *div.* (= *familia*), and *subordo* for additional suprageneric names. Link (1827) summarized his classification (pp. 267–272), in part, and the rank of *Sectio* is explicitly changed to *subordo*. Furthermore, the next lower rank is

unnamed and the terminations are used in a very irregular way. So although these can be considered as alternative names (possible before 1953), they only function as unranked, suprageneric names. If, following the first part of Art 18.2 of the Melbourne Code, *ordo* is taken to mean family rank, then all of Link's names would be invalid because their ranks would be misplaced. However, applying the second clause of Art. 18.2 ["unless this treatment would result in a taxonomic sequence with a misplaced rank-denoting term"] and literally accepting the ranks in the modern sense of order, suborder, and family, the problem of misplaced ranks is avoided, the names are validly published, and the terminations of these names can simply be corrected as necessary. This was the interpretation of Reveal (2015) and is adopted by us. Consequently, none of Link's (1827) names can be applied at



**Table 1** A worldwide phylogenetic classification of the family Poaceae Barnhart [1895] (nom. alt.: Gramineae Juss. [1789]). Accepted suprageneric names appear in **bold** type. The indigenous range of each genus is colored as follows: **Western Hemisphere**, **Eurasia** (including genera that in Africa are exclusively Mediterranean), **Australasia**, **Africa**. Genera with bimodal distributions are **bicolored**, those with broader distributions **tricolored**, or are **red** if more widely distributed. Genera in synonymy (syn. – ...) are colored if the accepted genus is more widely distributed, i.e., in more than one area. Genera in *italics* have been sampled in DNA studies. Comments are in brackets { }. Publication dates for suprageneric taxa appear in square brackets [ ].

subfam. **Anomochloideae** Pilg. ex Potz. [1957] (syn. – Streptochoeteae Butzin [1965]):

tribe **Anomochloae** C.E. Hubb. [1934]: *Anomochloa*.

tribe **Streptochoeteae** C.E. Hubb. [1934]: *Streptochoeta*.

subfam. **Pharoidae** L.G. Clark & Judz. [1996] (syn. – Leptaspidoideae C.O. Morales [1998], supertribe Pharoidae L. Liu [1980]):

tribe **Phareae** Stapf [1898] (syn. – Leptaspideae Tzvelev [1987]): *Leptaspis*, *Pharus*, *Scrotochloa*.

subfam. **Puelioideae** L.G. Clark, M. Kobay, S. Mathews, Spangler & E.A. Kellogg [2000]:

tribe **Atractocarpeae** Jacq.-Fél. ex Tzvelev [1987 Mar-Sep] (syn. – Atractocarpeae Jacq.-Fél. [1962, nom. inval.], Puelieae Soderstr. & R.P. Ellis [“1987” March 1988], subtribe Atractocarpinae E. Camus [1913], Puelliinae Stapf [1917]): *Puelia* (syn. – *Atractocarpa*).

tribe **Guaduelliaceae** Soderstr. & R.P. Ellis [1987]: *Guaduella*.

“**BOP**” clade {Clark et al., 1995; Clark et al., 2000, as **BEP**}

subfam. **Oryzoideae** Kunth ex Beilschm. [1833] (syn. – Ehrhartoideae Caro [1982], Oryzoideae Caro [1982, isonym]; Ehrhartinae Link [1827, unranked], Oryzeae Burmeist. [1837, unranked]):

*incertae sedis*: *Suddia* {probably Phyllorachideae}.

tribe **Streptogyneae** C. E. Hubb. ex C. E. Calderón & Soderstr. [1980] (syn. – Streptogyneae C.E. Hubb. [1956, nom. inval.]; subtribe Streptogyninae Pilg. ex Potz. [1969]): *Streptogyna*.

tribe **Ehrharteae** Nevski [1937]: *Ehrharta*, *Microlaena*, *Tetrarrhena*, *Zotovia*.

tribe **Oryzeae** Dumort. [1824] (syn. – Zizanieae Hitchc. [1920]):

subtribe **Oryzinae** Griseb. [1853]: *Leersia*, *Oryza* (syn. – *Porteresia*).

subtribe **Zizaniinae** Benth. [1881] (syn. – subtribe Luziolinae Terrell & H. Rob. [1974]): *Chikusichloa*, *Hygroryza*, *Luziola*, *Maltebrunia*, *Potamophila* (syn. – *Maltebrunia?*), *Prospytochloa*, *Rhynchoryza*, *Zizania*, *Zizaniopsis*.

tribe **Phyllorachideae** C.E. Hubb. [1939] {may be better in Oryzeae as a subtribe}: *Humbertochloa*, *Phyllorachis*.

subfam. **Bambusoideae** Luer. [1893] (syn. – Olyroideae Pilg. [1956], Parianoideae Butzin [1965]):

supertribe **Arundinarodae** L. Liu [1980]:

tribe **Arundinarieae** Asch. & Graebn. [1902] (syn. – Chimonocalameae Keng f. [1982, nom. inval.], Shibataeae Nakai [1933]):

subtribe **Arundinariinae** Nees ex Lindl. [1836] (syn. – Aruninariinae Benth. [1881, isonym], Hack. [1887, isonym], Phyllostachyridinae Keng f. [1992], Pleioblastinae Keng & Keng f.

[1959], Sasinae Keng. f. [1992], Shibataeinae (Nakai) Soderstr. & R.P. Ellis [1987], Sinobambusinae Z.B. Wang [1987], Thamnocalaminae Keng. f. [1992]): *Acidosasa*, *Ampelocalamus*, *Arundinaria*, *Bashania*, *Bergbambos*, *Chimonobambusa* (syn. – *Menstruocalamus*), *Chimonocalamus*, *Drepanostachyum*, *Fargesia* (syn. – *Borinda*, *Sinarundinaria*), *Ferrocalamus*, *Gaoligonshania*, *Gelidocalamus*, *Himalayacalamus*, *Indocalamus* (s.s.), *Indosasa*, *Kuruna*, *Oldeania*, *Oligostachyum*, *Phyllostachys*, *Pleioblastus*, *Pseudosasa*, *Sarocalamus*, *Sasa*, *Sasaella*, *Sasamorpha*, *Semiarundinaria* (syn. – *Brachystachyum*), *Shibataea*, *Sinobambusa*, *Thamnocalamus* s.s., *Vietnamocalamus*, *Yushania*.

supertribe **Bambusoidae** L. Liu [1980]:

tribe **Olyreae** Kunth ex Spenn. [1825] (syn. – supertribe Olyrodae L. Liu [1980]; tribes Buergersiochloae S.T. Blake [1946], Parianeae C.E. Hubb. [1934]).

subtribe **Buergersiochloinae** L.G. Clark & Judz [2007]: *Buergersiochloa*.

subtribe **Olyrinae** Kromb. [1875]: *Agnesia*, *Arberella*, *Cryptochloa*, *Diandrolyra*, *Ekmanochloa*, *Froesiochloa*, *Lithachne*, *Maclurolyra*, *Mniochloa*, *Olyra*, *Parodiolyra*, *Piresiella*, *Raddia*, *Raddiella*, *Rehia*, *Reitzia* (syn. – *Piresia*), *Sucrea*.

subtribe **Parianinae** Hack. [1887]: *Eremitis*, *Pariana*, *Parianella*.

tribe **Bambuseae** Kunth ex Dumort. [1829] (syn. – Arthrostylidiinae E. Camus [1913], Bacciferae E. Camus [1913, nom. inval.], Chusqueae E. Camus [1913], Hickeliinae A. Camus [1935, nom. inval.], Oxytenanthereae Tzvelev [1987]):

subtribe **Melocanninae** Benth. [1881] (syn. – Schizostachydinae Soderstr. & R.P. Ellis [1987]): *Cephalostachyum*, *Davidsea*, *Dendrochloa*, *Melocanna*, *Neohouzeaua*, *Ochlandra*, *Pseudostachyum*, *Schizostachyum* (syn. – *Leptocanna*), *Stapletonia*, *Teinostachyum*.

subtribe **Hickeliinae** A. Camus (syn. – Nastinae Soderstr. & R.P. Ellis [1987]): *Cathariostachys*, *Decaryochloa*, *Hickelia* (syn. – *Pseudocoix*), *Hitchcockella*, *Nastus* (syn. – *Oreiostrachys*), *Perrierbambus*, *Sirochloa*, *Valiha*.

subtribe **Bambusinae** J. Presl [1830] (syn. – Dendrocalaminae Benth. [1881]): *Bambusa* (syn. – *Dendrocalamopsis*, *Neosinocalamus*), *Bonia*, *Cyrtochloa*, *Dendrocalamus* (syn. – *Klemachloa*, *Sinocalamus*), *Dinochloa*, *Fimbribambusa*, *Gigantochloa*, *Greslania*, *Holttumochloa*, *Kinabaluchloa*, *Maclurochloa*, *Melocalamus*, *Mullerochloa*, *Nianhochloa*, *Neololeba*, *Neomicrocalamus*, *Oreobambos*, *Oxytenanthera* (syn. – *Houzeaubambus?*), *Parabambusa*, *Phuphanochloa*, *Pinga*, *Pseudobambusa*, *Pseudoxytenanthera*, *Soejatmia*, *Sphaerobambos*, *Temburongia*, *Temochloa*, *Thrysostachys*, *Vietanamosasa*.

subtribe **Racemobambosinae** Stapleton [1984]: *Racemobambos* s.s.

subtribe **Chusqueinae** Soderstr. & R.P. Ellis [1987] (syn. – Neurolepidinae Soderstr. & R.P. Ellis [1987]): *Chusquea* (syn. – *Neurolepis*, *Platonina*, *Rettbergia*, *Swallenochloa*).

subtribe **Guaduinae** Soderstr. & R.P. Ellis [1987]: *Apoclada*, *Eremocaulon* (syn. – *Criciuma*), *Guadua*, *Olmecca*, *Otatea*.

subtribe **Arthrostylidiinae** Soderstr. & R.P. Ellis [1987]: *Actinocladum*, *Alvimia*, *Arthrostylidium*, *Athroostachys*, *Atractantha*, *Aulonemia* (syn. – *Colantheria*, *Matudacalamus*), *Cambajuva*, *Didymogonyx*, *Elytostachys*, *Filgueirasia*, *Glaziophyton*, *Merostachys*, *Myriocladus*, *Rhipidocladum*.

subfam. **Pooideae** Benth. [1861] (syn. – Secaloideae Rouy [1913]; Agrostidoideae Kunth ex Beilschm. [1833]; Hordeaceae Burmeist. [1837, unranked], Phalarideae Burmeist. [1837, unranked], Stipaceae Burmeist. [1837, unranked]):

tribe **Brachyelytreae** Ohwi [1941] (syn. – Brachyelytrinae Ohwi [1942]): *Brachyelytrum*.

tribe **Nardeae** W.D.J. Koch. [1837] (syn. – subtribe Nardinae Kromb. [1875]) {sister to Lygeae}:  
*Nardus*.

tribe **Lygeae** J. Presl [1846] (syn. – Lygeinae Röser [2009], Spartineae Trin. [1824, nom. inval, based on *Lygeum*]) {sister to Nardeae}: *Lygeum*.

tribe **Phaenospermateae** Renvoize & Clayton [1985] (syn. – Duthieae Röser & Jul.Schneider [2011], subtribe Duthieinae Pilg. ex Potztl [1969]): *Anisopogon*, *Danthoniastrum*, *Duthiea* s.s. (s.l., syn. – *Triavenopsis*), *Metcalfia*, *Phaenosperma*, *Pseudodanthonia*, *Sinochasea*, *Stephanachne* (syn. – *Pappagrostis*).

tribe **Brylkinieae** Tateoka [1960] {sister to Meliceae, may be better in Meliceae as subtribe} (syn. – Brylkininae Ohwi [1941]): *Brylkinia*, *Koordersiochloa* (syn. – *Streblochaete*) {placement within Meliceae s.s. is doubtful, due to presence of cylindrical to lanceoloid (non-globose) styles, punctiform hilum}.

tribe **Meliceae** Link ex Endl. [1830] (syn. – Glycerieae Link ex Endl. [1830] {sister to Brylkinieae}; subtribe Glyceriinae Dumort. [1829], Melicinae Fr. [1835]): *Glyceria*, *Lyclochloa*, *Melica*, *Pleuropogon*, *Schizachne*, *Triniochloa*.

tribe **Ampelodesmeae** Tutin [1978] (syn. – Ampelodesminae Conert [1961]): *Ampelodesmos* {apparently an ancient hybrid between parents from Stipeae and Phaenospermateae; see Romaschenko et al., 2012}.

tribe **Stipeae** Dumort. [1824] (syn. – supertribe Stipodae L. Liu [1980]; subtribe Stipinae Griseb. [1846]; Aciachninae Caro [1982], Ortachninae Caro [1982]): *Achnatherum* {Eurasian/African, syn. – *Aristella*; Western Hemisphere species are in limbo, none belong in *Achnatherum* s.s, most are *Eriocoma* but not yet transferred}, *Aciachne*, *Amelichloa* {nested within *Nassella*, but an intergeneric hybrid origin has not been ruled out}, *Anatherostipa* (syn. – *Nicoraella*), *Anemanthele*, *Austrostipa*, *Celtica*, *Eriocoma* {incl. most American spp. of *Achnatherum*}, *Hesperostipa*, *Jarava*, *Lorenzochloa*, *Macrochloa*, *Nassella*, *Oloptum*, *Ortachne*, *Orthoraphium*, *Oryzopsis*, *Pappostipa*, *Patis*, *Piptochaetium*, *Piptatheropsis*, *Piptatherum*, *Psammochloa*, *Ptilagrostis*, *Stipa*, *Stipellula* (*Stipella* nom. illeg. hom.), *Timouria*, *Trikeriaia*.

tribe **Diarrheneae** C.S. Campb. [1985] (syn. – subtribe Diarrheninae Ohwi [1941]): *Diarrhena*, *Neomolinia*.

tribe **Brachypodieae** Harz [1880] (syn. – subtribe Brachypodiinae Hack. [1887]; Brachypodieae Hayek [1925, isonym]): *Brachypodium* (syn. – *Trachynia*).

supertribe **Poodae** L. Liu [1980] (syn. – Poodae T.D. Macfarl. & L. Watson [1982], isonym):

tribe **Poeae** R.Br. [1814] (syn. – Agrostideae Martinov [1820]{as Koleno = tribe, indirect ref. to Kunth}, Agrostidiaceae Dumort. [1824], Airopsidae Gren. & Godr. [1855], Alopecureae W.D.J. Koch [1837], Anthoxantheae Link ex Endl. [1830], Aveneae Dumort. [1824], Beckmannieae Nevski [1937], Calamagrostideae Trin. [1824], Cinneae Ohwi [1941], Coleantheae Husn. [1896], Cynosureae Dumort. [1824], Dupontieae A. Löve & D. Löve, [1961, nom. nud.], Festuceae Dumort. [1824], Gaudinieae Rouy [1913], Graphophoreae (Asch. & Graebn.) Hyl. [1953], Hainardieae Greuter [1967], Holceae J. Presl [1846], Lolieae Link ex Endl. [1830], Koelerieae Schur [1866, nom. nud.], Milieae Link ex Endl. [1830], Phalarideae Kunth [1829], Phleaeae Dumort. [1824], Scolochloaeae Tzvelev [1968], Seslerieae W.D.J. Koch [1837], Triseteeae Gren. & Godr. [1855], Vilfeae Trin. [1824]):

## Poeae CHLOROPLAST GROUP 1 (Aveneae type):

subtribe **Torreyochloinae** Soreng [2003]: *Amphibromus*, *Torreyochloa*.

subtribe **Aveninae** J. Presl [1830] (syn. – Gaudiniinae Holub ex Tzvelev [1976, nom. nud.], Graphephorinae Asch. & Graebn. [1900], Koeleriinae Asch. & Graebn. [1900]): *Arrhenatherum*, *Avellinia*, *Avena*, *Gaudinia*, *Graphephorum*, *Helictotrichon* s.s. (syn. – *Pseudarrhenatherum*; excl. *Avenula*, *Helictochloa*), *Koeleria* (syn. – *Parafestuca*), *Lagurus*, *Leptophyllochloa*, *Peyritschia*, *Rostraria*, *Sphenopholis*, *Trisetaria*, *Tricholemma*, *Trisetum*.

subtribe **Phalaridinae** Fr. [1835]: *Phalaris*.

subtribe **Anthoxanthinae** A. Gray [1856] (syn. – Foenodorinae Krause [1909, nom. inval.]): *Anthoxanthum* (syn. – *Ataxia*, *Hierochloa*).

subtribe **Brizinae** Tzvelev s.s. [1968]: *Airopsis*, *Briza* (syn. – *Macrobriza*; excl. *Brizochloa*).

subtribe **Calothecinae** Soreng [2015]: *Chascolytrum* (syn. – *Calotheca*, *Erianthecium*, *Gymnachne*, *Lombardochloa*, *Microbriza*, *Poidium*, *Rhombolytrum*), *Relchela*.

subtribe **Agrostidinae** Fr. [1835] (syn. – Chaeturaceae Link [1827, unranked], Calamagrostidinae Lindl. [1836, nom. nud.], Vilfinae Steud. [1954]): *Agrostis*, *Ammophila*, *Ancistragrostis*, *Bromidium*, *Calamagrostis* p.p. (syn. – *Deyeuxia*) {polyphyletic, p.p. in Western Hemisphere}, *Chaetopogon*, *Dichelachne*, *Echinopogon*, *Hypseochloa*, *Gastridium*, *Lachnagrostis*, *Limnodea*, *Pentapogon*, *Podagrostis*, *Polypogon*, *Triplachne*.

## Poeae CHLOROPLAST GROUP 2 (Poeae type):

*incertae sedis*: *Avenula* (syn. – *Homalotrichon*) {s.s., p.p. typica – *A. pubescens*; excl. *Helictochloa*. *Avenula* s.s. is a floater, probably allied to the set of Coleanthinae, Poinae s.l., and Miliinae}.

subtribe **Scolochloinae** Tzvelev [1987] (syn. – subtribe Scolochloae Tzvelev [1968]): *Dryopoa*, *Scolochloa* {this subtribe seems to share plastids with the classical Poeae and nrDNA with early GROUP 1 above}.

subtribe **Sesleriinae** Parl. [1845] (syn. – subtribe Miborinae Asch. & Graebn. [1899]): *Mibora*, *Echinaria*, *Oreochloa*, *Sesleria*, *Sesleriella* {this subtribe seems to share plastids with the old Poeae and nrDNA with early Aveninae GROUP 1 above}.

subtribe **Coleanthinae** Rouy [1913] (syn. – Puccinelliinae Soreng & Davis [2003]): *Catabrosa*, *Catabrosella*, *Coleanthus*, *Colpodium* (syn. – *Keniochloa*), *Hyalopoa* {apparently heterogenous}, *Paracolpodium* {apparently heterogenous}, *Phippsia*, *Puccinellia* (syn. – *Pseudosclerochloa*), *Sclerochloa*, *Zingeria* {probably best united with *Colpodium* s.s.}.

subtribe **Miliinae** Dumort. [1829] {possibly part of Poinae s.l., possibly sister to *Poa* or *Phleum*}: *Milium*.

subtribe **Poinae** Dumort. s.l. [1829] (syn. – subtribe Alopecurinae Dumort. [1829]; Beckmanniinae Nevski [1937], Cinninae Caruel. [1892], Gramininae Krause [1909, nom. inval.], Phleinae Dumort. [1868], Phleinae Benth. [1881, isonym], Ventenatinae Holub [1958, nom. nud.; Tzvelev, 1976, nom. inval., without Latin]): *Agrostopoa*, *Alopecurus*, *Aniselytron*, *Apera*, *Arctagrostis*, *Arctophila*, *Beckmannia*, *Bellardiochloa*, *Brizochloa*? {usually placed in *Briza*}, *Cinna*, *Cornucopiae*, *Cyathopus*, *Dupontia*, *Dupontiopsis*, *Gaudiniopsis*, *Hookerochloa* (syn. – *Festucella*), *Limnas*, *Nephelochloa*, *Nicoraepoa* {hybrids with *Poa* are known}, *Parvotrisetum*, *Phleum* (syn. – *Maillea*),



*Pholiurus*, *Poa* (syn. – *Anthochloa*, *Aphanelytrum*, *Austrofestuca*, *Dissanthelium*, *Eremopoa*, *Libyella*, *Lindbergella*, *Neuropoa*, *Oreopoa*, *Parodiochloa*, *Tovarochloa*, *Tzvelevia*), *Pseudophleum*, *Rhizocephalus*, *Saxipoa*, *Simplicia*, *Sylvipoa*, *Ventenata*.

subtribe **Airinae** Fr. [1835] (syn. – Corynephorinae subtrib V. Jirásek & Chrtek) {a heterogenous subtribe with no satisfactory resolution}: *Aira*, *Antinoria*, *Avenella*, *Corynephorus*, *Helictochloa* {incl. *Avenula* p.p. non-typica, A. subg. *Pratavenastrum*}, *Molineriella*, *Periballia*.

subtribe **Holcinae** Dumort. [1868] (syn. – Deschampsinae Holub [1958, nom. nud.], Aristaveninae F. Albers & Butzin [1977], Scribneriinae Soreng [2003]): *Deschampsia* s.s. (syn. – *Scribneria*) {excl. *Avenella*; possibly better as its own tribe}, *Holcus*, *Vahlodea*.

subtribe **Loliinae** Dumort. [1829] (syn. – Festucinae J. Presl [1830], Psilurinae Pilg. ex Potzta [1969]): *Castellia*, *Drymochloa*, *Festuca* (syn. – *Ctenopsis*, *Dielsiochloa*, *Hellerochloa*, *Loliolum*, *Micropyrum*, *Narduroides*, *Psilurus*, *Vulpia*, *Wangenheimia*), *Leucopoa* (syn. – *Xanthochloa*), *Lolium* (syn. – *Micropyropsis*, *Schedonorus*), *Megalachne*, *Patzkea*, *Podophorus*, *Pseudobromus* {the latter seems odd here. DNA data show a long branch, but outgroup selection has not clarified its placement}.

subtribe **Dactylidinae** Stapf [1898]: *Dactylis*, *Lamarckia*.

subtribe **Cynosurinae** Fr. [1835]: *Cynosurus*.

subtribe **Ammochloinae** Tzvelev [1976]: *Ammochloa*.

subtribe **Parapholiinae** Caro [1982] (syn. – Monerminae Tzvelev [1987, nom. inval.]): *Agropyropsis*, *Catapodium*, *Cutandia*, *Desmazeria*, *Hainardia*, *Parapholis*, *Sphenopus*, *Vulpiella*.

supertribe **Triticodae** T.D. Macfarl. & L. Watson [1982]:

tribe **Littledaleeae** Soreng & J.I. Davis [2015] (syn. – Littledaleinae Röser [2009]: *Littledalea* {this isolated genus appears to be the sister to Bromeae plus Triticeae}.

tribe **Bromeae** Dumort. [1824]: *Bromus* (syn. – *Anisantha*, *Boissiera*, *Bromopsis*, *Ceratochloa*, *Nevskiella*, *Stenofestuca*, *Trisetobromus*).

tribe **Triticeae** Dumort. [1824] (syn. – Aegilopineae Orb. [1841], Hordeae Kunth ex Spenn. [1825], Frumentae Krause [1903, nom. illeg.], Secaleinae Rchb. [1828, unranked]):

subtribe **Hordeinae** Dumort. [1829] (syn. – Elyminae Benth. [1881], Agropyrinae Nevski [1933], Clinelyminae Nevski [1933, nom. illeg.], Roegneriinae Nevski [1933], Henrardiinae C.E. Hubb. [1948]): *Agropyron*, *Anthosachne*, *Australopyrum*, *Connorochloa*, *Crithopsis*, *Douglasdewya*, *Elymus* (syn. – *Campeiostachys*, *Elytrigia*, *Hystrix*, *Roegneria*, *Sitanion*), *Eremopyrum*, *Festucopsis*, *Henrardia*, *Heteranthelium*, *Hordelymus*, *Hordeum* (syn. – *Critesion*), *Kengyilia*, *Leymus* (syn. – *Aneurolepidium*, *Eremium*, *Macrohystrix*, *Microhystrix*), *Pascopyrum*, *Peridictyon*, *Psathyrostachys*, *Pseudoroegneria*, *Secale*, *Stenostachys*, *Taeniatherum*.

subtribe **Triticinae** Fr. [1835] (syn. – Aegilopinae Nevski [1933]): *Aegilops*, *Amblyopyrum*, *Dasyphyrum*, *Thinopyrum*, *Triticum*.

“**PACMAD**” clade {Sánchez-Ken & Clark, 2010; also known as PACC (Davis & Soreng, 1993), PACCAD (GPWG, 2001), or PACCMAD (Sánchez-Ken et al. 2007)}

subfam. **Aristidoideae** Caro [1982] {sister to rest of PACMAD}:

tribe **Aristideae** C.E. Hubb. [1960]: *Aristida*, *Sartidia*, *Stipagrostis*.

subfam. **Panicoideae** A. Braun [1864] (syn. – Andropogonoideae Rouy [1913], Centothecoideae

Soderst. [1981]; Andropogineae Burmeist. [1837, unranked], Paniceae Burmeist. [1837, unranked], Paniceae Link [1827, unranked], Rottboëllaceae Burmeist. [1837, unranked]):

*incertae sedis*: *Chandrasekharania* {C3}, *Jansenella* {C3} {both genera were treated in Arundinellae by Clayton & Renvoize, 1986}.

tribe **Thysanolaeneae** C.E. Hubb. [1934] {possibly better within Centotheceae}: *Thysanolaena*.

tribe **Cyperochloaeae** L. Watson & Dallwitz ex Sánchez-Ken & L.G. Clark [2010] (syn. – Cyperochloaeae L. Watson & Dallwitz [1992, nom. nud.]): *Cyperochloa*, *Spartochloa*.

tribe **Centotheceae** Ridl. [1907] (subtribe Centothecinae Benth. [1881]): *Centotheca*, *Megastachya*.

tribe **Chasmanthieae** W.V. Br. & B.N. Smith ex Sánchez-Ken & L.G. Clark [2010]: *Bromuniola*, *Chasmanthium* (syn. – *Gouldochloa*).

tribe **Zeugiteae** Sánchez-Ken & L.G. Clark [2010] (syn. – Zeugitinae Caro [1982]): *Chevalierella*, *Lophatherum*, *Orthoclada*, *Pohlidium*, *Zeugites* (syn. – *Calderonella*).

tribe **Steyermarkochloaeae** Davidse & R.P. Ellis [1984] {DNA places with Chasmanthieae s.l. or Tristachyideae, the placement remains tentative}: *Arundoclaytonia*, *Steyermarkochloa*.

tribe **Tristachyideae** Sánchez-Ken & L.G. Clark [2010] (syn. – Trichopteryginae Jacq.-Fél. [1962, nom. inval.]): *Danthoniopsis*, *Dilophotriche*, *Gilgiochloa*, *Loudetia*, *Loudetiopsis*, *Trichopteryx*, *Tristachya*, *Zonotriche*.

tribe **Gynerieae** Sánchez-Ken & L.G. Clark [2001]: *Gynerium*.

{Paniceae sensu Clayton & Renvoize (1986) was revised following Morrone et al., 2012. Supertribes added here}.

Supertribe **Panicodae** L. Liu [1980]:

tribe **Paniceae** R.Br. [1814] (syn. – Cenchreae Rchb. [1828, unranked], Digitariae J.J.Schmitz & Regel [1841], Paniceae Horan. [1847, as Panicinae], Spiniferae Dumort. [1829], Melinideae Hitchc. [1920], Boivinelleae A. Camus [1925], Anthephoreae Pilg. ex Potztl [1957], Trachideae Pilg. ex Potztl [1957], Cyphochlaeneae Bosser [1965], Neurachneae S.T. Blake [1972]):

*incertae sedis*: *Chloachne*, *Oryzidium*, *Hydrothauma*, *Hylebates*, *Poecilostachys* p.p., *Sacciolepis*, *Thedachloa*, *Trichantheicum*.

subtribe **Anthephorinae** Benth. [1881] (syn. – Digitariinae Butzin [1972]; Trachidinae Pilg. [1940, nom. inval.], Trachydastrae Stapf [1917]): *Anthephora*, *Chaetopoa*, *Chlorocalymma*, *Digitaria*, *Megaloprotachne*, *Taeniorhachis*, *Tarigidia*, *Thyridachne*, *Trachys*.

subtribe **Dichantheiinae** Zuloaga [2014]: *Adenochloa*, *Dichantheium*.

subtribe **Boivinellinae** Pilg. [1940]: *Acroceras*, *Alloteropsis* (syn. – *Coridochloa*), *Amphicarpum*, *Cyphochlaena*, *Cyrtococcum*, *Echinochloa*, *Entolasia*, *Lasiacis*, *Mayariochloa*, *Morronea*, *Microcalamus*, *Oplismenus*, *Ottochloa*, *Parodiophyllochloa*, *Pseudechinolaena*.

subtribe **Neurachninae** Clayton & Renvoize [1986]: *Ancistrachne*, *Calyptochloa*, *Cleistochloa*, *Neurachne*, *Paraneurachne*, *Thyridolepis*.

*incertae sedis* {clade of ambiguous placement among latter set of subtribes}: *Homopholis*, *Walwhalleya*.

subtribe **Melinidinae** Stapf [1917, as Melinidastrae] Pilg. (syn. – Brachiariinae Butzin [1970], Thuarinae Ohwi [1942], Tristegininae Harv. [1869, nom. illeg.]; Melinidinae Pilg.

[1940]): *Chaetium*, *Eriochloa* *Eccoptocarpha*, *Leucophrys*, *Megathrysus*, *Melinis* (syn. – *Rhynchelytrum*), *Mildbraediochloa*, *Moorochloa*, *Rupichloa*, *Scutachne*, *Thuarea*, *Tricholaena*, *Urochloa* (syn. – *Brachiaria* s.s, *Pseudobrachiaria?*), *Yvesia*.

subtribe **Panicinae** Fr. [1835]: *Arthragrostis*, *Louisiella*, *Panicum*, *Yakirra*.

subtribe **Cenchrinae** Dumort. [1829] (syn. – Pennisetinae Rchb. [1828, unranked], Setariinae Dumort. [1829]; Pseudoraphidinae Keng & Keng f. [1990], Snowdeniinae Butzin [1972] Spinificinae Owhi [1942], Uranthoeciinae Butzin [1970], Xerochloinae Butzin [1970]): *Acritochaete*, *Alexfloydia*, *Cenchrus* (syn. – *Odontelyrum*, *Pennisetum*, *Snowdenia*), *Chamaeraphis*, *Dissochondrus* {Hawaii}, *Holcolemma*, *Hygrochloa*, *Ixophorus*, *Paractaenium*, *Paratheria*, *Plagiosetum*, *Pseudochaetochloa*, *Pseudoraphis*, *Setaria* (syn. – *Paspalidium*), *Setariopsis*, *Spinifex*, *Stenotaphrum*, *Stereochlaena*, *Streptolophus*, *Uranthoecium*, *Whiteochloa*, *Xerochloa*, *Zuloagaea*, *Zygochloa*.

tribe **Paspaleae** J. Presl [1830] (syn. – Arthropogoneae Pilg. ex Butzin [1972], Lecomtelleae Pilg. ex Potztal [1957]):

*incertae sedis*: *Reynaudia* {basal to the other subtribes}.

subtribe **Paspalinae** Griseb. [1846] (syn. – Lecomtelliinae Pilg. [1940]; Paspalinae Griseb. [1853], Paspalidinae Keng & Keng f. ex S.L. Chen & Y.X. Jin [1984], Reimarochloinae Caro [1982]): *Aakia*, *Acostia*, *Anthaenantiopsis*, *Axonopus* (syn. – *Centrochloa*, *Ophiochloa*), *Baptorhachis*, *Echinolaena* (syn. – *Chaseochloa*), *Gerritea*, *Hopia*, *Ichnanthus*, *Lecomtella*, *Ocellochloa*, *Osvaldoa*, *Paspalum* (syn. – *Thrasya*, *Thrasyopsis*, *Reimarochloa*), *Renvoizea*, *Spheneria*, *Streptostachys*.

subtribe **Otachyriinae** Butzin [1970]: *Aconisia* {tentatively accepted}, *Anthaenantia* (syn. – *Leptocoryphium*), *Hymenachne* (syn. – *Dallwatsonia*), *Otachyrium*, *Plagiantha*, *Rugolola*, *Steinchisma* (syn. – *Cliffordiochloa*, *Fasciculochloa*).

subtribe **Arthropogoninae** Butzin [1972]: *Achlaena*, *Altoparadisium*, *Apochloa*, *Arthropogon*, *Canastra*, *Coleataenia* (syn. – *Sorengia*), *Cyphonanthus*, *Homolepis*, *Keratochlaena* (syn. – *Sclerochlamys*), *Mesosetum*, *Oncorachis*, *Oplismenopsis*, *Phanopyrum*, *Stephostachys*, *Tatianyxa*, *Triscenia*.

supertribe **Andropogonodae** L. Liu [1980] {Arundinelleae—Sacchareae clade}:

tribe **Arundinelleae** Stapf [1898] (syn. – Garnotieae Tateoka [1957]; subtribe Arundinelliinae Honda [1930], Garnotiinae Pilg. [1956]): *Arundinella*, *Garnotia*.

tribe **Andropogoneae** Dumort. [1824] (syn. – Sacchareae Dumort. [1824], Coiceae Nakai [1943], Euchlaeneae Nakai [1943], Imperateae Godr. & Gren. [1855], Maydeae Dumort. [1824, nom. illeg.], Ophiureae Dumort. [1824], Rottboellieae Kunth [1829], Sacchareae Rchb. ex Horan. [1847, as Saccharinae], Tripsaceae C.E. Hubb. ex Nakai [1943], Zeeae Rchb. [1828, unranked], Zeeae Nakai [1943]) {Papers by Hodkinson et al., 2002, Skendzic et al., 2007, and Estep, et al. 2014, portend lots of problems for classification within this tribe, of which some obvious ones are noted below.}:

*incertae sedis* {*Eriochrysis*, *Imperata*, *Pogonatherum*, *Tripidium*, formerly placed in Saccharrinae, may be allied to Germaniinae. *Chrysopogon* and *Thelepogon* appear to be sisters and isolated from other tribes}: *Apluda*, *Chrysopogon* (syn. – *Vetiveria*), *Eriochrysis* (syn. – *Leptosaccharum*), *Imperata*, *Phacelurus* (syn. – *Thysia*) {apparently polyphyletic}, *Pogonatherum*, *Spathia*, *Spodiopogon* (syn. – *Eccoilopus*), *Thelepogon*, *Tripidium*.

subtribe **Arthraxoninae** Benth. [1881]: *Arthraxon*.

subtribe **Tripsacinae** Dumort. [1829] (syn. – Maydinae Harv. [1868, nom. illeg.], Zeinae Tzvelev [1968]): *Tripsacum*, *Zea*.

- subtribe **Chionachninae** Clayton [1981]: *Chionachne*, *Polytoca*, *Sclerachne*, *Trilobachne*.
- subtribe **Coicinae** Clayton & Renvoize [1986, inadvertent transfer of rank, may have been done earlier.] {Apparently sister to Rottoelliinae.}: *Coix*.
- subtribe **Rottboelliinae** J. Presl [1830] (syn. – Vossiastae Stapf [1917]): *Chasmopodium*, *Elyonurus* {orth. var. *Elyonurus*}, *Eremochloa*, *Glyphochloa*, *Hemarthria*, *Heteropholis*, *Lasiurus*, *Loxodera*, *Manisuris*, *Mnesithea* (syn. – *Coelorachis*, *Hackelochloa*), *Ophiuros*, *Oxyrhachis*, *Ratzeburgia*, *Rhytachne*, *Rottboellia*, *Thaumastochloa*, *Urelytrum*, *Vossia*.
- subtribe **Ischaeminae** J. Presl [1830] (syn. – Apludinae Hook.f. [1896]) {entangled with Saccharinae}: *Andropterum*, *Ischaemum*, *Kerriochloa*, *Pogonachne*, *Triplopogon*, *Sehima*.
- subtribe **Dimeriinae** Hack ex C.E. Hubb. [1934] (syn. – Dimeriinae Hack [1887, sin. descr.]) {apparently nested within Ischaeminae}: *Dimeria*.
- subtribe **Germaniinae** Clayton [1972] (syn. – Apocopidinae Keng [1939, nom. inval.]): *Apocopis*, *Germania*, *Trachypogon*.
- subtribe **Sorghinae** Stapf [1917], as Sorghastrae (syn. – Amphilophiastrae Stapf [1917]; Sorgha Bluff, Nees & Schauer [1836, unranked]): *Asthenochloa*, *Euclasta* (syn. – *Indochloa*), *Hemisorghum*, *Pseudodichanthium*, *Sorghastrum* {placement better in Saccharinae/Ischaeminae?}, *Sorghum* (syn. – *Cleistachne*, *Sarga*, *Vacoparis*).
- subtribe **Saccharinae** Griseb. [1846] (syn. – Erianthinae Hack. [1883]; Polliniastrae Stapf [1917]): *Erianthus*, *Eulalia* s.s. {s.l. is apparently polyphyletic}, *Eulaliopsis*, *Homozeugos*, *Lophopogon*, *Microstegium* (syn. – *Ischnochloa*), *Miscanthus* (syn. – *Diadranthus*, *Rubomons*, *Triarrhena*), *Miscanthidium*, *Narenga*, *Polliniopsis*, *Polytrias*, *Pseudopogonatherum*, *Pseudosorghum*, *Saccharum* s.s., *Sclerostachya* {better in *Miscanthus*?}, *Veldkampia*.
- subtribe **Andropogoninae** J. Presl [1830] (syn. – Hyparrheniastrae Stapf [1917], Hypogyniastrae Stapf [1917], Schizachyriastrae Stapf [1917]) {the subtribe is apparently sister to Anthistiriinae + *Eulalia* p.p. s.l.}: *Andropogon* (syn. – Hypogynium), *Bhidea*, *Diectomis*, *Diheteropogon*, *Hyparrhenia*, *Schizachyrium*.
- subtribe **Anthistiriinae** J. Presl [1830] (syn. – Anadelphiastrae Stapf [1917], Bothriochloinae Keng [1939, nom. inval.], Heteropogonastrae Stapf [1917], Themedastrae Stapf [1917]): *Agonium*, *Anadelphia*, *Bothriochloa*, *Capillipedium*, *Clausospicula*, *Cymbopogon*, *Dichanthium* (syn. – *Eremopogon*?), *Elymandra*, *Exotheca*, *Heteropogon*, *Hyperthelia*, *Iseilema*, *Monocymbium*, *Parahyparrhenia*, *Pseudanthistiria*, *Themeda*.
- subfam. **Arundinoideae** Kunth ex Beilschm. [1833] (syn. – Arundinoideae Tateoka [1957, isonym], Phragmitoideae Parodi [1958, nom. inval.], Phragmitoideae Parodi ex Caro [1982]; Arundinaceae Burmeist. [1837, unranked], {sister to Micrairoideae}):
- tribe **Arundineae** Dumort. [1824] (syn. – Amphipogoneae L. Watson & T.D. Macfarl. [2002]; subtribe Arundininae Miq. [1857]): *Amphipogon* (syn. – *Diplopogon*), *Arundo*, *Monachather*.
- tribe **Molinieae** Jirásek [1966] (syn. – subtribes Crinipinae Conert, [1961], Molininae Ohwi [1941]) {see Linder et al. (1997) on the Crinipoid group}; Phragmiteae Horan. [1847, unranked]): *Crinipes*, *Dichaetaria*, *Dregeochloa*, *Elytrophorus*, *Hakonechloa*, *Leptagrostis*, *Molinia*, *Moliniopsis*, *Nematopoa*, *Phragmites*, *Piptophyllum*, *Styppeiochloa*, *Zenkeria*.



subfam. **Micrairoideae** Pilg. [1956] {sister to Arundinoideae}:

tribe **Micraireae** Pilg. [1956]: *Micraira*.

tribe **Eriachneae** Eck-Borsboom [1980]: *Eriachne* (syn. – *Massia*), *Pheidochloa*.

tribe **Isachneae** Benth. [1881] (syn. – subtribe Isachninae Stapf [1898]): *Coelachne*, *Heteranthoecia*, *Isachne*, *Limnopoa*, *Sphaerocaryum*.

tribe **Hubbardieae** C.E. Hubb. [1960]: *Hubbardia*.

subfam. **Danthonioideae** H.P. Linder & N.P. Baker [2001] {sister to Chloridoideae}:

*incertae sedis*: *Alloeochaete*, *Danthonidium*, *Phaenanthoecium*.

tribe **Danthonieae** Zotov. [1963] (syn. – Cortaderieae Zotov. [1963]; subtribe Cortaderinae Conert [1961], Danthoniinae Fr. [1835]): *Austroderia*, *Capeochloa*, *Chaetobromus*, *Chimaerochloa*, *Chionochoa*, *Cortaderia* (syn. – *Lamprothyrsus*) *Danthonia*, *Geochloa*, *Merxmuellera*, *Notochloe*, *Pentameris* (syn. – *Pentastichis*, *Poagrostis*, *Prionanthium*), *Plinthanthesis*, *Pseudopentameris*, *Rytidosperma* (syn. – *Monostachya*, *Notodanthonia*, *Pyrrhanthera*), *Schismus* (syn. – *Karroochloa*), *Tenaxia*, *Tribolium*.

subfam. **Chloridoideae** Kunth ex Beilschm. [1833] (syn. – Eragrostoideae Pilg. [1956]; Chlorideae Burmeister [1837, unranked], Pappophorae Burmeister. [1837, unranked]) {sister to Danthonioideae}:

*incertae sedis*: *Decaryella*, *Indopoa*, *Lepturopetium*, *Myriostachya*, *Neostapfiella*, *Pogonochloa*, *Pseudozoysia*, *Silentvalleya*, *Viguiarella*.

tribe **Centropodieae** P.M. Peterson, N.P. Barker & H.P. Linder [2011]: *Centropodia*, *Ellisochloa*.

tribe **Triraphideae** P.M. Peterson [2010] (syn. – Triraphidinae Stapf [1917]): *Habrochloa*, *Neyraudia*, *Triraphis*.

tribe **Eragrostideae** Stapf [1898] (syn. – supertribe Eragrostodae L. Liu [1980], Uniroleae Roshev. ex C.S. Campb. [1985]):

subtribe **Cotteinae** Reeder [1965]: *Cottea*, *Enneapogon*, *Kaokochloa*, *Schmidtia*.

subtribe **Uniolinae** Clayton [1982]: *Entoplocamia*, *Fingerhuthia*, *Tetrachaete*, *Tetrachne*, *Uniola*.

subtribe **Eragrostidinae** J. Presl [1830]: *Catalepis*, *Cladoraphis*, *Ectrosia* (syn. – *Ectrosiopsis*, *Planichloa*), *Eragrostis* (syn. – *Acamptocladus*, *Diandrochloa*, *Neeragrostis*), *Harpachne*, *Heterachne*, *Pogonarthria* *Psammagrostis*, *Richardsiella*, *Steirachne*, *Stiburus*.

tribe **Zoysieae** Benth. [1881] (syn. – Spartineae Steele [1847], Sporoboleae Stapf [1898]):

subtribe **Zoysiinae** Benth. [1878]: *Urochondra*, *Zoysia*.

subtribe **Sporobolinae** Benth. [1881] (syn. – Crypsidinae Maire & Weiler [1953, nom. inval.], Spartiniinae Maire & Weiler [1953, nom. inval.]): *Psilolemma*, *Sporobolus* (nom. cons. prop. 2332, syn. – *Calamovilfa*, *Crypsis*, *Heleochloa*, *Spartina*, *Thellungia*).

tribe **Cynodonteae** Dumort. [1824] (syn. – Aeluropodieae Nevski ex Bor [1965], Chlorideae Rchb. [1828, unranked], Chlorideae Trin. [1824, nom. illeg. superfl, later than Dumort. and included *Cynodon*], Jouveae Pilg. [1956], Leptureae Dumort. [1824, as Lepiureae], Monermeae C.E. Hubb. [1948, nom. inval.], Nazieae Hitchc. [1920, nom. illeg.], Pappophoreae Kunth [1829], Perotideae C.E. Hubb. [1960], Pommereulleae Bor [1960], Trageae Hitchc. [1927], Triodieae S.W.L. Jacobs [2004], Hubbardochoinae Auquier [1980]):

*incertae sedis*: *Allolepis*, *Brachychloa*, *Cleistogenes*, *Dactyloctenium*, *Halopyrum*, *Hubbardochoa*, *Jouvea*, *Kalinia*, *Kampochloa*, *Lepturidium*, *Neobouteloua*, *Orinus*, *Pogononeura*, *Sohnsia*, *Vietnamochloa*.

subtribe **Aeluropodinae** P.M. Peterson [2010] (syn. – Aeluropodinae Jacq.-Fél. [1962, nom. inval.]): *Aeluropus*, *Odyssea* s.s.

subtribe **Triodiinae** Benth. [1881]: *Monodia*, *Symplectrodia*, *Triodia* (syn. – *Plectrachne*).

subtribe **Orcuttiinae** P.M. Peterson & Columbus [2007]: *Neostapfia*, *Orcuttia*, *Tuctoria*.

subtribe **Gouiniinae** P.M. Peterson & Columbus [2007]: *Gouinia*, *Schenckochloa*, *Tridentopsis*, *Triplasis*, *Vaseyochloa*.

subtribe **Cteniinae** P.M. Peterson, Romaschenko & Herrera Arrieta [2014]: *Ctenium*.

subtribe **Trichoneurinae** P.M. Peterson, Romaschenko & Herrera Arrieta [2014]: *Trichoneura*.

subtribe **Perotidinae** P.M. Peterson, Romaschenko & Herrera Arrieta [2014]: *Mosdenia*, *Perotis* (syn. – *Lopholepis*, *Toliara*), *Trigonochloa*.

subtribe **Farragininae** P. M. Peterson, Romaschenko & Herrera Arrieta [2014]: *Craspedorhachis*, *Farrago*.

subtribe **Gymnopogoninae** P. M. Peterson, Romaschenko & Herrera Arrieta [2014]: *Bewsia*, *Dignathia*, *Gymnopogon*, *Leptocarydion*, *Leptothrium*, *Lophacme*.

subtribe **Eleusininae** Dumort. [1829] (syn. – Astreblinae Clayton [1982], Chloridinae J. Presl [1830], Cynodontinae (Dumort.) Tzvelev [1968], Diplachninae Rouy [1913], Lepturinae Benth. [1881], Monerminae Janch. [1953, nom. nud.], Pommereullinae Potztl [1969]): *Acrachne*, *Afrotrichloris*, *Apochiton*, *Astrebla*, *Austrochloris*, *Chloris* (syn. – *Ochthochloa*), *Chrysochloa*, *Coelachyrum* (syn. – *Coelachyropsis*), *Cynodon*, (syn. – *Brachyachne*) *Daknopholis*, *Dinebra* (syn. – *Drake-Brockmania*, *Heterocarpha*, *Oxydenia*), *Diplachne*, *Disakisperma* (syn. – *Cypholepis*), *Eleusine*, *Enteropogon*, *Eustachys*, *Harpochloa*, *Leptochloa* (syn. – *Trichloris*), *Lepturus*, *Lintonia*, *Microachne*, *Microchloa* (syn. – *Rendlia*), *Oxychloris*, *Pommereulla*, *Rendlia*, *Rheochloa*, *Saugetia*, *Schoenefeldia*, *Sclerodactylon*, *Stapfochloa*, *Tetrapogon*.

subtribe **Tripogoninae** Stapf [1917]: *Desmostachya*, *Eragrostiella*, *Melanocenchris*, *Oropetium*, *Tripogon*.

subtribe **Pappophorinae** Dumort. [1829] (syn. – Tridentinae Keng & Keng f. [1960]): *Neesiochloa*, *Pappophorum*, *Tridens* s.s. {excl. *Tridentopsis*}.

subtribe **Traginae** P.M. Peterson & Columbus [2007] (syn. – Lappagininae Link ex Endl.

[1830, nom. illeg.], Tragineae Rchb. [1845, unranked]): *Monelytrum*, *Polevansia*, *Tragus*, *Willkommia* (syn. – *Willbleibia*).

subtribe **Hilariinae** P.M. Peterson & Columbus [2007]: *Hilaria* (syn. – *Pleuraphis*).

subtribe **Monanthochloinae** Pilg. ex Potzta [1969] (syn. – Distichlinae Parodi [1946, nom. nud.]): *Distichlis* (syn. – *Monanthochloe*, *Reederochloa*).

subtribe **Boutelouinae** Stapf [1917]: *Bouteloua* (syn. – *Buchloe*, *Buchlomimus*, *Cathestecum*, *Chondrosium*, *Cyclostachya*, *Griffithsochloa*, *Opizia*, *Pentarrhaphis*, *Pringleochloa*, *Soderstromia*).

subtribe **Scleropogoninae** Pilg. [1956] (syn. – Munroinae Parodi ex P.M. Peterson [1995]): *Blepharidachne*, *Dasyochloa*, *Erioneuron*, *Munroa*, *Scleropogon*, *Swallenia*.

subtribe **Muhlenbergiinae** Pilg. [1956] (syn. – Lycurinae Pilg. [1956]): *Muhlenbergia* (syn. – *Aegopogon*, *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Pereilema*, *Redfieldia*, *Schaffnerella*, *Schedonnardus*).

the level of subfamily, tribe, or subtribe. Earlier, in our printed Catalogue of New World Grasses (Judziewicz et al., 2000) and in Soreng et al. (2014) we attributed the names Panicoideae and Ehrhartoideae to Link (1827) but as a consequence now use Panicoideae A. Braun [1864], and for Ehrhartoideae revert back to the previously, more widely used, Oryzoideae Kunth ex Beilschm. [1833].

#### Nomenclatural changes

Subtribe **Calothecinae** Soreng, **subtribe nov.** Spikelets generally similar to Brizinae s.s., but basal sheaths fibrous. TYPE genus *Calotheca* Desv., *Nouv. Bull. Sci. Soc. Philom. Paris* 2: 190. 1810. (= *Chascolytrum* Desv.). Sometimes referred to as the “Calotheca clade” or the “Brizinae s.l. clade,” the two genera (sensu Essi et al., 2011), *Chascolytrum* and *Relchella* Steud., are confined to the Western Hemisphere occurring almost entirely in South America. Brizinae s.s. is native to Eurasia and North Africa.

Tribe **Littledaleeae** Soreng & Davis, **tribe et stat nov.** (based on—Littledaleinae Röser, *Taxon* 58(2): 420. 2009): TYPE genus *Littledalea* Hemsl., in *Hooker's Icon. Pl.* 25: pl. 2472. 1896. The species in this monogeneric tribe are confined to high altitudes on the Tibetan Plateau and adjacent Central Asian mountains.

## Discussion

### Anomochlooideae, Pharoideae, and Puelioideae

The basal lineages in the family include three small subfamilies Anomochlooideae (*Anomochloa* Brongn. and *Steptochoeta* Schrad. ex Nees), Pharoideae (*Pharus* P. Browne, *Leptaspis* R. Br., and *Scrotochloa* Judz.), and Puelioideae (*Guaduella* Franch. and *Puelia* Franch.) totaling 31 species. These form a grade (in the order listed) leading to the split between the BOP and PACMAD clades. Possible morphological synapomorphies for these three subfamilies were identified by the Grass Phylogeny Working Group (2001).

### Oryzoideae

Subfamily Oryzoideae is the basal lineage of the BOP clade and includes 116 species in 20 genera divided into 4 tribes: Streptogyneae with two species in a single genus, Ehrharteae with 38 species in 4 genera, Phyllorachideae with 3 species in 2 genera, and the Oryzeae with 72 species in 11 genera, divided into 2 subtribes (Oryzinae with 40 species in 2 genera and Zizaniinae with 32 species in 9 genera). The branching position of Phyllorachideae in Fig. 1 is based on the analysis of Zhang (2000). The Oryzeae are economically important since *Oryza sativa* L. (rice) and *Zizania palustris* L. (wild rice) are members. The rice plastid genome was the first to be completely sequenced in the monocots (Hiratsuka et al., 1989). *Suddia sagittifolia* Renvoize is not placed in a subtribe (*incertae sedis*) and is currently on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Ali, 2010).

### Bambusoideae

Subfamily Bambusoideae includes 1641 species in 120 genera in 3 tribes. The classification largely follows BPG (2012). Tribe Arundinarieae with only the subtribe Arundinariinae contains 621 species in 31 genera that are almost exclusively distributed in Eurasia; only the three species of *Arundinaria* Michx. reach North America (Triplett & Clark, 2010; Triplett et al., 2010). The species are principally temperate in distribution, and all are woody. Tribe Olyreae (herbaceous bamboos) includes 127 species in 21 genera, and these, with the exception of *Buergersiochloa* Pilg. from Malaysia and *Olyra latifolia* L. populations in Africa, occur in the western hemisphere, primarily in the tropical forests of South and Central America. Recent molecular analyses may change circumscription among the genera (Attigala et al., 2014; Oliveira et al., 2014; Triplett et al., 2014). Tribe Bambuseae (woody subtropical and tropical bamboos) includes 893 species in 68 genera placed in 7 subtribes. Subtribes Melanocanninae (95 species in 10 genera), Hickeliinae (38 species in 8 genera), Racemobambosinae (19 species in 1 genus), and Bambusinae (368 species in 29 genera) form a clade distributed in Eurasia, Australasia, or

Africa, and these share a common ancestor with subtribes Arthrostylidiinae (167 species in 14 genera), Guaduininae (41 species in 5 genera), and Chusqueinae (165 species in 1 genus) distributed in the western hemisphere, primarily in South and Central America.

### Pooideae

Subfamily Pooideae includes 4234 species in 197 genera in 14 tribes. The species are known as the “cool season” or “poid” grasses and all are  $C_3$  and distributed in temperate climates. The tribe Brachyelytreae is the deepest split in the subfamily, with three species in a single genus: one distributed in southeastern Asia and two from the southeastern USA (Saarela et al., 2003). The monotypic tribes Lygeeae and Nardeae, each with a single species, share a common ancestor and are the only poidids with bicellular microhairs (Soreng & Davis, 1998). Schneider et al. (2011) united these two species in one tribe, but we feel they are worthy of separate tribal status because each species appears on a long branch in our phylogenetic trees suggesting ancient diversification. The Phaenospermateae (14 species in 8 genera) are sister to the remaining tribes. Brylkinieae (4 species in 2 genera) and Meliceae (154 species in 6 genera), and Stipeae (582 species in 28 genera) and Ampelodesmeae (1 species of putative ancient hybrid origin derived from Stipeae and Phaenospermateae; Romschenko et al., 2012), each share a common ancestor. Recent work on the Stipeae and relatives supports the inclusion of *Duthiea* Hack. in the Phaenospermateae (Romschenko et al., 2010, 2012) rather than in a separate tribe (Schneider et al., 2011). In our current analysis, as in Romschenko et al. (2012), Stipeae (plus Ampelodesmeae) are sister to the remaining poid tribes. The pattern of speciation in two Stipeae genera, *Patis* Ohwi and *Ptiliagrostis* Griseb. revealed a past hybridization followed by two plastid capture events preceded migration of *Patis coreana* (Honda) Ohwi and *Ptiliagrostis porteri* (Rydb.) W.A. Weber from Asia to North America (Romschenko et al., 2014). Diarrheneae (5 species in 2 genera) and Brachypodieae (20 species in 1 genus) are the next 2 sequentially diverging lineages. Brachypodieae and the remaining tribes are frequently referred to as the “core Pooideae” (Soreng & Davis, 1998).

Early molecular studies using plastid restriction sites led Soreng et al. (1990) to identify Aveneae and Poeae groups which correspond to the 2 plastid clades in the tribe Poeae (2776 species in 118 genera) (Fig. 1). The Poeae include many temperate forage and lawn species in the genera *Agrostis* L., *Festuca* L., *Lolium* L., *Phleum* L., *Poa* L., and *Avena* L. (includes *A. sativa* L.: cultivated oats). The following seven subtribes share a common ancestor in chloroplast group 1 (Aveneae type): Agrostidinae (604 species in 16 genera), Calothecinae (26 species in 2 genera; see Essi et al., 2008, 2010, 2011), Brizinae (5 species in 2 genera), Aveninae (302 species in 15 genera), Anthoxanthinae (69 species in 1 genus), Phalaridinae (17 species in 1 genus), and Torreyochloinae (16 species in 2 genera). Generic limits among the core Agrostidinae genera, such as *Calamagrostis* Adans. and *Trisetum* Pers., are not well understood and more study is needed (Saarela et al., 2010). This group has also been studied by Quintanar et al. (2007, 2010). The following 11 subtribes share a common ancestor in chloroplast group 2 (Poeae type): Coleanthinae (163 species in 10 genera), Airinae (41 species in 7 genera), Miliinae (5 species

in 1 genus), Poinae s.l. (697 species in 29 genera), Holcinae (52 species in 3 genera), Parapholiinae (26 species in 8 genera), Ammochloinae (3 species in 1 genus), Cynosurinae (10 species in 1 genus), Dactylidinae (2 species in 2 genera), Sesleriinae (37 species in 5 genera), Loliinae (698 species in 9 genera), and the Scolochloinae (3 species in 2 genera). *Avenula* (Dumort.) Dumort. s.s. remains *incertae sedis*. Poinae s.l. here includes Alopecurinae, Cinninae, and Phleinae but Poinae s.s. could include only *Poa* L. (Gillespie et al., 2010; Soreng et al., 2015). Loliinae and allied subtribes, which include *Festuca* s.l., have been extensively studied (Inda et al., 2008; Catalán et al., 2009; Díaz-Pérez et al., 2014). Since the genera with traditional Aveneae and Poeae morphologies are intermingled among the two plastid groups, the Aveneae were melded into tribe Poeae (Soreng & Davis, 2000; GPWG, 2001). Subsequent phylogenetic studies of the nuclear ribosomal spacer regions show the whole lineage with Aveneae type plastids emerge from among lineages with Poeae type plastids, indicating deep reticulation in the tribe. Subtribe Sesleriinae is considered hybrid in origin since *Sesleria* Scop. shares a distinctly Poeae type plastid and a nuclear ribosomal type that places it among early diverging elements of subtribe Aveninae (Quintanar et al., 2010; Saarela et al., 2010).

Littledaleeae (4 species in 1 genus) is sister to Bromeneae (166 species in 1 genus) and Triticeae (503 species in 27 genera, not counting some 20 nothogenera!). Bromeneae was investigated by Saarela et al. (2007, 2014) where it was treated as monotypic. Triticeae includes subtribes Triticinae (448 species in 22 genera) and Hordeinae (55 species in 5 genera). Triticeae includes *Triticum aestivum* L. (wheat), *Hordeum vulgare* L. (barley), and *Secale cereale* L. (rye), and is one of the most intensively studied grass tribes. Triticinae is derived from within Hordeinae s.l., but no new infratribal classification has been offered (Seberg & Petersen, 2007). The tribe is well known for reticulate evolution and the classification of genera is largely based on genome types and pairings (Barkworth et al., 2009; Anamthawat-Jonsson, 2014; Sha et al., 2014; Sun 2014; Wang & Lu, 2014; Zhang et al., 2014).

### Aristidoideae

Subfamily Aristidoideae includes 1 tribe, Aristideae (364 species in 3 genera): *Aristida* L., *Sartidia* De Winter, and *Stipagrostis* Nees. Within *Aristida* (304 species) there is a single species, *A. longifolia* Trin. from South and Central America, that has been verified as  $C_3$ , and it was found to be basal in a survey of 67 species in the genus (Cerros-Tlatilpa et al., 2011). Apparently, all four species of *Sartidia* are  $C_3$ , whereas all examined species of *Stipagrostis* are  $C_4$  grasses. Therefore, at least two independent  $C_4$  origins, each with unique anatomical and genetic features, are hypothesized for Aristidoideae (Cerros-Tlatilpa et al., 2011).

### Panicoideae

Subfamily Panicoideae includes 3560 species in 12 tribes. The species are predominantly distributed in tropical to warm-temperate habitats with summer precipitation, and in tropical forests and savannas. Important genera include *Zea mays* L. (corn or mays), *Saccharum officinarum* L. (sugarcane), *Sorghum bicolor* L. (sorghum), *Cenchrus* L., *Panicum* L., and *Setaria* P. Beauv. Within the subfamily there are six major clades. Two monotypic genera, *Chandrasekharania* V. J Nair,



Ramachandran, Srekumar and *Jansenella* Bor, both placed in Arundinelleae by Clayton & Renvoize (1986), are here considered *incertae sedis* in Panicoideae pending future DNA studies, leaving Arundinelleae as strictly C<sub>4</sub>. These two genera are hypothesized to belong to Tristachyideae, which was separated from Arundinelleae (Sánchez-Ken & Clark, 2010). The basal lineage of subfamily Panicoideae consists of the following seven tribes and has loosely been referred to as the “centothecoid” clade: Thysanolaeneae (2 species in 1 genus), Cyperochloae (2 species in 2 genera), Centothecae (6 species in 2 genera), Chasmanthieae (7 species in 2 genera), Zeugiteae (18 species in 5 genera), Tristachyidae (71 species in 8 genera), and Steyermarkochloae (3 species in 2 genera). The phylogenetic relationships of *Arundoclaytonia* Davidse & R.P. Ellis and *Steyermarkochloa* Davidse & R.P. Ellis, both in Steyermarkochloae (Sánchez-Ken & Clark, 2007, 2010), are not well established. Steyermarkochloae is tentatively placed in Fig. 1 based on the study of Morrone et al. (2012), but also see Sánchez-Ken & Clark (2010) for further discussion. These seven tribes were formerly classified as subfamily Centothecoideae or placed in Arundinoideae, or mixed among Arundinelleae and Paniceae (Soderstrom, 1981; Clayton & Renvoize, 1986; Sánchez-Ken & Clark, 2007). Tristachyideae is sometimes resolved among the basal elements of Paniceae or Paspaleae (Sánchez-Ken & Clark, 2010) after the divergence of Gynerieae. The Gynerieae (1 species in 1 genus) is the next diverging lineage (Fig. 1).

Tribe Paniceae (1498 species in 84 genera) includes the following seven subtribes: Anthephorinae (298 species in 9 genera), Dichantheiinae (66 species in 2 genera), Boivinellinae (135 species in 15 genera), Neurachninae (21 species in 6 genera), Melinidinae (215 species in 14 genera), Panicinae (343 species in 4 genera), and Cenchrinae (394 species in 24 genera). Tribes Paniceae and Paspaleae have been extensively revised by Morrone et al. (2007, 2008, 2012) with a series of new genera proposed over the last decade by Acosta et al. (2014), Denham & Zuloaga (2007), Donadio et al. (2009), Salariato et al. (2010), Scataglini et al. (2014a, 2014b), Scataglini & Zuloaga (2014), Sede et al. (2009a, 2009b, 2010), and Zuloaga et al. (2007, 2010). The following 10 genera in Paniceae are *incertae sedis*: *Chloachne* Stapf, *Homopholis* C.E. Hubb., *Hydrothauma* C.E. Hubb., *Hylebates* Chippin., *Oryzidium* C.E. Hubb. & Schweick., *Poecilostachys* Hack., *Sacciolepis* Nash, *Thedachloa* S.W.L. Jacobs, *Trichanthecium* Zuloaga & Morrone, and *Walwhalleya* Wills & J.J. Bruhl. Tribe Paspaleae is the next diverging lineage in Fig. 1 and includes 673 species in 40 genera distributed in the following three subtribes: Paspalinae (556 species in 16 genera), Otachyriinae (40 species in 7 genera), and Arthropogoninae (75 species in 16 genera). *Reynaudia filiformis* (Spreng. ex Schult.) Kunth is *incertae sedis* within the Paspaleae. Relationships of the Andropogoneae–Arundinelleae clade to Paniceae and Paspaleae are still unsettled, and genera tenuously assigned as *incertae sedis* are in need of additional study.

The remaining clade in Panicoideae includes the Arundinelleae (88 species in 2 genera) and the Andropogoneae (1189 species in 90 genera), all of which are C<sub>4</sub>. Arundinelleae here is restricted to include 88 species in 2 genera. Andropogoneae includes the following 12 subtribes: Arthraxoninae (27 species in 1 genus), Tripsacinae (22 species in 2 genera), Chionachninae (12 species in 4 genera), Coicinae (4 species in 1 genus),

Rottboelliinae (134 species in 18 genera), Ischaeminae (98 species in 6 genera), Dimeriinae (61 species in 1 genus), Germainiinae (30 species in 3 genera), Sorghinae (53 species in 6 genera), Saccharinae (144 species in 16 genera), Andropogoninae (249 species in 6 genera), and Anthistiriinae (244 species in 16 genera). Based on interpretations of recent DNA studies (Estep et al., 2014; Liu et al., 2014b; Welker et al., 2015) there are at least ten *incertae sedis* genera in Andropogoneae: *Apluda* L., *Chrysopogon* Trin., *Eriochrysis* P. Beauv., *Imperata* Cirillo, *Phacelurus* Griseb., *Pogonarthrum* P. Beauv., *Spathia* Ewart, *Spodiopogon* Trin., *Thelepogon* Roth., and *Tripidium* H. Scholz. Hybridization has played a major role in the diversification of the Andropogoneae (Estep et al., 2014; Liu et al., 2014b; Welker et al., 2015) and we anticipate significant rearrangements to occur in the classification, which is currently based on that of Clayton & Renvoize (1986).

#### Arundinoideae

Subfamily Arundinoideae was fairly large and quite heterogeneous sensu Watson & Dallwitz (1992). It formerly included 736 species, but now is reduced to 40 species in 16 genera in 2 tribes. Arundineae sensu GPWG (2001) is paraphyletic in a recent phylogeny (GPWG II, 2012), and in our analysis, if Amphipogoneae is recognized. We recognize two main lineages as tribes: Arundineae (16 species in 3 genera: *Amphipogon* R. Br., *Arundo* L., and *Monachather* Steud.); and Molinieae (24 species in 13 genera, including the *Crinipes* group). Further dividing these two tribes into subtribes seems reasonable, but more data are needed. *Dichaetaria* Steud. (monotypic) and *Dregeochloa* Conert (2 species) are strongly supported as members of Molinieae (Jordan Teisher, preliminary data, pers comm.), along with *Styppeiochloa* De Winter, *Elytrophorus* P. Beauv., and *Eragrostis walteri* Pilg. The following six genera were referred to as the *Crinipes* group (Barker, 1997; Linder et al., 1997): *Crinipes* Hochst. (2 species), *Leptagrostis* C.E. Hubb. (monotypic), *Nematopoa* C.E. Hubb. (monotypic), *Piptophyllum* C.E. Hubb. (monotypic), *Styppeiochloa* (2 species), and *Zenkeria* (5 species). The *Crinipes* group has had scant representation in molecular studies and its monophyly is uncertain. All species currently placed in this subfamily are C<sub>3</sub> grasses.

#### Micrairoideae

Subfamily Micrairoideae includes 186 species in 4 tribes: Micraireae (15 species in 1 genus), Eriachneae (50 species in 2 genera), Isachneae (119 species in 5 genera), and Hubbardieae (2 species in 1 genus). Sánchez-Ken et al. (2007) recognized 8 genera in 3 tribes by sinking Hubbardieae within Isachneae. We include Hubbardieae in the subfamily since Clayton & Renvoize (1986) indicate it is apparently derived from Isachneae. Only *Eriachne* R. Br. and *Pheidochloa* S.T. Blake (*Eriachneae*) appear to be C<sub>4</sub>.

#### Danthonioideae

The primarily southern hemisphere subfamily, Danthonioideae consists of 293 species in 20 genera. Molecular phylogenetic analyses and generic classifications for this subfamily have been completed (Pirie et al., 2008; Linder et al., 2010). However, 3 genera: *Alloeochoetae* C.E. Hubb. (6 species), *Danthoniastrum* C.E. Hubb. (monotypic), and *Phaenanthoecium* (monotypic), were not mentioned by Linder

et al. (2010) even though other agrostologists thought they were allied to *Rytidosperma* Steud. (Clayton & Renvoize, 1986; Phillips, 1995). We treat these three genera as *incertae sedis* in the subfamily because their lemmas have well developed, flattened, coiled, geniculate awns diverging between relatively slender lateral lobes, typical of Danthoideae, but not found in Arundinoideae. Embryological features for these three taxa are also unknown. Linder et al. (1997) specifically included *Alloeochoetae* in Danthoideae, and indicated that *Danthodium* was probably misplaced in Arundinoideae. All the species in this subfamily as currently circumscribed are C<sub>3</sub>.

### Chloridoideae

Subfamily Chloridoideae is sister to Danthoideae. It consists of 1601 species in 131 genera and 5 tribes. The species are predominantly found in arid temperate grasslands with warm-season precipitation or in arid tropical grasslands. The following nine chloridoid genera have not yet been included in any molecular studies and their affinities are uncertain: *Decaryella* A. Camus, *Indopoa* Bor, *Lepturopetium* Morat, *Myriostachya* (Benth.) Hook.f., *Neostapfella* A. Camus, *Pogonochloa* C.E. Hubb., *Pseudozoysia* Chiov., *Silentvalleya* V.J. Nair, *Viguiella* A. Camus. The basal lineage, tribe Centropodieae, includes two genera (*Centropodia* Rchb. and *Ellisochloa* P.M. Peterson & Barker) and six species distributed in Africa and Asia (Peterson et al., 2011). *Ellisochloa* is currently the only genus within the chloridoids that includes C<sub>3</sub> grasses.

Tribe Triphideae includes 14 species in 3 genera distributed in Africa, Asia, and Australasia. Based on preliminary DNA studies *Habrochloa* C.E. Hubb. belongs in this Tribe (Peterson & Romaschenko, unpublished).

Tribe Eragrostideae includes 488 species in 20 genera and is composed of 3 subtribes: Eragrostidinae (449 species in 11 genera), Unioliinae (11 species in 5 genera), and Cotteinae (28 species in 4 genera). Eragrostidinae and Unioliinae form a clade, and together are sister to Cotteinae. Earlier morphological studies of *Eragrostis* Wolf (416 species) concluded that the genus was polyphyletic (Van den Borre & Watson, 1994) but more recent studies indicate that it is monophyletic or possibly paraphyletic since other genera appear to be derived from within (Ingram & Doyle, 2004; Peterson & Romaschenko, in preparation). *Eragrostis tef* (Zucc.) Trotter (*tef*) is widely cultivated in Africa and its grain includes all eight essential amino acids for humans (El-Alfy et al., 2010).

Tribe Zoysieae includes 244 species in 4 genera and 2 subtribes: Zoysiinae (12 species in 2 genera) and Sporobolinae (232 species in 2 genera). Based on DNA studies Peterson et al. (2014b) found *Sporobolus* R. Br. (231 species) to be paraphyletic with *Calamovilfa* (A. Gray) Hack. ex Scribn. & Southw., *Crypsis* Aiton, *Spartina* Schreb., *Thellungia* Stapf, and *Eragrostis megalosperma* F. Muell. ex Benth. embedded within.

Tribe Cynodonteae includes 839 species in 93 genera and 18 subtribes. The following 15 genera have not been placed in a subtribe: *Allolepis* Soderstr. & H.F. Decker, *Brachychloa* S.M. Phillips, *Cleistogenes* Keng, *Dactyloctenium* Willd., *Halopyrum* Stapf, *Hubbardochloa* Auquier, *Jouvea* E. Fourn., *Kalinia* H.L. Bell & Columbus, *Kampochloa* Clayton, *Lepturidium* Hitchc. & Eckman, *Neobouteloua* Gould, *Orinus* Hitchc., *Pogononeura* Napper, *Sohnsia* Airy Shaw, and *Vietnamochloa* Veldkamp & Nowack. The following 6 subtribes form a clade in a study previously determined by Peterson et al. (2014a): Gouiniinae

(17 species in 5 genera, western hemisphere), Cteniinae (20 species in 1 genus, African/western hemisphere), Trichoneurinae (8 species in 1 genus, western hemisphere), Gymnopogoninae (25 species in 6 genera, African), Farragininae (4 species in 2 genera, African), and the Perotidinae (20 species in 5 genera, African and Eurasian). The Eleusininae (238 species in 31 genera), a larger subtribe and topic of a recent DNA study (Peterson et al., 2015) is sister to these six subtribes (Peterson et al., 2012). *Eleusine coracana* (L.) Gaertn. (finger millet) is an important cereal crop in semi-arid regions of the world (Liu et al., 2011, 2014a). Aleuropodinae (11 species in 2 genera) and Troidiinae (69 species in 3 genera) distributed in Australasia and Africa form a clade that is sister to the six previously mentioned subtribes and Eleusininae. Subtribes Tripogoninae (60 species in 5 genera, primarily Australasian and African), Pappophorinae (28 species in 3 genera, western hemisphere), Tragiinae (14 species in 4 genera, primarily African and Australasian), Hilariinae (10 species in 1 genus), Muhlenbergiinae (182 species in 1 genus), Scleropogoninae (15 species in 6 genera), Boutelouinae (58 species in 1 genus), and Monanthochloinae (10 in 1 genus) form a clade that is sister to all other Cynodonteae. The latter four subtribes are primarily distributed in the western hemisphere with only six species of *Muhlenbergia* Schreb. known to occur in Asia (Peterson et al., 2010a, 2010b).

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### References

- Acosta JM, Scatagliini MA, Reinheimer R, Zuloaga FO. 2014. A phylogenetic study of subtribe Otachyriinae (Poaceae, Panicoideae, Paspaleae). *Plant Systematics and Evolution* 300: 2155–2166.
- Ali MM. 2010. The IUCN Red List of Threatened Species, version 2014.3 [online]. Available from [www.iucnredlist.org](http://www.iucnredlist.org) [accessed 28 Jan 2015].
- Anamthawat-Jonsson K. 2014. Molecular cytogenetics of *Leymus*: Mapping the Ns genome-specific repetitive sequences. *Journal of Systematics and Evolution* 52: 716–721.
- Attigala L, Triplett JK, Kathriarachchi HS, Clark LG. 2014. A new genus and a major temperate bamboo lineage of the Arundinarieae (Poaceae: Bambusoideae) from Sri Lanka based on a multi-locus plastid phylogeny. *Phytotaxa* 174: 187–205.
- Bamboo Phylogeny Group (BPG). 2012. An updated tribal and subtribal classification for the Bambusoideae (Poaceae). *Bamboo Science & Culture. The Journal of the American Bamboo Society* 25: 3–27.

- Barker NP. 1997. The relationships of *Amphipogon*, *Elytrophorus* and *Cyperochloa* (Poaceae) as suggested by *rbcl* sequence data. *Telopea* 7: 205–213.
- Barkworth ME, Cutler DR, Rollo JS, Jacobs SWL, Rashid A. 2009. Morphological identification of genomic genera in the Triticeae. *Breeding Science* 59: 561–570.
- Bentham G. 1881. Notes on Gramineae. *Journal of the Linnean Society, Botany* 19: 14–134.
- Bouchenak-Khelladi Y, Salamin N, Savolainen V, Forest F, Van der Bank M, Chase MW, Hodkinson TR. 2008. Large multi-gene phylogenetic trees of the grasses (Poaceae): Progress towards complete tribal and generic level sampling. *Molecular Phylogenetics and Evolution* 47: 488–505.
- Bouchenak-Khelladi Y, Slingsby JA, Verboom GA, Bond WJ. 2014. Diversification of  $C_4$  grasses (Poaceae) does not coincide with their ecological dominance. *American Journal of Botany* 101: 300–307.
- Brown R. 1814. Gramineae. In: Flinders M ed. *A voyage to Terra Australis*. London: W. Bulmer & Company. 580–583.
- Catalán P, Soreng RJ, Peterson PM. 2009. *Festuca aloha* and *F. molokaiensis* (Poaceae: Loliinae), two new species from Hawai'i. *Journal of the Botanical Research Institute of Texas* 3: 51–58.
- Cerros-Tlatilpa R, Columbus JT, Barker NP. 2011. Phylogenetic relationships of *Aristida* and relatives (Poaceae, Aristidoideae) based on noncoding chloroplast (*trnL-F*, *rpl16*) and nuclear (ITS) DNA sequences. *American Journal of Botany* 98: 1868–1886.
- Christin P-A, Spriggs E, Osborne CP, Strömberg CAE, Salamin N, Edwards EJ. 2014. Molecular dating, evolutionary rates, and the age of the grasses. *Systematic Biology* 63: 153–165.
- Clark LG, Kobayashi M, Matthews S, Spangler RE, Kellogg EA. 2000. The Puelioideae, a new subfamily of Poaceae. *Systematic Botany* 25: 181–187.
- Clark LG, Zhang WP, Wendel JF. 1995. A phylogeny of the grass family (Poaceae) based on *ndhF* sequence data. *Systematic Botany* 20: 436–460.
- Clayton WD. 1981. Early sources of tribal names in Gramineae. *Kew Bulletin* 36: 483–485.
- Clayton WD, Renvoize SA. 1986. Genera graminum. Grasses of the world. *Kew Bulletin, Additional Series* 13: 1–389.
- Davis JI, Soreng RJ. 1993. Phylogenetic structures in the grass family (Poaceae) as inferred from chloroplast DNA restriction site variation. *American Journal of Botany* 80: 1444–1454.
- Davis JI, Soreng RJ. 2007. A phylogenetic analysis of Poaceae tribe Poeae sensu lato based on morphological characters and sequence data from three plastid-encoded genes: evidence for reticulation, and a new classification for the tribe. *Kew Bulletin* 62: 425–454.
- Davis JI, Soreng RJ. 2010. Migration of endpoints of two genes relative to boundaries between regions of the plastid genome in the grass family (Poaceae). *American Journal of Botany* 97: 874–892.
- Denham SS, Zuloaga FO. 2007. Phylogenetic relationships of the Decumbentes group of *Paspalum*, *Thrasya*, and *Thrasypopsis* (Poaceae: Panicoideae: Paniceae). *Aliso* 23: 545–562.
- Díaz-Pérez AJ, Sharifi-Tehrani M, Inda LA, Catalán P. 2014. Polyphyly, gene-duplication and extensive allopolyploidy framed the evolution of the ephemeral *Vulpia* grasses and other fine-leaved Loliinae (Poaceae). *Molecular Phylogenetics and Evolution* 79: 92–105.
- Donadio S, Giussani LM, Kellogg EA, Zuloaga FO, Morrone O. 2009. A preliminary molecular phylogeny of *Pennisetum* and *Cenchrus* (Poaceae-Paniceae) based on the *trnL-F*, *rpl16* chloroplast markers. *Taxon* 58: 392–404.
- El-Alfy TS, Ezzat SM, Sleem AA. 2010. Chemical and biological study of the seeds of *Eragrostis tef* (Zucc.) Trotter. *Natural Product Research* 26: 612–629.
- Essi L, Longhi-Wagner HM, Souza-Chies TT. 2008. Phylogenetic analysis of the *Briza* complex (Poaceae). *Molecular Phylogenetics and Evolution* 47: 1018–1029.
- Essi L, Longhi-Wagner HM, Souza-Chies TT. 2011. New combinations within the *Briza* complex (Poaceae, Pooideae, Poaeae). *Novon* 21: 326–330.
- Essi L, Souza-Chies TT, Longhi-Wagner HM. 2010. Three new taxa of *Chascolytrum* (Poaceae, Pooideae, Poaeae) from South America. *Novon* 20: 149–156.
- Estep MC, KcKain MR, Diaz DV, Zhong J, Hodge JG, Hodkinson TR, Layton DJ, Malcomber ST, Pasquet R, Kellogg EA. 2014. Allopolyploidy, diversification, and the Miocene grassland expansion. *Proceedings of the National Academy of Sciences USA* 111: 15149–15154.
- Gillespie LJ, Soreng RJ, Paradis M, Bull RD. 2010. Phylogeny and reticulation in subtribe Poinae and related subtribes (Poaceae) based on nrITS, ETS, and *trnTLF* data. In: Seberg O, Petersen G, Barfod AS, David JI eds. *Diversity, phylogeny, and evolution in the monocotyledons*. Aarhus: Aarhus University Press. 589–618.
- Grass Phylogeny Working Group (GPWG). 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden* 88: 373–457.
- Grass Phylogeny Working Group (GPWG II). 2012. New grass phylogeny resolves deep evolutionary relationships and discovers  $C_4$  origins. *New Phytologist* 193: 304–312.
- Hilu KW, Alice LA. 2001. A phylogeny of Chloridoideae (Poaceae) based on *matK* sequences. *Systematic Botany* 26: 386–405.
- Hiratsuka J, Shimada H, Whittier R, Ishibashi T, Sakamoto M, Mori M, Kondo C, Honji Y, Sun CR, Meng BY, Li YQ, Kanno A, Nishizawa Y, Hirai A, Shinozaki K, Sugiura M. 1989. The complete sequence of the rice (*Oryza sativa*) chloroplast genome intermolecular recombination between distinct tRNA genes accounts for a major plastid DNA inversion during the evolution of the cereals. *Molecular and General Genetics* 217: 185–194.
- Hitchcock AS. 1935. Manual of Grasses of the United States. *US Department of Agriculture Miscellaneous Publication* 200: 1–1040.
- Hitchcock AS, Chase A. 1951. Manual of Grasses of the United States (revised). *US Department of Agriculture Miscellaneous Publication* 200: 1–1051.
- Hodkinson TR, Chase MW, Lledo MD, Salamin N, Renvoize SA. 2002. Phylogenetics of *Miscanthus*, *Saccharum* and related genera (Saccharinae, Andropogoneae, Poaceae) based on DNA sequences from ITS nuclear ribosomal DNA and plastid *trnL* intron and *trnL-F* intergenic spacers. *Journal of Plant Research* 115: 381–392.
- Inda LA, Segarra-Moragues JG, Mueller J, Peterson PM, Catalán P. 2008. Dated historical biogeography of the temperate Loliinae (Poaceae, Pooideae) grasses in the northern and southern hemispheres. *Molecular Phylogenetics and Evolution* 46: 932–957.
- Ingram AL, Doyle JJ. 2004. Is *Eragrostis* (Poaceae) monophyletic? Insights from nuclear and plastid sequence data. *Systematic Botany* 29: 545–552.
- Judziewicz EJ, Soreng RJ, Davidse G, Peterson PM, Filgueiras TS, Zuloaga FO. 2000. Catalogue of New World grasses (Poaceae): I. subfamilies Anomochlooideae, Bambusoideae, Ehrhartoideae, and Pharoideae. *Contributions from the United States National Herbarium* 39: 1–128.

- Linder HP. 2005. Evolutionary history of Poales. *Annual Review of Ecology and Systematics* 36: 107–124.
- Linder HP, Baeza CM, Barker NP, Galley C, Humphreys AM, Lloyd KM, Orlovich DA, Pirie MD, Simon BK, Walsh N, Verboom GA. 2010. A generic classification of the Danthonioideae (Poaceae). *Annals of the Missouri Botanical Garden* 97: 306–364.
- Linder HP, Verboom GA, Barker NP. 1997. Phylogeny and evolution in the Crinipes group of grasses (Arundinoideae: Poaceae). *Kew Bulletin* 52: 91–110.
- Link HF. 1827. Classis I. Endogeneae. Divisio I. Paralleinerviae. Ordo I. Gramineae. Ordo II. Cyperoideae. *Hortus Regius Botanicus Berolinensis* 1: 1–274.
- Liu Q, Jiang B, Wen J, Peterson PM. 2014a. Low-copy nuclear gene McGISH resolves polyploid history of *Eleusine coracana* and morphological character evolution in *Eleusine*. *Turkish Journal of Botany* 38: 1–12.
- Liu Q, Liu H, Wen J, Peterson PM. 2014b. Infrageneric phylogeny and temporal divergence of *Sorghum* (Andropogoneae, Poaceae) based on low-copy nuclear and plastid sequences. *PLoS ONE* 9: 1–14.
- Liu Q, Triplett JK, Wen J, Peterson PM. 2011. Allotetraploid origin and divergence in *Eleusine* (Chloridoideae, Poaceae): evidence from low-copy nuclear gene phylogenies and a plastid gene chronogram. *Annals of Botany* 108: 1287–1298.
- Michelangeli FA, Davis JI, Stevenson DW. 2003. Phylogenetic relationships among Poaceae and related families as inferred from morphology, inversions in the plastid genome, and sequence data from the mitochondrial and plastid genomes. *American Journal of Botany* 90: 93–106.
- Morrone O, Aagesen L, Scataglini MA, Salarato DL, Denham SS, Chemisquy MA, Sede SM, Giussani LM, Kellogg EA, Zuloaga FO. 2012. Phylogeny of the Paniceae (Poaceae: Panicoideae): integrating plastid DNA sequences and morphology into a new classification. *Cladistics* 28: 333–356.
- Morrone O, Denham SS, Aliscioni SS, Zuloaga FO. 2008. *Parodiophylloclhoa*, a new genus segregated from *Panicum* (Paniceae, Poaceae) based on morphological and molecular data. *Systematic Botany* 33: 66–76.
- Morrone O, Scataglini MA, Zuloaga FO. 2007. *Cyphonanthus*, a new genus segregated from *Panicum* (Poaceae: Panicoideae: Paniceae) based on morphological, anatomical and molecular data. *Taxon* 56: 521–532.
- Oliveira RP, Clark LG, Schnadelbach AS, Monteiro SHN, Borba EL, Longhi-Wagner HM, Van den Berg C. 2014. A molecular phylogeny of *Raddia* and its allies within the tribe Olyreae (Poaceae, Bambusoideae) based on noncoding plastid and nuclear spacers. *Molecular Phylogenetics and Evolution* 78: 105–117.
- Peterson PM, Romaschenko K, Barker NP, Linder HP. 2011. Centropodieae and *Ellisochloa*, a new tribe and genus in Chloridoideae (Poaceae). *Taxon* 60: 1113–1122.
- Peterson PM, Romaschenko K, Herrera Arrieta Y. 2014a. A molecular phylogeny and classification of the Cteniinae, Farragininae, Gouiniinae, Gymnopogoninae, Perotidinae, and Trichoneurinae (Poaceae: Chloridoideae: Cynodonteae). *Taxon* 63: 275–286.
- Peterson PM, Romaschenko K, Herrera Arrieta Y. 2015. A molecular phylogeny and classification of the Eleusininae with a new genus, *Microachne* (Poaceae: Chloridoideae: Cynodonteae). *Taxon* 64: in press.
- Peterson PM, Romaschenko K, Herrera Arrieta Y, Saarela J. 2014b. A molecular phylogeny and new subgeneric classification of *Sporobolus* (Poaceae: Chloridoideae: Sporobolinae). *Taxon* 63: 1212–1243.
- Peterson PM, Romaschenko K, Johnson G. 2010a. A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. *Molecular Phylogenetics and Evolution* 55: 580–598.
- Peterson PM, Romaschenko K, Johnson G. 2010b. A phylogeny and classification of the Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae) based on plastid and nuclear DNA sequences. *American Journal of Botany* 97: 1532–1554.
- Peterson PM, Romaschenko K, Snow N, Johnson G. 2012. A molecular phylogeny and classification of *Leptochloa* (Poaceae: Chloridoideae: Chloridoideae) sensu lato and related genera. *Annals of Botany*, n.s. Oxford 109: 1317–1329.
- Peterson PM, Romaschenko K, Soreng RJ. 2014c. A laboratory guide for generating DNA barcodes in grasses: a case study of *Leptochloa* s.l. (Poaceae: Chloridoideae). *Webbia* 69: 1–12.
- Peterson PM, Soreng RJ, Davidse G, Filgueiras TS, Zuloaga FO, Judziewicz EJ. 2001. Catalogue of New World grasses (Poaceae): II. subfamily Chloridoideae. *Contributions from the United States National Herbarium* 41: 1–255.
- Phillips SP. 1995. Flora of Ethiopia and Eritea. Addis Ababa, Ethiopia: The National Herbarium, Biology Department, Addis Ababa University and Department of Systematic Botany, Uppsala University.
- Pirie MD, Humphreys AM, Galley C, Barker NP, Verboom GA, Orlovich DA, Draffin SJ, Lloyd KM, Baeza CM, Negritto M, Ruiz E, Sánchez Cota JH, Reimer E, Linder HP. 2008. A novel supermatrix approach improves resolution of phylogenetic relationships in a comprehensive sample of danthonioid grasses. *Molecular Phylogenetics and Evolution* 48: 1106–1119.
- Quintanar A, Castroviejo Bolibar S, Catalán P. 2007. Phylogeny of the tribe Aveneae (Pooideae, Poaceae) inferred from plastid *trnT-F* and nuclear ITS sequences. *American Journal of Botany* 94: 1554–1569.
- Quintanar A, Catalán P, Castroviejo S. 2010. A review of the systematics and phylogenetics of the Koeleriinae (Poaceae: Poaceae). In: Seberg O, Petersen G, Barfod AS, Davis JI eds. *Diversity, phylogeny, and evolution in the monocotyledons*. Aarhus: Aarhus University Press. 511–538.
- Rambaut A. 2006–2014. Tree Figure Drawing Tool, version 1.4.2, Institute of Evolutionary Biology, University of Edinburgh [online]. Available from <http://tree.bio.ed.ac.uk/software/figtree/> [accessed 10 February 2015].
- Reveal JL. 2015. Nominum Supragenericorum Plantarum Vascularium [online]. Available from <http://www.plantsystematics.org/reveal/pbio/WWW/supragen.html> [accessed 12 February 2015].
- Romaschenko K, Garcia-Jacas N, Peterson PM, Soreng RJ, Vilatersana R, Susanna A. 2014. Miocene–Pliocene speciation, introgression, and migration of *Patis* and *Ptilagrostis* (Poaceae: Stipeae). *Molecular Phylogenetics and Evolution* 70: 244–259.
- Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Futorna O, Susanna A. 2008. Molecular phylogenetic analysis of the American Stipeae (Poaceae) resolves *Jarava* sensu lato polyphyletic: evidence for a new genus, *Pappostipa*. *Journal of the Botanical Research Institute of Texas* 2: 165–192.
- Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Futorna O, Susanna A. 2012. Systematics and evolution of the needle grasses (Poaceae: Pooideae: Stipeae) based on analysis of multiple chloroplast loci, ITS, and lemma micromorphology. *Taxon* 61: 18–44.
- Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Susanna A. 2010. Phylogenetics of Stipeae (Poaceae: Pooideae) based on plastid and nuclear DNA sequences. In: Seberg O, Petersen G,



- Barfod AS, Davis JI eds. *Diversity, phylogeny, and evolution in the monocotyledons*. Aarhus: Aarhus University Press. 511–538.
- Saarela JM, Liu Q, Peterson PM, Soreng RJ, Paszko B. 2010. Phylogenetics of the grass 'Aveneae-type plastid DNA clade'. In: Seberg O, Petersen G, Barfod AS, Davis JI eds. *Diversity, phylogeny, and evolution in the monocotyledons*. Aarhus: Aarhus University Press. 557–588.
- Saarela JM, Peterson PM, Keane RM, Cayouette J, Graham SW. 2007. Molecular phylogenetics of *Bromus* (Poaceae: Pooideae) based on chloroplast and nuclear DNA sequence data. *Aliso* 23: 450–467.
- Saarela JM, Peterson PM, Soreng RJ, Chapman R. 2003. A taxonomic revision of the eastern North American and eastern Asian disjunct genus *Brachyelytrum* (Poaceae): Evidence from morphology, phytogeography and AFLPs. *Systematic Botany* 28: 674–692.
- Saarela JM, Peterson PM, Valdés-Reyna J. 2014. A taxonomic revision of *Bromus* (Poaceae: Pooideae: Bromeae) in Mexico and Central America. *Phytotaxa* 185: 1–147.
- Salariato DL, Zuloaga FO, Giussani LM, Morrone O. 2010. Molecular phylogeny of the subtribe Melinidinae (Poaceae: Panicoideae: Paniceae) and evolutionary trends in the homogenization of inflorescences. *Molecular Phylogenetics and Evolution* 56: 355–369.
- Sánchez-Ken JG, Clark LG. 2007. Phylogenetic relationships within the Centothecoideae+Panicoideae clade (Poaceae) based on *ndhF* and *rpl16* intron sequences and structural data. *Aliso* 23: 487–502.
- Sánchez-Ken JG, Clark LG. 2010. Phylogeny and a new tribal classification of the Panicoideae s.l. (Poaceae) based on plastid and nuclear sequence data and structural data. *American Journal of Botany* 97: 1732–1748.
- Sánchez-Ken JG, Clark LG, Kellogg EA, Kay EE. 2007. Reinstatement and emendation of subfamily Micrairoideae (Poaceae). *Systematic Botany* 32: 71–80.
- Scataglini MA, Aliscioni S, Zuloaga FO, Giussani LM, Denham SS, Morrone O. 2014a. Phylogeny of New World *Paspalum* (Poaceae, Panicoideae, Paspaleae) based on plastid and nuclear markers. *Plant Systematics and Evolution* 300: 1051–1070.
- Scataglini MA, Lizarazu MA, Zuloaga FO. 2014b. A peculiar amphitropical genus of Paniceae (Poaceae, Panicoideae). *Systematic Botany* 39: 1108–1119.
- Scataglini MA, Zuloaga FO. 2014. *Morronea*, a new genus segregated from *Panicum* (Paniceae, Poaceae) based on morphological and molecular data. *Systematic Botany* 38: 1076–1086.
- Schneider J, Winterfeld G, Hoffmann MH, Röser M. 2011. Duthieae, a new tribe of grasses (Poaceae) identified among the early diverging lineages of subfamily Pooideae: Molecular phylogenetics, morphological delineation, cytogenetics and biogeography. *Systematics and Biodiversity* 9: 27–44.
- Seberg O, Petersen G. 2007. Phylogeny of Triticeae (Poaceae) based on three organelle genes, two single-copy nuclear genes, and morphology. *Aliso* 23: 362–371.
- Sede SM, Escobar A, Morrone O, Zuloaga FO. 2010. Chromosome studies in American Paniceae (Poaceae, Panicoideae). *Annals of the Missouri Botanical Garden* 97: 128–138.
- Sede SM, Morrone O, Aliscioni SS, Giussani LM, Zuloaga FO. 2009a. *Oncorhachis* and *Sclerochlamys*, two new segregated genera from *Streptostachys* (Poaceae, Panicoideae, Paniceae): A revision based on molecular, morphological and anatomical characters. *Taxon* 58: 365–374.
- Sede SM, Zuloaga FO, Morrone O. 2009b. Phylogenetic studies in the Paniceae (Poaceae-Panicoideae): *Ocellochloa*, a new genus from the New World. *Systematic Botany* 34: 684–692.
- Sha L-N, Fan X, Zhang H-Q, Kang H-Y, Wang Y, Wang X-L, Zhang L, Ding C-B, Yang R-W, Zhou Y-H. 2014. Phylogenetic relationships in *Leymus* (Triticeae; Poaceae) evidence from chloroplast *trnH-psbA* and mitochondrial *cox11* intron sequences. *Journal of Systematics and Evolution* 52: 722–734.
- Simon BK. 2014. GrassWorld [online]. Available from <http://grass-world.myspecies.info/> [accessed 2 February 2015].
- Skendzic E, Columbus J, Cerros-Tlatilpa R. 2007. Phylogenetics of Andropogoneae (Poaceae: Panicoideae) based on nuclear ribosomal internal transcribed spacer and chloroplast *trnL-F* sequences. *Aliso* 23: 530–544.
- Soderstrom TR. 1981. The grass subfamily Centothecoideae. *Taxon* 30: 614–616.
- Soderstrom TR, Ellis R. 1987. The position of bamboo genera and allies in a system of grass classification. In: Soderstrom TR, Hilu KW, Campbell CS, Barkworth ME eds. *Grass systematics and evolution*. Washington, DC: Smithsonian Institution Press. 225–238.
- Soreng RJ, Davidse G, Peterson PM, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Morrone O, Romaschenko K. 2014. A World-wide Phylogenetic Classification of the Poaceae (Gramineae): Cão (草), capim, çayır, çimen, darbha, ghaas, ghas, gish, gramas, graminus, gräser, grasses, gyokh, he-ben-ke, hullu, kasa, kusa, nyasi, pastos, pillu, pullu, zlaki, etc. [online]. Available from <http://www.tropicos.org/projectwebportal.aspx?pagename=ClassificationNWG&projectid=10> [accessed 26 January 2015].
- Soreng RJ, Davis JI. 1998. Phylogenetics and character evolution in the grass family (Poaceae): Simultaneous analysis of morphological and chloroplast DNA restriction site character sets. *Botanical Review* 64: 1–85.
- Soreng RJ, Davis JI. 2000. Phylogenetic structure in Poaceae subfamily Pooideae as inferred from molecular and morphological characters: Misclassification versus reticulation. In: Jacobs SWL, Everett J eds. *Grasses: Systematics and evolution*. Melbourne: CSIRO. 61–74.
- Soreng RJ, Davis JI, Doyle JJ. 1990. A phylogenetic analysis of chloroplast DNA restriction site variation in Poaceae subfam. Pooideae. *Plant Systematics and Evolution* 172: 83–97.
- Soreng RJ, Gillespie LJ, Koba H, Boudko K, Bull RD. 2015. Molecular and morphological evidence for a new grass genus, *Dupontiopsis* (Poaceae tribe Poeae subtribe Poinae s.l.), endemic to alpine Japan, and implications for the reticulate origin of *Dupontia* and *Arctophila* within Poinae s.l. *Journal of Systematics and Evolution* 53: 138–162.
- Soreng RJ, Peterson PM, Davidse G, Judziewicz EJ, Zuloaga FO, Filgueiras TS, Morrone O. 2003. Catalogue of New World grasses (Poaceae): IV. subfamily Pooideae. *Contributions from the United States National Herbarium* 48: 1–730.
- Sun GL. 2014. Molecular phylogeny revealed complex evolutionary process in *Elymus* species. *Journal of Systematics and Evolution* 52: 706–711.
- Triplett JK, Clark LG. 2010. Phylogeny of the temperate bamboos (Poaceae: Bambusoideae: Bambuseae) with an emphasis on *Arundinaria* and allies. *Systematic Botany* 35: 102–120.
- Triplett JK, Clark LG, Fisher AE, Wen J. 2014. Independent allopolyploidization events preceded speciation in the temperate and tropical woody bamboos. *New Phytologist* 204: 66–73.
- Triplett JK, Oltrogge KA, Clark LG. 2010. Phylogenetic relationships and natural hybridization among the North American woody bamboos (Poaceae: Bambusoideae: *Arundinaria*). *American Journal of Botany* 97: 471–492.

- Tzvelev N. 1976. *Zlaki SSSR [Grasses of the Soviet Union]*. Leningrad: Nauka Publishers, Leningrad Section.
- Tzvelev N. 1989. The system of grasses (Poaceae) and their evolution. *The Botanical Review* 55: 141–204.
- Van den Borre A, Watson L. 1994. The infrageneric classification of *Eragrostis* (Poaceae). *Taxon* 43: 383–422.
- Vicentini A, Barber JC, Aliscioni SS, Giussani LM, Kellogg EA. 2008. The age of the grasses and clusters of origins of C<sub>4</sub> photosynthesis. *Global Change Biology* 14: 2963–2977.
- Wang RRC, Lu B-R. 2014. Biosystematic and evolutionary relationships of perennial Triticeae species revealed by genomic analyses. *Journal of Systematics and Evolution* 56: 697–705.
- Watson L, Dallwitz M. 1992. *The grass genera of the World*. Cambridge: C.A.B. International.
- Welker CAD, Souza-Chies TT, Longhi-Wagner HM, Peichoto MC, McKain MR, Kellogg EA. 2015. Phylogenetic analysis of *Saccharum* s.l. (Poaceae: Andropogoneae), with emphasis on the circumscription of the South American species. *American Journal of Botany* 102: 248–263.
- Zhang WP. 2000. Phylogeny of the Grass Family (Poaceae) from *rpl16* Intron sequence data. *Molecular Phylogenetics and Evolution* 15: 135–146.
- Zhang H-Q, Yang R-W, Yang C-R, Huang Y, Fan X, Sha L-N, Kang H-Y, Wang Y, Zhou Y-H. 2014. What became of *Hystrix*? *Journal of Systematics and Evolution* 52: 712–715.
- Zuloaga FO, Giussani LM, Morrone O. 2007. *Hopia*, a new monotypic genus segregated from *Panicum* (Poaceae). *Taxon* 56: 145–156.
- Zuloaga FO, Morrone O, Davidse G, Filgueiras TS, Peterson PM, Soreng RJ, Judziewicz EJ. 2003. Catalogue of New World grasses (Poaceae): III. subfamilies Panicoideae, Aristidoideae, Arundinoideae, and Danthoioideae. *Contributions from the United States National Herbarium* 46: 1–662.
- Zuloaga FO, Scataglini MA, Morrone O. 2010. A phylogenetic evaluation of *Panicum* sects. *Agrostoides*, *Megista*, *Prionita* and *Tenera* (Panicoideae, Poaceae): Two new genera, *Stephostachys* and *Sorengia*. *Taxon* 59: 1535–1546.
- Zwickl DJ. 2006. *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Austin: University of Texas.