

TAXONOMIC TREATMENT

Twelve subfamilies are recognized formally in this classification system (Table 1). A description is provided for each subfamily, and where appropriate, synonymy is indicated. To permit easy comparison with previous work, we have listed for each subfamily which of the tribes recognized by Clayton and Renvoize (1986) are to be included. In some cases (e.g. Pharoideae or Danthonioideae), the new circumscription of subfamilies makes tribal recognition largely unnecessary. For example, the subfamily Pharoideae includes three genera in a single tribe; the tribe is effectively redundant, and serves no useful function in the subfamilial classification. Nonetheless we list the names for comparison.

Our sample of taxa was explicitly designed to explore relationships among major clades that can be recognized at the subfamilial level, but it is not dense enough to evaluate tribal limits. We have in many cases combined molecular data from several species to represent a genus (as is also commonly done for morphological analyses), and in a few cases have combined data from several genera that represent a putatively monophyletic group. Such combinations assume, rather than test, monophyly. We therefore refrain from formal discussion of tribal limits, which cannot be addressed by our data; these limits will have to be re-evaluated by future studies. Three tribes and two genera are placed as *Incertae Sedis* at the end of the classification, although the genera may be provisionally placed as noted below.

This classification reflects our attempt to use the phylogeny as the basis for recognizing subfamilies while remaining nomenclaturally conservative. Except for Centothecoideae, all subfamilies recognized are well supported as monophyletic in our analyses. While we could create an unranked classification for the grasses using our phylogeny, we feel that the practical interests of the potential users of this classification currently are best served by retaining the Linnaean hierarchy. Nonetheless we have applied informal names to several of the well-supported clades (see above).

The most significant changes in our proposed subfamily classification are the breakup of the traditional Bambusoideae and Arundinoideae and the expansion of Pooideae. The diversity encompassed by the traditional Bambusoideae (or Bambusoideae s. l.) is now recognized as Anomochlooideae, Pharoideae, Puelioideae, Bambusoideae s. s., and Ehrhartoideae. Elements of the traditional Arundinoideae are now recognized as Aristidoideae, Danthonioideae, and Arundinoideae s. s., with *Thysanolaeneae* placed in the Centothecoideae and *Gynerium* as *Incertae Sedis*. *Centropodia* and *Merxmuellera rangei* are placed in Chloridoideae. Pooideae has grown by inclusion of Brachyelytreae, Lygeae, Nardeae, Phaenospermatidae, Diarrheneae, Stipeae, and Ampelodesmeae, all formerly classified within either Bambusoideae or Arundinoideae by some authors; note, however, that Clayton and Renvoize (1986) placed Lygeae, Nardeae and Stipeae in Pooideae in agreement with the classification proposed here. A detailed comparison of the GPWG classification with other major grass classification systems of this century is presented in Table 1.

Primary sources for suprageneric names were the STAR Database (<http://matrix.nal.usda.gov:8080/star/supragenericname.html>), the Catalog of New World Grasses (<http://mobot.mobot.org/W3T/Search/nwgc.html>), and Clayton and Renvoize (1986). Diagnoses of the subfamilies were extracted from various sources including Clayton and Renvoize (1986) and Watson and Dallwitz (1992). Tribes in Chloridoideae and Panicoideae (except for the exclusion of Eriachneae) follow the treatment of Clayton and Renvoize (1986); tribes listed for the other

subfamilies generally are treated according to more recent studies and/or consultation with specialists in those groups.

Poaceae (R. Br.) Barnh., Bull. Torrey Bot. Club 22: 7. 1895. (nom. alt. Gramineae Juss., Gen. Pl.: 28. 1789.)

A monophyletic family, recognizable by the following synapomorphic characters: Inflorescence highly bracteate. Perianth reduced or lacking. Pollen lacking scrobiculi, but with intraaxinous channels. Seed coat fused to inner ovary wall at maturity, forming a caryopsis. Embryo highly differentiated with obvious leaves, shoot and root meristems, and lateral in position.

I. Anomochloideae Pilg. ex Potz. in Willdenowia 1: 772. 1957. Type: *Anomochloa* Brongn. (Fig. 4C and D)

Syn.: Streptochoaetoideae (Nakai) Butzin, Neue Unters. Blüte Gram.: 148. 1965.

Plants perennial, rhizomatous, herbaceous, of shaded tropical forest understories. Culms hollow or solid. Leaves with phyllotaxis either a distichous or spiral; abaxial ligule absent; adaxial ligule a short fringe of cilia or absent, not membranous; pseudopetioles short to very long, with dark, turgid swellings (pulvini) at both ends (*Anomochloa*) or only at the summit (*Streptochoaeta*); sheaths non-auriculate; blades with parallel venation, usually large and broad. Inflorescences spicate, with complicated branching patterns, bracts outside of the spikelet equivalents present, large and with a blade or small and bladeless. Ultimate structures of the inflorescence (“spikelet equivalents”) of uncertain homology with typical grass spikelets but one-flowered and bisexual; bracts within the spikelet equivalents with phyllotaxis distichous or spiral, lacking uncinata macrohairs, sometimes awned but if so, the awns single; lodicules absent, or, in *Anomochloa*, their position occupied by a ring of short brownish cilia borne on a low membranous ring; stamens 4 or 6; ovary glabrous, apical appendage absent, haustorial synergids presumed absent, style 1, stigma(s) 1 or 3. Caryopsis with the hilum linear, shallow and inconspicuous; endosperm hard, containing compound starch grains; embryo large, epiblast present or not, scutellar cleft present but shallow, mesocotyl internode absent, embryonic leaf margins overlapping or not. Basic chromosome numbers: $x = 11$ or 18 (note: Clark & Judziewicz 1996 erroneously cited these as 12 or 18).

Foliar anatomy. Mesophyll non-radiate, an adaxial palisade layer absent, with fusoid cells very large and well developed, arm cells only weakly developed; kranz anatomy absent; midrib complex; adaxial bulliform cells present.

Foliar micromorphology. Stomata with low dome-shaped and triangular subsidiary cells; bicellular microhairs very large (0.075-0.15 mm), the pointed apical cell usually one and a half times as long as the basally constricted basal cell; papillae absent.

Photosynthetic pathway. Presumed C_3 .

Included tribes:

Anomochloae C. E. Hubb. in Hutchinson, Fam. Fl. Pl. 2: 219. 1934.

Streptochoaetae C. E. Hubb. in Hutchinson, Fam. Fl. Pl. 2: 205. 1934.

Notes. There is no unique morphological synapomorphy for this subfamily, but both tribes lack lodicules and they apparently also lack grass-type spikelets. As noted above (Unresolved

Questions), this lineage may not be monophyletic, in which case two subfamilies would need to be recognized. The subfamily includes 4 species.

II. Pharoideae (Stapf) L. G. Clark & Judz., *Taxon* 45: 643. 1996. Type: *Pharus* P. Browne. Syn.: Leptaspidoideae (Tzvelev) C. O. Morales, *Sendtnera* 5: 244. 1998. Nom. superfl. (Fig. 4B)

Plants perennial, rhizomatous, monoecious, herbaceous, of shaded tropical to warm temperate forest understories. Culms hollow or solid. Leaves distichous; pseudopetiolate, this prominent and twisted, blade resupinate, with lateral nerves diverging obliquely from midnerve and running straight to margins; abaxial ligule absent; adaxial ligule a fringed membrane; sheaths non-auriculate. Inflorescences paniculate, the main axis and branches disarticulating or not, covered with uncinata macrohairs, bracts outside of the spikelets lacking. Spikelets unisexual, one-flowered, mostly in male-female pairs on short branchlets, or some female spikelets solitary. Female spikelets large, short-stalked; glumes 2, shorter than the floret; lemma tubular or inflated, covered wholly or in part by uncinata macrohairs, awnless; palea well developed; lodicules absent; ovary glabrous, apical appendage absent, haustorial synergids presumed absent, style 1, stigmas 3. Caryopsis with the hilum linear, extending the full length; endosperm hard, without lipid; embryo small, epiblast present, scutellar cleft present but shallow, mesocotyl internode absent, embryonic leaf margins overlapping. Male spikelets small, short- to long-stalked, membranous; glumes 2, shorter than the floret; lodicules 3 or 0, if present then minute, elliptic, glabrous, and nerveless; stamens 6. Basic chromosome number: $x = 12$.

Foliar anatomy. Mesophyll non-radiate, an adaxial palisade layer absent, fusoid cells large and well developed, arm cells weakly to moderately well developed; kranz anatomy absent; midrib complex; inflated adaxial interstomatal cells present, bulliform cells poorly developed or absent. Foliar micromorphology. Stomata with parallel-sided to dome-shaped subsidiary cells; bicellular microhairs and papillae absent.

Photosynthetic pathway. Presumed C₃.

Included tribe (now identical to subfamily and thus redundant):

Phareae Stapf in *Thiselton-Dyer*, *Fl. Cap.* 7: 319. 1898.

Notes. In his original description of the tribe, Stapf specifically included *Olyra* (based on its unisexual spikelets), but did not explicitly list *Pharus* or *Leptaspis*, although his choice of the name Phareae implicitly recognized the membership of *Pharus* in the tribe and automatically placed *Pharus* as its type, according to Art. 10.6 of the Code (Greuter et al., 1994). As long as *Olyra* was retained in the same tribe as *Pharus*, Phareae was a superfluous name for the Olyreae. When *Pharus* and *Leptaspis* are segregated into their own tribe, and *Olyra* is excluded, then Phareae becomes the valid, correct name for the tribe. Clark and Judziewicz (1996) based the name of the subfamily on this tribal name. Tzvelev (1989) argued that the name Phareae was illegitimate because the type of the previously described tribe Olyreae was included in it, and provided the name Leptaspidae for this tribe. Morales (1998) agreed with Tzvelev and rejected the name Pharoideae for this subfamily according to Art. 52.1 of the Code (Greuter et al., 1994), replacing it with Leptaspidoideae. Under Art. 52.3, however, "A name that was nomenclaturally superfluous when published is not illegitimate...if it is based on the stem of a legitimate generic name." We therefore accept the name Pharoideae for this subfamily, as *Pharus* is a legitimate generic name. The subfamily includes 12 species.

III. Puelioideae L. G. Clark, M. Kobay., S. Mathews, Spangler & E. A. Kellogg, Syst. Bot. 25: 181-187. 2000. Type: *Puelia* Franch. (Fig. 4A).

Plants perennial, rhizomatous, herbaceous, of shaded rainforest understories. Culms hollow. Leaves distichous, pseudopetiolate; abaxial ligule absent (*Guaduella*) or present (*Puelia*); adaxial ligule a fringed membrane; sheaths non-auriculate. Inflorescences racemose or paniculate, bracts outside of the spikelets sometimes present. Spikelets with two glumes and several florets, the 1-3 proximal florets male, the next several florets female-fertile, with distal incomplete florets (*Guaduella*), or the proximal 3-6 florets male or neuter with the single distal floret female (*Puelia*), disarticulating above the glumes and between the florets (*Guaduella*) or not (*Puelia*); lemmas lacking uncinuate macrohairs, awnless; palea well developed, sometimes tubular; lodicules 3, membranous, ciliate; stamens 6; ovary glabrous or hairy, an apical appendage present or not, haustorial synergids presumed absent, styles 2 or 3, the bases close, stigmas 2 or 3. Caryopsis with a long-linear hilum; embryo small. Basic chromosome number: $x = 12$.

Foliar anatomy. Mesophyll non-radiate, an adaxial palisade layer absent, fusoid cells well developed, arm cells only weakly developed; kranz anatomy absent; midrib complex or less commonly simple; adaxial bulliform cells present.

Foliar micromorphology. Stomata with dome-shaped to triangular subsidiary cells; microhairs absent (*Puelia*) or multicellular, uniseriate microhairs present (*Guaduella*); papillae present or more commonly absent.

Photosynthetic pathway. Presumed C₃.

Included tribes:

Puelieae Soderstr. & R. P. Ellis in Soderstrom et al. (eds.), Grass Syst. Evol.: 238. 1987.

Guaduelleae Soderstr. & R. P. Ellis in Soderstrom et al. (eds.), Grass Syst. Evol.: 238. 1987.

Notes. This subfamily, which comprises approximately 14 species, is poorly known and morphological, anatomical, cytological, and ecological studies are needed.

IV. Bambusoideae Luer., Grundz. Bot., ed. 5: 451. 1893. Type: *Bambusa* Schreb.

Syn.: Olyroideae Pilger, Nat. Pfl.-Fam. ed. 2, 14d: 168. 1956. (Fig. 4F)

Parianoideae (Nakai) Butzin, Neue Unters. Blüte Gram.: 148. 1965.

Plants perennial (rarely annual), rhizomatous herbaceous or woody, of temperate and tropical forests, tropical high montane grasslands, riverbanks, and sometimes savannas. Culms hollow or solid. Leaves distichous, pseudopetiolate; abaxial ligule absent (Olyreae) or present (Bambuseae); adaxial ligule membranous or chartaceous, fringed or unfringed; sheaths often auriculate. Inflorescences spicate, racemose or paniculate, completing development of all spikelets in one period of growth and subtending bracts and prophylls usually absent, or pseudospikelets with basal bud-bearing bracts producing two or more orders of spikelets with different phases of maturity and subtending bracts and prophylls usually present. Spikelets (or spikelets proper of the pseudospikelets) bisexual (Bambuseae) or unisexual (Olyreae), consisting of 0, 1, 2 or several glumes, one to many florets; lemma lacking uncinuate macrohairs, if awned, the awns single; palea well developed; lodicules usually 3 (rarely 0 to 6 or many), membranous, vascularized, often

ciliate; stamens usually 2, 3, or 6 (10-40 in *Pariana*, 6-120 in *Ochlandra*); ovary glabrous or hairy, sometimes with an apical appendage, haustorial synergids absent, styles 2 or 3, sometimes very short but close, stigmas (1-) 2 or 3. Caryopsis with hilum linear (or rarely punctate), extending its full length (or rarely less than full length); endosperm hard, without lipid, containing compound starch grains; embryo small, not waisted, epiblast present, scutellar cleft present, mesocotyl internode absent, embryonic leaf margins overlapping. Basic chromosome numbers: $x = 7, 9, 10, 11,$ and 12.

Foliar anatomy. Mesophyll non-radiate, an adaxial palisade layer absent, fusoid cells large and well developed, arm cells usually well developed and strongly invaginated; kranz anatomy absent; midrib complex or simple; adaxial bulliform cells present.

Foliar micromorphology. Stomata with dome-shaped, triangular, or parallel-sided subsidiary cells; bicellular microhairs present, panicoid-type; papillae common and abundant.

Photosynthetic pathway. C_3 .

Included tribes:

Bambuseae Dumort., Anal. Fam. Pl.: 63. 1829.

Olyreae Kunth ex Spenn., Fl. Friburg. 1: 172. 1825. (including *Buergersiochloae* Blake, *Blumea*, Suppl. 3: 62. 1946; *Parianeae* C. E. Hubbard in Hutch., Fam. Fl. Pl. 2: 219. 1934.)

Notes. The current circumscription of this subfamily is much narrower than the traditional view. In their recent analysis, Zhang and Clark (2000) recovered two robustly supported clades, the olyroid bamboos and the woody bamboos, which they recognized as tribes *Olyreae* and *Bambuseae*, respectively. Following Zhang and Clark (2000), *Buergersiochloae* and *Parianeae* are included in *Olyreae*. This subfamily includes approximately 1,200 species.

V. Ehrhartoideae Link, Hort. Berol. 1: 233. 1827. Type: *Ehrharta* Thunb.

Syn.: *Oryzoideae* Kunth ex Beilschm., Flora 16(2): 52, 109. 1833. (Fig. 4G)

Plants annual or perennial (rhizomatous or stoloniferous), herbaceous to suffrutescent, of forests, open hillsides, or aquatic habitats. Culms hollow or solid. Leaves distichous, sometimes pseudopetiolate, rarely basally cordate or sagittate (*Phyllorachideae*); abaxial ligule absent; adaxial ligule a fringed or unfringed membrane, or a fringe of hairs; sheaths sometimes bearing auricles. Inflorescences paniculate or racemose, bracts outside of the spikelets rarely present

(*Humbertochloa*). Spikelets bisexual or unisexual, with glumes 2 (absent in some *Oryzeae*), sterile florets 0 to 2, and female-fertile floret 1, disarticulating above the glumes or infrequently primary branches disarticulating as units; lemma lacking uncinulate macrohairs, if awned, the awn single; palea well developed; lodicules 2, membranous or rarely fleshy, heavily vascularized; stamens usually 3 or 6 (sometimes 1, 2, or 4); ovary glabrous, apical appendage absent, haustorial synergids absent, styles 2, free, fused basally or for their full length (*Zizaniopsis*), close, stigmas 2.

Caryopsis with the hilum long-linear; endosperm hard, without lipid, containing compound starch grains (rarely simple); embryo small, waisted or not, epiblast usually present (absent in *Ehrharta*), scutellar cleft usually present (absent in *Leersia* and *Potamophila*), mesocotyl internode absent (present but short in *Microlaena*), embryonic leaf usually with overlapping margins (meeting in *Potamophila*). Basic chromosome numbers: $x = 12$ (10 in *Microlaena*; 15 in *Zizania*).

Foliar anatomy. Mesophyll nonradiate, an adaxial palisade layer usually absent, fusoid cells absent or sometimes present (*Zizania* and *Zizaniopsis*), arm cells absent or present; kranz anatomy absent; midrib simple or complex; adaxial bulliform cells present.

Foliar micromorphology. Stomata with dome-shaped or triangular subsidiary cells; bicellular microhairs present, panicoid-type; papillae often present in Oryzeae, otherwise absent. Photosynthetic pathway. C_3 .

Included tribes:

- Ehrharteae Nevski, Trudy Bot. Inst. Akad. Nauk SSSR 4: 227. 1937.
- Oryzeae Dumort., Observ. Gramin. Belg.: 83. 1824.
- Phyllorachideae C. E. Hubb. in Hook. Ic. Pl. 34: t 3386, p. 5. 1939.

Notes. Although we did not sample Phyllorachideae, we place it here based on morphological similarity. Nonetheless, any future studies of this clade should include this tribe to test its relationship to Ehrharteae and Oryzeae. Under the present circumscription, this subfamily includes approximately 120 species.

VI. Pooideae Benth., Fl. Hongk. 407. 1861. Type: *Poa* L. (Fig. 4E and H)

Syn.: Agrostidoideae Kunth ex Beilschm., Flora (Beib.) 16(2): 52, 104. 1833.

Anthoxanthoideae Link, Hort. Berol. 1: 232, 271. 1827.

Avenoideae Link, Hort. Berol. 1: 108. 1827.

Cynosuroideae Link, Hort. Berol. 1: 198. 1827.

Echinarioideae Link, Hort. Berol. 1: 197. 1827.

Festucoideae Link, Hort. Berol. 1: 137. 1827.

Glycerioideae Link, Hort. Berol. 1: 160. 1827.

Hordeoideae Burmeist., Handb. Naturgesch. 202. 1837.

Phalaroideae Burmeist., Handb. Naturgesch. 208. 1837.

Secaloideae Rouy, Fl. France 14: 2, 298. 1913.

Stipoideae Burmeist., Handb. Naturgesch. 199. 1837.

Plants annual or perennial (rhizomatous, stoloniferous, or neither), herbaceous, of cool temperate and boreal regions, extending across the tropics in the high mountains. Culms hollow (rarely solid). Leaves distichous, rarely pseudopetiolate (*Phaenosperma*); abaxial ligule absent; adaxial ligule scarious or membranous, the margin not or infrequently short ciliate fringed (rarely long ciliate, *Anisopogon*); sheaths sometimes auriculate. Inflorescences spicate, racemose, or paniculate, bracts outside of the spikelets lacking or rarely present (*Sesleria*, *Echinaria*, *Ammochloa*). Spikelets bisexual, infrequently unisexual or mixed, usually with two glumes (rarely without glumes, *Lygeum*, or the first absent, *Hainardia*, *Lolium*, *Nardus*, except on terminal florets), 1-many female-fertile florets with apical or infrequently basal reduction, compressed laterally, infrequently not or dorsally compressed, disarticulating above the glumes (infrequently below the glumes, some Poeae, or at the nodes of the inflorescence, various genera); lemma lacking uncinat macrohairs, if awned, the awn single; palea usually present and well developed, but variable and sometimes very reduced or absent; lodicules 2 (rarely 3, *Anisopogon*, *Ampelodesmeae*, many *Stipeae* and few *Poeae*; fused, *Meliceae*; rarely absent, *Lygeum*, *Nardus*, and few *Poeae*), usually lanceolate, broadly membranous apically (fleshy, truncate, *Meliceae*), often lobed (*Triticeae*, *Poeae*), obscurely few-nerved, or infrequently more or less distinctly few-nerved, not or conspicuously ciliate on the margins; stamens usually 3 (infrequently 1-2); ovary glabrous or pubescent, rarely with an apical appendage (*Bromus*, *Diarrhena*), haustorial synergids absent, styles usually 2, close, stigmas 2 (rarely 1, *Lygeum*, *Nardus*, and a few others, or 3, scattered genera). Caryopsis with the hilum linear and up to as long as the fruit, or basal and

punctiform, linear, ellipsoidal, ovate, or circular and less than 1/3 the length of the fruit; endosperm hard or sometimes soft or liquid (some Poeae), with or without lipids (some Poeae), containing compound starch grains, or simple starch grains (Brachyelytreae, Bromeae, Triticeae, some Stipeae); embryo small, not waisted, epiblast present (rarely absent), scutellar cleft absent (rarely present, but not deeply incised), mesocotyl internode absent (rarely short, *Brachyelytrum*), embryonic leaf margins meeting (infrequently margins overlapping). Basic chromosome numbers: $x = 7$ (Bromeae, Triticeae, Poeae generally, few Brachypodieae), 2, 4, 5, 6, 8, 9, 10, 11, 12, 13 represented in a few Poeae and the other tribes, generally medium or large.

Foliar anatomy. Mesophyll nonradiate, an adaxial palisade layer absent, fusoid cells absent, arm cells absent; kranz anatomy absent; midrib simple; adaxial bulliform cells present.

Foliar micromorphology. Stomata with parallel-sided subsidiary cells; bicellular microhairs absent (rarely present, *Lygeum*, where chloroid, *Nardus*, where panicoid), unicellular microhairs absent (rarely present, few Stipeae); papillae usually absent, when present rarely more than one per long cell.

Photosynthetic pathway. C₃.

Included tribes:

- Brachyelytreae Ohwi, Bot. Mag. Tokyo 55: 361. 1941.
- Nardeae W. D. J. Koch, Syn. Fl. Germ. Helv.: 830. 1837.
- Lygeae J. Presl, Wsobecny Rostl. 2: 1708, 1753. 1846.
- Phaenospermatideae Renvoize & Clayton, Kew Bull. 40: 478. 1985.
- Meliceae Link ex Endl., Fl. Poson.: 116. 1830.
- Diarrheneae (Ohwi) C. S. Campb., J. Arn. Arb. 66: 188. 1985.
- Stipeae Dumort., Observ. Gramin. Belg.: 83. 1824.
- Ampelodesmeae (Conert) Tutin, Bot. J. Linn. Soc. 76: 369. 1978.
- Bromeae Dumort., Observ. Gramin. Belg.: 83. 1824.
- Brachypodieae (Hack.) Hayek, Oesterr. Bot. Z. 74(10): 253. 1925.
- Triticeae Dumort., Observ. Gramin. Belg.: 82, 84, 91. 1824.
- Brylkinieae Tateoka, Canad. J. Bot. 38: 962. 1960.
- Poeae R. Br., Voy. Terra Austral. 2: 582. 1814. (including Aveneae Dumort., Observ. Gramin. Belg.: 82. 1824.; Agrostideae Dumort., Observ. Gramin. Belg.: 83. 1824.)

Notes. Relationships among some of the major lineages of the core Pooideae clade remain unresolved, and conflicts between molecular data and morphologically based tribal classifications exist (e.g., Poeae vs. Aveneae); this is one of several reasons that we do not offer a formal classification of tribes at this point. Relationships among the earlier diverging lineages of the whole pooid clade are only weakly supported, and also require further investigation. The tribal classification presented here is almost certain to change as additional data accumulate, and thus should be taken only as an indication of the taxa included within the subfamily. The subfamily includes approximately 3,300 species.

VII. Aristidoideae Caro, Dominguezia 4: 16. 1982. Type: *Aristida* L. (Fig. 5C)

Plants annual or perennial, caespitose, herbaceous, xerophytic or less commonly mesophytic, of temperate, subtropical and tropical zones, often in open habitats. Culms solid or hollow. Leaves distichous, without pseudopetioles; abaxial ligule absent or present as a line of hairs; adaxial ligule

a fringed membrane or a fringe of hairs; sheaths non-auriculate. Inflorescences paniculate, bracts outside of the spikelets absent. Spikelets with bisexual florets, glumes 2, female-fertile floret 1, and no rachilla extension, cylindrical or laterally compressed, disarticulating above the glumes; lemmas with three awns, the awns separate from each other, or fused below into a twisted column; palea short, less than half the lemma length; lodicules present or rarely absent, when present 2, free, membranous, glabrous, heavily vascularized; stamens 1-3; ovary glabrous, apical appendage absent, haustorial synergids absent, styles 2, free, close, stigmas 2. Caryopsis with the hilum short or long-linear; endosperm hard, without lipid, containing compound starch grains; embryo small (*Sartidia*) or large (*Aristida*, *Stipagrostis*), waisted or not waisted, epiblast absent, scutellar cleft present or absent (*Sartidia*), mesocotyl internode elongated, embryonic leaf margins meeting. Basic chromosome numbers: $x = 11, 12$.

Foliar anatomy. Mesophyll radiate or non-radiate (*Sartidia*), an adaxial palisade layer absent, fusoid cells absent, arm cells absent; kranz anatomy absent (*Sartidia*) or present (*Stipagrostis*, *Aristida*), when present with one (*Stipagrostis*) or two (*Aristida*) parenchyma sheaths, although both not equally well-developed throughout the genus; midrib simple; adaxial bulliform cells present.

Foliar micromorphology. Stomata dome-shaped or triangular; bicellular microhairs present, panicoid-type; papillae absent.

Photosynthetic pathway. C_3 (*Sartidia*); C_4 (*Aristida*, NADP-ME; *Stipagrostis*, not biochemically typed, but anatomically NAD-ME; Hattersley and Watson, 1992)

Included tribe (now identical to the subfamily and thus redundant):

Aristideae C. E. Hubbard in Bor, Grasses Burma Ceylon India Pakistan: 685. 1960.

Notes. The presence of a basal column of the awn is a potential morphological synapomorphy for this clade. *Sartidia* diverges from *Stipagrostis* and *Aristida* in other respects, and should be sampled in future analyses. The subfamily includes approximately 350 species.

VIII. Arundinoideae Burmeist., Handb. Naturgesch.: 204. 1837. Type: *Arundo* L. (Fig. 5A)
Syn.: Phragmitoideae Parodi ex Caro, Dominguezia 4: 13. 1982.

Plants perennial (rarely annual), rhizomatous, stoloniferous, or caespitose, herbaceous to somewhat woody, of temperate and tropical areas, mesophytic or xerophytic, the reeds found in marshy habitats. Culms hollow or less commonly solid. Leaves distichous, without pseudopetioles; abaxial ligule absent or rarely present as a line of hairs (*Hakonechloa*); adaxial ligule a fringed or unfringed membrane or a fringe of hairs; sheaths usually non-auriculate. Inflorescences usually paniculate, rarely spicate or racemose, bracts outside of the spikelets absent. Spikelets with bisexual florets, glumes 2, a sterile lemma sometimes present, female-fertile florets 1-several, apical reduction usually present, usually laterally compressed, disarticulating above the glumes; lemma lacking uncinuate macrohairs, if awned, awn usually single, sometimes awns three, but then lacking a basal column; palea usually well developed; lodicules 2, free (rarely joined at the base), fleshy, glabrous or infrequently ciliate, not or scarcely vascularized to heavily vascularized; stamens (1-) 3; ovary glabrous, apical appendage absent, haustorial synergids absent, styles 2, usually free, close, stigmas 2. Caryopsis with the hilum short or long-linear (*Molinia*); endosperm hard, without lipid, containing compound starch grains; embryo large or small (*Amphipogon*), waisted or not, epiblast absent, scutellar cleft present, mesocotyl internode elongated, embryonic leaf margins meeting or overlapping (*Hakonechloa*). Basic chromosome numbers: $x = 6, 9, 12$.

Foliar anatomy. Mesophyll non-radiate or rarely radiate (*Arundo*, *Amphipogon*), without an adaxial palisade layer, without fusoid cells, arm cells absent or present (*Phragmites*); kranz anatomy absent; midrib simple; adaxial bulliform cells present.

Foliar micromorphology. Stomata with low dome-shaped or triangular subsidiary cells; bicellular microhairs present or less commonly absent, when present of panicoid-type except in *Amphipogon*, which has unique microhair morphology; papillae absent except in *Amphipogon*.

Photosynthetic pathway. C₃.

Included tribe (now identical to subfamily and thus redundant):

Arundineae Dumort., Obs. Gram. Belg.: 82. 1824.

Notes. The traditional Arundinoideae was well known as a dustbin group (e.g., Clayton & Renvoize 1986; Kellogg & Campbell 1987). A number of studies indicated that this subfamily as traditionally circumscribed was polyphyletic (e.g., Barker et al. 1995; Clark et al. 1995) although some support for a monophyletic Arundinoideae (including Arundinoideae s. s., Danthonioideae, Aristidoideae, *Micraira* and *Eriachne*) was found by Hsiao et al. (1999). The results of the combined analysis presented here suggest that a monophyletic core arundinoid group does exist, even though individual data sets do not strongly support the group. The exact generic membership of the subfamily remains to be determined, however, we include the following genera:

Amphipogon, *Arundo*, *Dregeochloa*, *Hakonechloa*, *Molinia* (and *Moliniopsis* if recognized), and *Phragmites*. We provisionally place the crinipoid group (*Crinipes*, *Dichaetaria*, *Elytrophorus*, *Leptagrostis*, *Nematopoa*, *Piptophyllum*, *Styppeiachloa*, and *Zenkeria*) here as well, based on molecular evidence from Linder et al. (1997) and Barker (1997), but further study of this group is needed. No morphological synapomorphies have been identified to support the monophyletic arundinoid clade, although Linder et al. (1997) linked *Arundo*, *Phragmites* and *Molinia* by the presence of hollow culm internodes, a punctiform hilum, and convex adaxial rib sides in the leaf blade. This subfamily clearly requires further study. The subfamily includes 33-38 species, counting the crinipoids.

IX. Danthonioideae Barker & Linder, subfam. nov. Type: *Danthonia* DC. (Fig. 5F)

DIAGNOSIS

Distinct from the other subfamilies of the grasses by the haustorial synergids, and by the conjunction of a ciliate ligule, the presence of an embryo mesocotyl, a several flowered spikelet, which, if 1-2 flowered, has a rachilla extension, usually distinctly separated style bases, the absence of Kranz anatomy and the absence of chloridoid microhairs.

Collaboratore haustorio, et ligulis ciliatis, atque mesocotyle embryonis presente, atque spiculis floribus pluribus sic floribus 1-2 nunc rhachillis extensis, atque plerumque basibus stylosum distantibus, atque anatomia "Kranz" et micropilis chloridis nullis a subfamilis graminis bene distincta.

Plants perennial (caespitose, rhizomatous or stoloniferous) or less commonly annual, herbaceous or rarely suffrutescent, of mesic to xeric open habitats in grasslands, heathlands and open woodlands. Culms solid or very rarely hollow. Leaves distichous, without pseudopetioles; abaxial ligule usually absent (sometimes present in *Cortaderia*, *Karoochloa* and *Pentaschistis*); adaxial

ligule a fringe of hairs or a fringed membrane; sheaths not auriculate except in *Pentameris thuarii*. Inflorescences paniculate or less commonly racemose or spicate, bracts outside of the spikelets absent (but the subtending leaf more or less spatulate and disarticulating with the inflorescence in *Urochlaena*). Spikelets bisexual (but sometimes without bisexual florets in *Cortaderia*) or unisexual (*Cortaderia*, *Lamprothyrsus*), glumes 2 and usually equal, female-fertile florets 1-6 (-20), with apical reduction and a rachilla extension usually present, laterally compressed, disarticulating above the glumes and between the florets, less commonly below the glumes; lemma lacking uncinata macrohairs, awn single and from a sinus; palea well developed, sometimes relatively short; lodicules 2, free (rarely joined), fleshy or rarely with an apical membranous flap, glabrous or ciliate, often with microhairs, sometimes heavily vascularized; stamens 3; ovary glabrous or rarely with apical hairs (*Pentameris*), apical appendage absent, haustorial synergids present, only weakly developed in a few taxa, styles 2, the bases usually widely separated, stigmas 2. Caryopsis with the hilum short or long-linear; endosperm hard, containing compound starch grains (simple in *Prionanthium*); embryo large or small, epiblast absent, scutellar cleft present, mesocotyl internode elongated, embryonic leaf margins meeting (overlapping in *Sieglingia*). Basic chromosome numbers: $x = 6, 7, 9$.

Foliar anatomy. Mesophyll nonradiate, an adaxial palisade layer absent, fusoid cells absent, arm cells absent; kranz anatomy absent; midrib simple, usually with one bundle, an arc of bundles in *Cortaderia*; adaxial bulliform cells present or absent.

Foliar micromorphology. Stomata with dome-shaped or parallel-sided subsidiary cells (rarely high dome-shaped or slightly triangular); bicellular microhairs present, panicoid-type, sometimes absent; papillae usually absent but often present in *Chionochloa* and *Merxmuellera*.

Photosynthetic pathway. C_3 .

Included tribe (now identical to subfamily and thus redundant):

Danthonieae Zotov, New Zealand J. Bot. 1 (1): 86. 1963. (including Cortaderieae Zotov, New Zealand J. Bot. 1 (1): 83. 1963.)

Notes. The presence of haustorial synergids in the ovule and distant styles support the monophyly of this clade (Verboom et al., 1994). Bilobed prophylls also may be a synapomorphy, but this feature has not been investigated sufficiently in the rest of the family. The results of this study indicate robust molecular support for the monophyly of this clade (excluding *Centropodia* and *Merxmuellera rangei*), but its placement within the larger PACCAD Clade is equivocal. Pending further studies of the diversity of the danthonioid grasses, we recognize only one tribe, which includes the following genera (sensu Barker et al., 2000): *Austrodanthonia*, *Chaetobromus*, *Chionochloa*, *Cortaderia*, *Danthonia*, *Joycea*, *Karoochloa*, *Lamprothyrsus*, *Merxmuellera* (minus *M. rangei*), *Notochloe*, *Notodanthonia*, *Pentameris*, *Pentaschistis*, *Plinthanthesis*, *Prionanthium*, *Pseudopentameris*, *Rytidosperma*, *Schismus*, and *Tribolium*. The subfamily includes approximately 250 species.

X. Centothecoideae Soderstr., Taxon 30: 615. 1981. Type: *Centotheca* Desv. (Fig. 5G)

Plants annual or perennial (rhizomatous or stoloniferous), herbaceous or reedlike, of warm temperate woodlands and tropical forests. Culms solid or hollow. Leaves distichous, often pseudopetiolate; abaxial ligule absent or present as a line of hairs (*Calderonella*, *Thysanolaena*); adaxial ligule membranous or ciliate, or membranous with ciliate margins; sheaths sometimes auriculate. Inflorescences racemose or paniculate, bracts outside of the spikelets absent. Spikelets

bisexual or unisexual, (1-) 2-many-flowered with reduction either above or below the fertile florets, often compressed laterally; lemma lacking uncinata macrohairs, if awned, the awn single; palea usually well developed, sometimes relatively short; lodicules 2 or absent, more or less cuneate, many-nerved or less commonly not or scarcely vascularized; stamens (1-) 2 or 3; ovary glabrous, apical appendage absent, haustorial synergids presumed absent, styles 2, free or fused, close, stigmas 2. Caryopsis with the hilum basal, punctiform; endosperm hard, without lipid, containing simple or compound starch grains; embryo small or large, the epiblast present, scutellar cleft present, mesocotyl internode present, embryonic leaf margins overlapping. Basic chromosome number: $x = 12$ ($x = 11$ or $12?$ in *Thysanolaena*).

Foliar anatomy. Mesophyll non-radiate, often with an adaxial palisade layer, fusoid-like cells frequently present as extensions of the outer parenchyma bundle sheath, arm cells absent; kranz anatomy absent; midrib simple; adaxial bulliform cells large.

Foliar micromorphology. Stomata with dome-shaped and/or triangular subsidiary cells; bicellular microhairs present, panicoid-type; papillae absent.

Photosynthetic pathway. C_3 .

Included tribes:

Centothecae Ridl., Mat. Fl. Malay Pen. 3: 122. 1907.

Thysanolaeneae C. E. Hubb. in Hutch., Fam. Fl. Pl. 2: 222. 1934.

Notes. Support for the monophyly of this subfamily as recognized here is moderate, and no morphological synapomorphies have been identified. The sister relationship between the centothecoid and panicoid clades, however, is relatively robust. The positions of *Gynerium* and *Danthoniopsis* are unstable. A majority of the Centothecae is characterized by unusual leaf anatomy, including the presence of palisade mesophyll and laterally extended bundle sheath cells, but additional study of this clade is required. The subfamily includes approximately 45 species.

XI. Panicoideae Link, Hort. Berol. 1: 202. 1827. Type: *Panicum* L. (Fig. 5B and E)

Syn.: Saccharoideae (Rchb.) Horan., Char. Ess. Fam.: 34. 1847.

Andropogonoideae Burmeist., Handb. Naturgesch.: 201. 1837.

Rottboellioideae Burmeist., Handb. Naturgesch.: 202. 1837.

Plants annual or perennial (rhizomatous, stoloniferous, caespitose or decumbent), primarily herbaceous, of the tropics and subtropics, but also diverse in the temperate zone. Culms solid or less commonly hollow. Leaves distichous, sometimes pseudopetiolate; abaxial ligule usually absent, occasionally present as a line of hairs; adaxial ligule a fringed or unfringed membrane, or a fringe of hairs, or sometimes absent; sheaths usually non-auriculate. Inflorescences panicles, racemes or spikes, or complex combinations of these, bracts outside of the spikelets present (Andropogoneae) or absent (Paniceae). Spikelets bisexual or unisexual (if the latter plants dioecious or monoecious), frequently paired in long-short combinations, usually with glumes 2, sterile lemma 1, and female-fertile floret 1, dorsally compressed or less commonly not compressed or laterally compressed, disarticulating below the glumes (above the glumes in Arundinelleae) or the inflorescence axes breaking apart; lemma lacking uncinata macrohairs, if awned, the awn single; palea well developed (Paniceae) or reduced to absent (Andropogoneae); lodicules 2 or sometimes absent, cuneate, free, fleshy, usually glabrous; stamens 3; ovary usually glabrous, apical appendage absent, haustorial synergids absent, styles 2, free or fused, close, stigmas 2 (rarely 1 or 3). Caryopsis with the hilum usually short; endosperm hard, without lipid, containing simple or less commonly compound starch grains; embryo usually large, waisted, epiblast absent or rarely

present, scutellar cleft present, mesocotyl internode elongated, embryonic leaf margins overlapping or rarely meeting. Basic chromosome numbers: $x = 5, (7), 9, 10, (12), (14)$.

Foliar anatomy. Mesophyll radiate or non-radiate, an adaxial palisade layer absent, fusoid cells absent except in *Homolepis* and *Streptostachys*, arm cells usually absent; kranz anatomy present or absent; midrib simple or rarely complex; adaxial bulliform cells present.

Foliar micromorphology. Stomata with triangular or dome-shaped subsidiary cells; bicellular microhairs present, panicoid-type, rarely absent; papillae absent or present (mostly in the Andropogoneae).

Photosynthetic pathway. C_3, C_4 (PCK, NAD-ME and NADP-ME), and some C_3/C_4 intermediates.

Included tribes:

- Steyermarkochloae Davidse & R. P. Ellis, Ann. Miss. Bot. Gard. 71 (4): 994. 1984.
- Hubbardieae C. E. Hubb. in Bor, Grasses India Burma Ceylon Pakistan: 685. 1960.
- Isachneae Benth., J. Linn. Soc. Bot. 19: 30. 1881.
- Paniceae R. Br., Voy. Terra Austr. 2: 582. 1814.
- Arundinelleae Stapf, Fl. Cap. 7: 314. 1898.
- Andropogoneae Dumort., Observ. Gramin. Belg.: 84. 1824.

Notes. While support for the panicoid/centothecoid clade is high, relationships within the clade remain unclear. No robust phylogeny for the Panicoideae is yet available, although work is in progress. Preliminary results indicate that the Paniceae as currently circumscribed may not be monophyletic, and that the large genus *Panicum* is polyphyletic (Zuloaga, Morrone, & Giussani 2000; Gomez-Martinez & Culham, 2000). Andropogoneae + *Arundinella* appears to be monophyletic (Spangler et al. 1999); other genera of the Arundinelleae are likely to be distributed among the Andropogoneae, Paniceae, and perhaps even the Centothecoideae (Kellogg, 2000b). This subfamily includes approximately 3270 species.

XII. Chloridoideae Kunth ex Beilschm., Flora 16(2): 52, 105. 1833. Type: *Chloris* Sw. (Fig. 5H and D)

Syn.: Pappophoroideae Burmeist., Handb. Naturgesch. 205. 1837.

Eragrostoideae Pilger, Nat. Pfl.-Fam. ed. 2, 14d: 167. 1956.

Plants annual or perennial (rhizomatous, stoloniferous, caespitose or decumbent), herbaceous (rarely woody), of dry climates, especially in the tropics and subtropics, also found in the temperate zone. Culms solid or hollow. Leaves distichous, without pseudopetioles; abaxial ligule usually absent, rarely present as a line of hairs; adaxial ligule a fringed or less commonly unfringed membrane; sheaths usually non-auriculate. Inflorescences paniculate, paniculate with spicate branches, racemose, or spicate, bracts outside of the spikelets absent. Spikelets bisexual or sometimes unisexual (if so the plants dioecious or monoecious), with glumes 2, rarely a sterile lemma, and female-fertile florets 1-many, apical reduction usually present, usually laterally compressed, sometimes dorsally compressed, usually disarticulating above the glumes (below in a few *Eragrostis* species); lemma lacking uncinata macrohairs, if awned, the awns single or if multiple, lacking a basal column; palea well developed; lodicules 2 or absent, fleshy, glabrous; stamens 1-3; ovary glabrous, apical appendage absent, haustorial synergids absent, styles 2, free, close, stigmas 2. Caryopsis with the pericarp often free or loose; hilum short; endosperm hard, without lipid, containing simple or compound starch grains; embryo large or rarely small, not waisted, epiblast present or rarely absent, scutellar cleft present, mesocotyl internode elongated,

embryonic leaf margins meeting or rarely overlapping. Basic chromosome numbers: $x = (7), (8), 9, 10$.

Foliar anatomy. Mesophyll usually radiate, without an adaxial palisade layer, fusoid cells absent, arm cells absent; kranz anatomy present; midrib simple; adaxial bulliform cells present.

Foliar micromorphology. Stomata with dome-shaped or triangular subsidiary cells; bicellular microhairs present, usually chloridoid-type; papillae absent or present.

Photosynthetic pathway. C_3 (*Eragrostis walteri*, *Merxmuellera rangei*), otherwise C_4 (PCK, NAD-ME, but NADP-ME in *Pappophorum*).

Included tribes:

Pappophoreae Kunth, Rév. Gramin. 1: 82. 1829.

Orcuttieae Reeder, Madroño 18: 20. 1965.

Cynodonteae Dumort., Observ. Gramin. Belg.:83. 1824.

Eragrostideae Stapf, Fl. Cap. 7: 316. 1898.

Leptureae Dumort., Observ. Gramin. Belg.: 83. 1824.

Incertae Sedis: *Centropodia* Reichenb., *Merxmuellera rangei* (Pilg.) Conert

Notes. Reduction in the number of veins in the lemma is a general trend within the subfamily, but is clearly not a synapomorphy. Except for the C_3 *Eragrostis walteri* and *Merxmuellera rangei*, the Chloridoideae are uniformly C_4 with both the NAD-ME and PCK subtypes. The current tribal classification for this subfamily conflicts with molecular data and is likely to be modified (Hilu et al., 1999). This subfamily includes approximately 1,400 species.

XIII. *Incertae Sedis*

Eriachneae (Ohwi) Eck-Borsb., Blumea 26: 128. 1980.

Micraireae Pilger, Nat. Pfl.-Fam. Ed. 2, 14d: 167. 1956.

Streptogyneae C. Calderón & Soderstr., Smithsonian Contr. Bot. 44: 18. 1980.

Cyperochloa Lazarides & L. Watson, Brunonia 9: 216. 1987.

Gynerium Willd. ex P. Beauv., Ess. Agrostogr. 138, 153, t. 24. 1812.

Notes. These five taxa are left *Incertae Sedis* because the data presented here do not firmly support their inclusion in any of the twelve subfamilies. This approach has also been taken by the APG (1998) for taxa of uncertain placement. Some possible placements of the five taxa above will require publication of new names, and we feel strongly that nomenclatural changes should not be made until appreciable data support the conclusion. That said, recent unpublished data (J. G. Sánchez-Ken, pers. comm.) suggest that *Gynerium* can be placed as its own tribe in Panicoideae, and the tribal name may be available by the time this paper is published (Sánchez-Ken & Clark, in review). It is likely that *Cyperochloa* will be placed in Centothecoideae, but this is based on its morphological similarities to *Spartochloa* and not on any data on *Cyperochloa* itself. Streptogyneae will probably fall within Ehrhartoideae, but limitations of our data and lack of support in our trees make us cautious about placing it there unequivocally; there may be an argument for recognition of the tribe as its own subfamily. The name Micrairoideae has been published (Pilger, 1956). Our data are too limited and the placement of the group too uncertain to add it as a thirteenth subfamily, although flora writers may choose to do so. Our data on *Eriachne* are weak, and show only that the genus does not fall within the Panicoideae where it has been placed traditionally. The placement near the base of the PACCAD Clade is based on a single-stranded *rbcL* sequence from one species, an ITS sequence from a second; the two species represent two sections of the genus,

one of which has actually been recognized as its own genus. We therefore feel that *Incertae Sedis* best reflects what we know of the position of the tribe - its position is uncertain.