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# THE SUBFAMILIES AND TRIBES OF GRAMINEAE (POACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

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THE FAMILY GRAMINEAE (POACEAE), the fourth largest family of flowering plants, is represented in the southeastern United States by about 575 species, 130 genera, and 21 tribes assigned to five subfamilies. In number of genera it matches the Compositae (Asteraceae) almost exactly and exceeds both the Leguminosae (Fabaceae) (ca. 72 genera) and the Orchidaceae (ca. 50 genera) in this area of some 444,000 square miles (1.15 million square kilometers). The present account contains a comprehensive family description; general

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FIGURE 1 was drawn by Donna Marino, and FIGURE 2 is by Scott E. Bergquist. FIGURES 3–11 were drawn by Karen Stoutsenberger in 1975, 1976, and 1977, largely under NSF Grant BMS-21469 (C. E. Wood, Jr., principal investigator); Carroll Wood or Kenneth R. Robertson and the author prepared the materials and supervised these illustrations. FIGURE 4 was based on living plants collected by Norton Miller near Chapel Hill, North Carolina, and grown by Carroll Wood in Cambridge, Massachusetts.


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comments on the systematics, phylogeny, origin and distribution, reproductive biology, and economic importance of the family; a general diagnosis of the family followed by a key to the subfamilies and tribes; and brief diagnoses and discussions of the subfamilies and tribes. Fuller descriptions of these taxa are given in the APPENDIX (a data matrix based on 84 characters) at the end of the paper. Two pages of figures illustrate variations in leaf epidermis and internal leaf anatomy; four genera are illustrated as in other papers in the Generic Flora series; and five pages of drawings show details of spikelets, florets, and various other parts of representatives of 17 of the 21 tribes.

## GRAMINEAE A. L. de Jussieu, Gen. Pl. 28. 1789.
## Nom. alt. POACEAE Barnhart, Bull. Torrey Bot. Club **22**: 7. 1925.

(GRASS FAMILY)

Annual or perennial herbs or shrubs with stems to 7.6 m high [trees to over 40 m in height and 30 cm in diameter], occasionally aquatic [or climbing]; hardness of woody stems not from secondary growth but from caps of fibers on both sides of the vascular bundles, lignified ground tissue, and to a lesser extent, silicified epidermis. Cyanogenic glycosides and various fructosans often present; major flavonoids flavone C-glycoside and tricin. Nucleoli disintegrating before or after metaphase, either enclosed within a lumen during interphase or not. Vessel members with mostly simple perforation plates. Primary roots usually ephemeral, the mature root system adventitious and fibrous (FIGURES 4a, 6a, 10a); prop roots sometimes adventive from lower stem nodes; epidermal cells all equal in size or alternating long and short; root hairs perpendicular to or obliquely angled from the surface of the root; roots sometimes forming mycorrhizae. Corms and bulbs sometimes present. Shoot apex with 1 or 2 tunica layers. Stems jointed, terete to somewhat flattened, rarely quadrangular, erect, ascending, or prostrate; in some biennials and perennials forming sterile tufts of leaves (innovations) that later grow into fertile stems; branching absent or at the upper nodes, sometimes from dormant buds, and near the ground by tillering intravaginally, the plants then often caespitose (FIGURE 10a), or extravaginally and then often stoloniferous or rhizomatous (FIGURE 4a); all vegetative branches bearing 2-keeled prophylls proximal on the adaxial surface of the branch and perpendicular to the plane of distichy of succeeding leaves; internodes growing by basal intercalary meristems, hollow or solidly filled with parenchyma; vascular bundles scattered to more or less concentrated toward the periphery; nodes transversely septate [armed with spines or thorns].

Leaves distichous [phyllotaxis 3/8 in the Australian endemic *Micraira* F. Mueller], green or glaucous from 2-$\beta$-diketone-containing waxes, and usually consisting of sheath, ligule, and blade, the sheaths and blades growing by basal intercalary meristems. Sheaths tightly encircling and supporting the stem (FIGURE 4b), the margins overlapping or, less commonly, united to form a tube. Ligules consisting of a membranaceous flange or a fringe of hairs at adaxial apex of sheath (FIGURES 4b, 6b, 8b, 10d), rarely absent. Blades simple, 1–150 cm [5 m] long, entire, usually linear, less often lanceolate to ovate [sagittate or cor-

date], flat, involute, convolute, or terete, sometimes deciduous from the sheath, continuous with the sheath or petiolate [the petiole twisting], sometimes dimorphic (much reduced on the main stem and normal on the branches), usually absent from leaves on rhizomes; venation parallel, rarely pinnate, cross-veins absent to prominent; small basal auricles often present (FIGURE 6b). Leaf epidermis (FIGURE 1) composed predominantly of files of long (length considerably greater than width) and short (more or less isodiametric) cells; walls of long cells sinuous or straight, with or without small epidermal protrusions (papillae); short cells usually occurring over veins, often absent from between veins, arranged in files of 5 or more, mainly paired or solitary, in short rows, or in mixtures of 1's, 2's, and short rows, often containing cork bodies or silica bodies, sometimes modified into usually apically pointing hooks or prickles (the latter larger than the former) or microhairs; silica bodies sinuous or crenate, cross to dumbbell shaped or nodular, tall and narrow, saddle shaped, crescentic, or oryzoid; microhairs usually in or between stomatal rows, usually bicellular, rarely unicellular [3- or 4-celled], the apical cell spherical to linear; stomata paracytic, biperigynous (i.e., the subsidiary and guard cells not derived from the same meristematic cell), raised above or at the same level as surrounding epidermal cells, with parallel-sided to triangular subsidiary cells; macrohairs unicellular, rarely multicellular, intergrading with prickles; 2-celled salt glands found in some halophytes and their relatives. Transverse-sectional anatomy of leaves (FIGURE 2) either $C_3$ or $C_4$—see discussion below; midrib bundle(s) 1 or more than 1 and either arranged in an arc or not, conspicuous or inconspicuous; vascular-bundle sheaths usually 2, an inner, thick-walled, endodermal mestome sheath and an outer parenchyma sheath, less often only 1 sheath present, rarely 3; sclerenchyma associated with all or nearly all vascular bundles, or only with larger bundles, as girders connecting the bundle and epidermis or as strands not reaching the epidermis; "arm" or "ratchet" cells with invaginated walls and large, elongated "fusoid" cells present or absent; simple, fan-shaped groups of bulliform cells present or absent in the adaxial epidermis; colorless cells sometimes traversing the mesophyll or forming deeply penetrating fans, narrow groups penetrating into the mesophyll, or arches over small bundles; palisade parenchyma rarely present.

Primary inflorescence a spikelet (FIGURES 3–11) composed of an axis, the rachilla (FIGURES 3F2, G2; 4g; 5A2, B2, C2; 6j, k; 7D2, I2), bearing distichously [spirally] arranged and closely overlapping basal bracts (glumes) and florets; disarticulating above the glumes or as a unit and with or without other spikelets; dorsally compressed (perpendicular to the plane of distichy; FIGURE 10n) or laterally (parallel to the plane of distichy; FIGURE 4c); the base sometimes formed into a hard, often pointed and/or hairy callus (FIGURE 3A3); sometimes viviparous (containing bulbils or bearing germinating seeds while still attached to the plant) or proliferating (i.e., converted into a leafless shoot, usually by growth of the lemmas); rarely subterranean. Spikelets borne in terminal or terminal and lateral secondary inflorescences of various kinds: panicles (FIGURES 4a; 10b, c), false panicles, cymes, racemes, rames (FIGURE 8a, k), and spikes (FIGURE 6c) that mature either basipetally or acropetally and basipetally from the middle and that may or may not be associated with leaves or bladeless

sheaths. Glumes proximal on the rachilla (FIGURE 4c), usually 2, equal (FIGURE 4d) or unequal (FIGURES 5A1, 10f) in size and appearance, sometimes 1 (FIGURE 5D2) (then usually the upper) or absent, awned or unawned, 0- to several-nerved, and subtending no axillary structures. Florets (FIGURES 3–11) maturing acropetally within a spikelet, made up of a bract (the lemma) subtending a flower and a bract (the palea) lying between the flower and the rachilla, 1–30 (–50) per spikelet; uppermost floret terminal or subterminal (with the rachilla therefore prolonged above it); base of florets sometimes formed into a hard, often hairy or pointed callus (FIGURES 4e, k; 5J3; 7C2). Lemmas similar or dissimilar to the glumes in texture or appearance, indurate or membranaceous, 0- to several-nerved; awn(s) 0, 1, or more, apical or abaxial, straight or hygroscopically sensitive and basally twisted and geniculate. Paleas with 2, infrequently 0, 1, or more than 2, nerves, often hyaline, sometimes absent, rarely awned, usually smaller than and more or less enclosed by the lemma.

Flowers (FIGURES 4i, 6h, 8h, 10h) small, perfect or imperfect (the plants then variously monoecious or dioecious), anemophilous, rarely entomophilous, mostly protandrous, greatly reduced relative to most other monocotyledons in the size and number of floral parts. Lodicules (the outermost floral parts) 2 and located adjacent to the lemma and opposite the palea, less often 3, rarely 1 [or more than 3], translucent, veined or veinless, glabrous or hairy, apically thick or thin, toothed, pointed or truncate, rarely adnate to palea. Stamens hypogynous, 6 in 2 whorls of 3 or, more commonly, only the 3 outer present, less often 1, 2, or 4 [to 30]; filaments slender, free or connate; anthers (FIGURES 4h, 6f, 8i) 4-sporangiate, 2-locular at anthesis, appearing versatile, dehiscing extrorsely (or in the stamen between the lodicules, introrsely) by longitudinal slits or terminal pores; anther wall formation of the monocotyledonous type; [staminodes present]. Pollen (FIGURES 6g, 8j) trinucleate when shed, monoporate, operculate, more or less spheroidal-ovoid, (14–)20–55(–130) $\mu$m in diameter, very ephemeral, the sexine granular. Gynoecium tricarpellate, syncarpous. Styles 2, less often 1 or 3, terminal or rarely subterminal, free or connate; stigmas (FIGURES 3C3; 4f, g, i, l; 6e, h, i, k; 7A2, A3; 8a, c, h; 9A1, A5, B5; 10e, h) dry, plumose, white or colored, free or connate. Ovary superior, unilocular, uniovular, smooth or hairy. Ovule anatropous, hemianatropous, campylotropous, or orthotropous, bitegmic, rarely the integuments 1 or none, pseudocrassinucellate or sometimes tenuinucellate; micropyle formed by the inner integument; megasporogenesis of the Polygonum (rarely Adoxa) type; antipodals proliferate (3).

Fruit (FIGURES 6n, 8m, 10j) a single-seeded caryopsis (grain), in which the pericarp is adnate to the seed, or when the pericarp is free, an achene or utricle [or berry], often associated with parts of the floret or spikelet for dispersal; hilum punctiform to linear and more than ½ the length of the fruit; endosperm (FIGURES 4m, 6m, 10k) present or absent, hard or milky, with or without lipids, its development nuclear; starch grains simple or compound. Embryogeny of the asterad type; embryo achlorophyllous, basal and lateral (FIGURES 4m, 6m, 10k), from $\frac{1}{10}$ of the length of the seed to equal to it; radicle ensheathed by the coleorhiza; plumule ensheathed by the coleoptile; scutellum large, flat, adjacent to the endosperm, haustorial, its base free from (FIGURES 8n, 10l) or adnate to

(FIGURE 4n) the coleorhiza; epiblast (a small, nonvascularized outgrowth opposite the scutellum; FIGURE 4n) present or absent; vascular bundles to scutellum and coleoptile separated by an internode (the embryo mesocotyl; FIGURES 8n, 10l) or not separated (FIGURE 4n); plumule leaves with many to few vascular bundles, margins either overlapping (FIGURES 8o, 10m) or not (FIGURE 4o).

Seedlings (FIGURE 8p–r) with adventitious roots present or absent at scutellar and coleoptilar nodes; first several leaves above coleoptilar node with or without a well-developed blade; first well-developed blades either broad and horizontal to ascending or more or less narrow and erect. Chromosomes mostly with median to submedian centromeres, the base numbers primarily 7, 9, 10, and 12.

(Including Agrostidaceae Burnett, Andropogonaceae Herter, Anomochloaceae Nakai, Arundinellaceae Herter, Avenaceae Burnett, Bambusaceae Burnett, Chloridaceae Herter, Eragrostidaceae Herter, Festucaceae Herter, Graminaceae Lindley, Hordeaceae Burnett, Lepturaceae Herter, Miliaceae Burnett, Oryzaceae Burnett, Panicaceae Herter, Parianaceae Nakai, Phalaridaceae Burnett, Saccharaceae Burnett, Spartinaceae Burnett, Sporobolaceae Herter, Stipaceae Burnett, and Streptochaetaceae Nakai.) TYPE GENUS: *Poa* L.

References used in family description: Anton & Astegiano; Arber (1925, 1934); Avdulov; Barnard; Beetle (1980); Bor; W. V. Brown (1958a, 1977); W. V. Brown, Harris, & Graham; W. V. Brown & Johnson; Burns; Calderón & Soderstrom (1973); Cheadle (1955); Clayton (1970, 1978); Clifford & Watson; Cronquist; Davis; Ellis (1976, 1979); Evans; Gibbs; Gould & Shaw; Hackel (1890); Harborne & Williams; Hitchcock; Hubbard (1973a); Jacques-Félix (1962); Lipschitz & Waisel; McClure (1973); Metcalfe (1960); Monod de Froideville; J. S. Page; Pohl; Reeder (1957); Roshevits; Row & Reeder; Soderstrom (1981a); Stapf; Stebbins (1982); Tulloch & Hoffman; Wagner; and Yakovlev & Zhukova.

A very natural family, the fourth largest in the flowering plants (about 600 genera and 10,000 species) and the foremost in ecological and economic importance. Species occur on all continents, in desert to freshwater and marine habitats, and at all but the highest elevations. Communities dominated by grasses (e.g., the North American prairie and plains, the South American pampas, the Eurasian steppes, and the African veld) account for about 24 percent of the earth's vegetation (Schantz). The grassland communities of the southeastern United States (e.g., the Pennyroyal area of Tennessee and the Black Belt of Alabama) occupy small areas, but grasses are major components of the flora, with 130 genera—about ten percent of the total number of angiosperm genera.

A division of the family into two major groups (the pooids and the panicoids) based on the structure of the spikelet, the basic unit of the inflorescence, and dating from Robert Brown (1810, 1814), was used in most floras through the first half of this century. Evidence from leaf and embryo anatomy, from chromosome number and size, and from a remarkably broad series of morphological, anatomical, physiological, chemical, cytological, and phenological studies has subsequently led to the recognition by most workers of from five to eight subfamilies and as many as 60 tribes. All five of the subfamilies recognized

here (Bambusoideae, Arundinoideae, Pooideae, Chloridoideae, and Panicoideae) have indigenous members in the southeastern United States, and the 21 tribes that occur there include most of the major ones in the family.

Difficulties with grass taxonomy at all levels stem from a number of features. First, the great reduction in size and complexity of reproductive parts has limited the use of characters that are taxonomically useful in many other families (Stebbins, 1982). Second, parallelism is believed to be frequent in the family (Arber, 1934; Hubbard, 1948; Prat, 1960; Stebbins & Crampton; Decker; Phipps; Guédès & Dupuy; Renvoize, 1981; Estes & Tyrl). Third, two common aspects of the breeding system of grasses—hybridization, with the attendant phenomena of polyploidy and apomixis, and inbreeding—have obscured taxonomic boundaries and made the biological species concept difficult to apply to many grasses.

## Systematics, Past and Present

In his sexual system of classification, Linnaeus recognized 38 genera of grasses in six groups. His knowledge of the morphology of grasses was as limited as his sytematic treatment, for he was not clear about the nature of the "spicula" (his term for the spikelet; see Jacques-Félix (1972) for a multilingual etymology of the parts of grass spikelets and flowers). Robert Brown (1814) interpreted the spikelet as a modified inflorescence consisting of an "outer envelope or gluma" (the latter term taken from Jussieu) and an "inner envelope" (the calyx of Jussieu, i.e., the lemma and palea). He considered the "inner valve" (the palea) to be homologous with two fused members of the "proper envelope" (outer perianth whorl) and the "squamae" (lodicules) to be derived from the inner perianth whorl. He defined (1810, 1814) the Paniceae (the Panicoideae of modern authors), a mostly tropical group bearing spikelets with two florets, of which the lower is imperfect, and the Poaceae (the Pooideae), a group mostly of temperate climates, the spikelets of which contain one to many florets, with the imperfect florets, if present, not basal. This remarkably perceptive taxonomic insight is supported by a wealth of data (see below), and it orders suprageneric studies in the family even to the present. The gradual accumulation of taxonomic knowledge of the tribes and genera of the family through the efforts of Palisot de Beauvois, Trinius (1820, 1824), Dumortier, Kunth, and others culminated in the cosmopolitan treatments of Bentham, Bentham & Hooker, and Hackel (1887). These classifications include a dozen or more tribes in two subfamilies corresponding to Brown's subdivisions.

The classifications of Bentham & Hooker and of Hackel rely almost exclusively on gross morphology, especially that of the inflorescences. At about the same time many workers were uncovering systematically useful variation in leaf anatomy (Duval-Jouve, T. Holm, Pée-Laby), in embryology (Van Tieghem), and in the nature of starch grains in the endosperm (Harz). In spite of the patent taxonomic value of these works, they were largely ignored, perhaps because of major incongruities with morphological classifications. The work of Avdulov (1931) on the size and base numbers of chromosomes and that of Prat (1932, 1936) on the leaf epidermis emphasized the synthesis of morphological and nonmorphological data in grass systematics. They initiated redef-

inition of the Pooideae by removing the chloridoid grasses. These had traditionally been grouped with the pooids because of spikelet characters, but new characters clearly showed them to be much closer to panicoids. Each also established an additional major subdivision, Avdulov's series Phragmitiformes and Prat's Bambusoideae.

The subsequent search for new taxonomic data and the use of these in establishing subfamilial relationships have been highly productive. While variation in some characters (e.g., pollen morphology (J. S. Page) and flavonoid chemistry (Harborne & Williams)) is small throughout the family, a diverse series of morphological, anatomical, physiological, chemical, cytological, and phenological features provides useful taxonomic information (see Reeder, 1957; Bor; Metcalfe, 1960; Prat, 1960; Tateoka, 1960; Stebbins & Crampton; Jacques-Félix, 1962; Auquier; Clifford & Watson; and Gould & Shaw for additional discussions of taxonomically useful variation). As a rule, this array of characters distinguishes not only the two extremes of the family, the panicoid and pooid groups, but also one or more of the other subfamilies recognized here.

The contrasts given in the paragraphs that follow are intended to show the breadth of characters separating the panicoids and pooids in the restricted, modern sense. The wider taxonomic use of each of these characters, if one exists, will be detailed later.

The pooids accumulate fructosans as the predominant reserve polysaccharide; panicoids accumulate starch (De Cugnac; D. Smith, 1968). Pooid caryopses contain consistently higher levels of alanine, methionine, and phenylalanine than do those of panicoids (Yeoh & Watson). Taira also pointed out differences in amino-acid composition of the two groups. Fairbrothers & Johnson and P. Smith demonstrated a clear serological distinction between pooid and panicoid grasses.

In pooids the nucleoli do not persist beyond metaphase and do not appear to lie within a lumen during interphase, but in panicoids they do persist and are surrounded by a lumen (Avdulov; Brown & Emery, 1957). Vessels tend to be more specialized in pooids than in panicoids (Cheadle, 1960). Pooid shoot apices mostly have two tunica layers, and panicoids one layer (Brown, Heimsch, & Emery). Goller established differences between pooid and panicoid anatomy of the cortex and stele of the root. Pooid root hairs are directed toward the root apex and come from relatively small epidermal cells alternating with larger cells, while panicoid root hairs tend to emerge at right angles from uniformly sized cells (Row & Reeder). Hitch & Sharman noted several differences in the vascular patterns of pooid and panicoid axes. Pooids tend to have a definite sheath pulvinus and no culm pulvinus; panicoids usually bear a culm pulvinus but a poorly developed sheath pulvinus (Brown, Pratt, & Mobley; Ebinger & Carlen). Brown, Harris, & Graham found that pooid stem internodes are mostly hollow, panicoid internodes mostly solid. On the basis of the nature of the vascular-bundle sheaths, De Wet (1960a) and Auquier & Somers set up groups that correspond well to those based on leaf transverse-sectional anatomy established by Brown (1958a, 1977) and Carolin and colleagues (see below). The second and third leaves of seedlings are less differentiated in pooids than in panicoids when the shoot breaks through the coleoptile (Stebbins & Crampton).

The absence of bicellular microhairs from the leaf epidermis of pooid grasses

separates them from panicoids (Tateoka *et al.*; Johnston & Watson, 1977). Pooids generally have horizontally elongated or crenate silica bodies and sunken stomata bordered by parallel-sided subsidiary cells, while in panicoids the epidermis bears cross- or dumbbell-shaped or nodular silica bodies, and the stomata are flush with the rest of the epidermal cells and have triangular subsidiary cells (Prat, 1936; Clifford & Watson; Watson & Johnston). Pooid guard cells tend to be semicircular in cross-sectional outline, and the membrane is absent or rudimentary, while panicoid guard cells are angular and have a well-developed membrane (Brown & Johnson).

In addition to the spikelet differences upon which Robert Brown founded his two subdivisions, pooid spikelets tend to be compressed laterally, to disarticulate above the glumes, and to have the rachilla extending above the uppermost floret. In contrast, panicoid spikelets tend to be compressed dorsally, to disarticulate below the glumes, and to have the rachilla ending at the uppermost floret. They also tend to be viviparous less often than pooid spikelets (Beetle, 1980). Vasculature of the spikelets of the two groups differs (N. Chandra, 1962). In pooids the three or four nodes below the inflorescence do not bear branches, while in panicoids all but the uppermost node below the inflorescence bear branches or buds (Latting). The lemmas of pooids do not have germination flaps, while all panicoid lemmas studied so far have them (Johnston & Watson, 1981). Lodicules are thin, nonvascularized, and truncate in pooids and thick, heavily vascularized, and acute in panicoids (Decker; Tateoka, 1967; Jirásek & Jozífová).

The diffusible pollen-wall antigens of pooids and panicoids are immunologically distinguishable from each other (Wright & Clifford, Watson & Knox). Pooid ovules often have short outer integuments, no periclinal divisions in the nucellar epidermis, and laterally positioned antipodals. Long outer integuments, periclinal divisions, and chalazally positioned antipodals characterize panicoid ovules (N. Chandra, 1963). Numerous studies have shown that gametophytic apomixis in pooids is mostly (three out of four genera) diplosporous, and that the mature apomictic megagametophyte has the usual complement of nuclei. Apomictic panicoids are usually (18 out of 19 genera) aposporous, and their asexually derived megagametophytes contain only four nuclei (Brown & Emery, 1958; Reddy; Connor, 1979).

Reeder (1957, 1962) used four characteristics of the mature embryo to sort grasses into six groups (see below), including a pooid and a panicoid group. Genera with liquid or soft endosperm are found only among pooid grasses (Terrell). Starch grains are mostly smooth walled and either simple or compound in the pooids, and angular walled and usually simple in the panicoids (Harz; Tateoka, 1962). The germination of pooid seeds is inhibited more by isopropyl carbamate and low oxygen tensions than is that of panicoid seeds (Al-Aish & Brown). Pooid seedlings have narrow and erect or ascending leaves and often produce transitionary node roots. Panicoid seedling leaves are broad and horizontal and do not have transitionary node roots (Avdulov, Kuwabara, Hoshikawa).

Large chromosomes with a base number of seven characterize pooids, while small ones in multiples of nine or ten are found in panicoids (Avdulov; Tateoka,

1960). Different viruses and fungi attack pooid and panicoid hosts (Watson; Watson & Gibbs; Savile). Finally, Robert Brown's early observation about the different geographic distributions in pooid and panicoid grasses has been supported by more recent studies (Hartley, 1950; Clayton, 1975, 1981a; Cross).

There are numerous exceptions to these differences between pooid and panicoid grasses. In addition, many characters define groups distinct from the pooids and panicoids and corresponding to other suprageneric taxa. Furthermore, there is a strong congruence between the various groups established on the basis of these diverse characters. The most striking congruences come from leaf anatomy, embryo anatomy, and karyotypes.

Some of the best evidence for relationships at the subfamilial and tribal levels in grasses is from leaf anatomy. The abaxial epidermis of the blade provides two excellent diagnostic features. First, bicellular microhairs are generally found in all subfamilies except the Pooideae (FIGURE 1a), from which they are uniformly absent (Tateoka *et al.*; Johnston & Watson, 1977). Variation in the shape and wall thickness of the distal cell is useful in distinguishing the Chloridoideae (FIGURE 1d) from the Panicoideae (FIGURE 1c). Second, the shape and distribution of silica bodies often characterize tribes or subfamilies (Prat, 1932, 1936; Metcalfe, 1960; Clifford & Watson; see APPENDIX, characters 52–58). The shape of stomatal subsidiary cells is of secondary value.

Light- and electron-microscope studies of the transverse-sectional anatomy of leaves (Duval-Jouve; Brown, 1958a, 1975, 1977; Carolin *et al.*; Johnson & Brown) have established two extremes in grasses. At one extreme is the presence of a well-developed mestome sheath (presumably with endodermal functions) around the vascular bundles; a parenchyma sheath (outside the mestome sheath) with chloroplasts similar to those of the surrounding mesophyll cells; and irregularly arranged chlorenchyma cells in the mesophyll. At the other extreme the mestome sheath is either present or absent, and there are specialized, thick-walled photosynthetic cells located in bundle sheaths or rarely in the mesophyll. The chloroplasts of these specialized sheath cells are radially or tangentially arranged and are larger and more numerous than the chloroplasts in the mesophyll; there are many plasmodesmatal connections between the specialized cells and mesophyll; and the mesophyll cells are more or less radially arranged around the vascular bundles. The first extreme reflects the $C_3$ photosynthetic pathway and characterizes the Pooideae (FIGURE 2b), the Bambusoideae (FIGURE 2a), most of the Arundinoideae, and 20 percent of the Panicoideae. The other extreme, known as the "kranz syndrome,"[2] is associated with the $C_4$ pathway. It occurs uniformly in the Chloridoideae (FIGURE 2c), in most Panicoideae (FIGURE 2d), and in about 10 percent of the genera of the Arundinoideae. The best histological predictor of the photosynthetic pathway is the "one cell distant criterion" (Hattersley & Watson, 1975, 1976): in $C_4$ plants no chlorenchyma mesophyll cell is more than one cell away from the parenchyma sheath, while

[2]"Kranz" is a German noun, meaning ring or wreath (W. V. Brown, 1977), and hence capitalized in German. In accounts in English, capitalization has been retained, as though of some significance. Since kranz is not a proper noun, lower case is used here to avoid possible confusion with the name of a person.

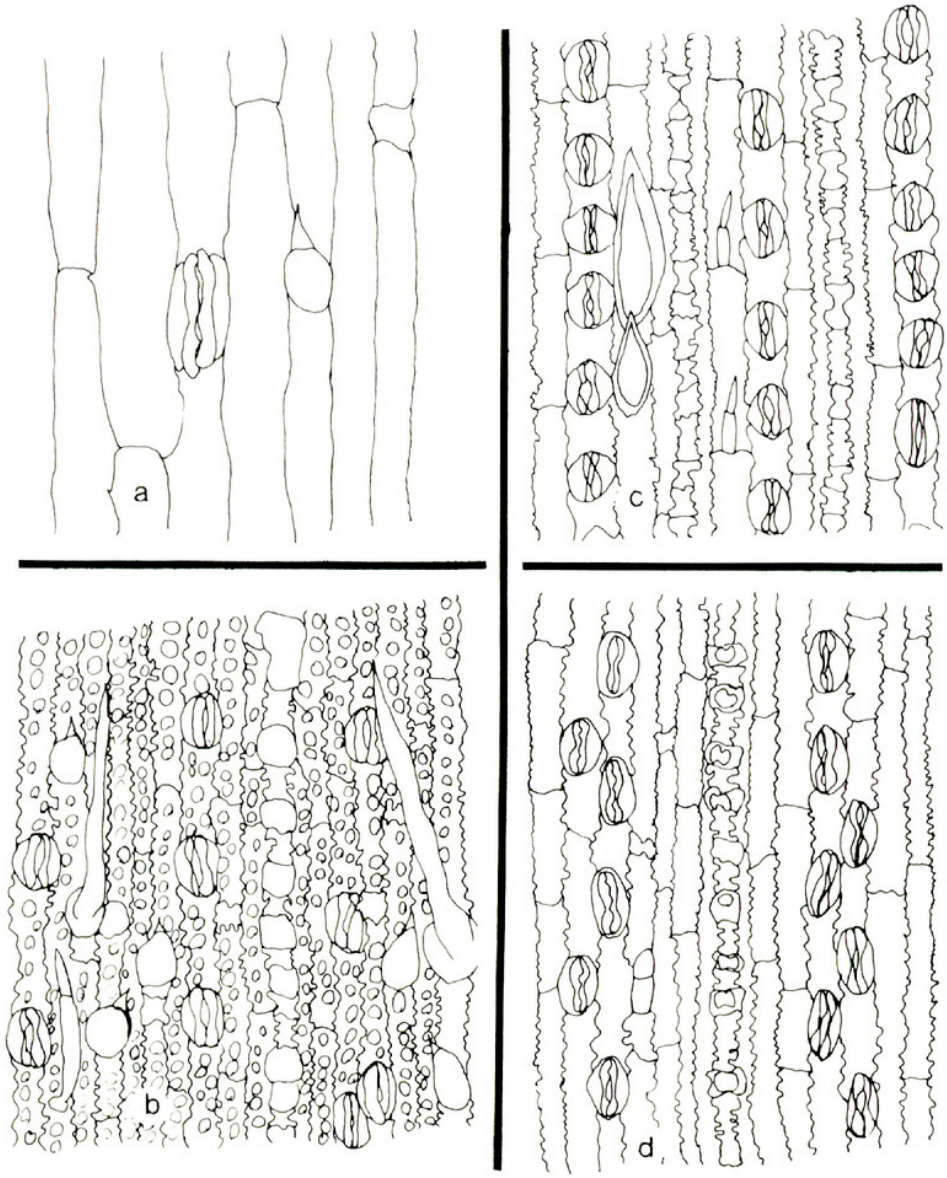


FIGURE 1. Camera-lucida drawings of abaxial leaf epidermises (leaf apex toward top) prepared according to hot-acids method of Steward and observed with phase-contrast microscopy, all × 130. a, *Elymus Hystrix* (*Hystrix patula*; Pooideae, Triticeae): note straight cell walls of long cells, parallel-sided stomatal subsidiary cells, and prickle hair. b, *Arundinaria gigantea* (Bambusoideae, Arundinarieae): note narrow distal cell of bicellular microhair, sinuous cell walls of long cells, papillae on long cells, nodular and more or less saddle-shaped silica bodies, dome-shaped stomatal subsidiary cells, and large macrohair. c, *Andropogon virginicus* (Panicoideae, Andropogoneae): note narrow distal cell of bicellular microhairs, sinuous cell walls of long cells, dumbbell-shaped to nodular silica bodies, more or less triangular stomatal subsidiary cells, and prickle hairs. d, *Tridens flavus* (Chloridoideae, Cynodonteae): note inflated distal cell of bicellular microhair, sinuous cell walls of long cells, dumbbell-shaped to nodular silica bodies alternating with cork cells, and more or less triangular stomatal subsidiary cells.

in $C_3$ plants some mesophyll cells are. All subfamilies, tribes, and genera (as circumscribed here) are uniformly either $C_3$ (non-kranz) or $C_4$ (kranz), except the Arundinoideae and Panicoideae (B. N. Smith & Brown; Brown, 1977; Renvoize, 1981), in which both pathways occur.

The kranz bundle-sheath of some $C_4$ grasses is derived from a mestome sheath (MS), and the chloroplasts are centrifugally positioned and contain either no grana or only small ones (Brown, 1977). In species with this MS subtype of kranz anatomy, the four-carbon compound transported into kranz cells is decarboxylated by NADP-malic enzyme (NADP-me). The kranz sheath of other $C_4$ grasses is derived from the parenchyma sheath (PS), and the four-carbon compound in this PS subtype of kranz anatomy is decarboxylated by one of two enzymes: PEP-carboxykinase (PCK or PEP-ck) is associated with a centrifugal position of the kranz bundle-sheath chloroplasts, NAD-malic enzyme (NAD-me) with a centripetal position. The significance of the difference between the PCK and NAD-me kinds of the PS subtype of kranz anatomy is not understood. There is, however, a clear association between systematics and variation in kranz anatomy (see discussion under the $C_4$ taxa and character 67 of the APPENDIX).

Plants with the $C_3$ pathway and those with the $C_4$ differ in numerous physiological ways: in the first intermediate into which atmospheric $CO_2$ is fixed, in carbon-isotope ratios, in light-saturation levels of photosynthesis, in temperature optima of photosynthesis, in photosynthetic translocation efficiency, and in $CO_2$ compensation point (Björkman & Berry; Brown, 1977; Ehleringer; Waller & Lewis). The $C_4$ pathway provides a high concentration of $CO_2$ in the parenchyma sheath and thereby allows higher photosynthetic rates in habitats with high light intensities and temperatures and low soil moisture (McWilliam & Mison). Low temperatures during growth offset the advantages of the $C_4$ pathway. Finally, the physiological differences between $C_3$ and $C_4$ grasses are associated with different geographic distributions. In North America the greatest relative abundance of $C_4$ species is found where the minimum temperature during the growing season is highest (Teeri & Stowe).

Other characters pertaining to transverse-sectional anatomy of the leaf have more or less unique states in certain subfamilies or tribes (Brown, 1958a; Clifford & Watson; also see below).

Reeder's (1957, 1962) embryological studies revealed four important characters, for each of which he determined two states, one found in the Panicoideae (designated "P") and the other in the Pooideae (designated "F" for Festucoideae, now a synonym of the Pooideae): presence (P) or absence (F) of an internode between the scutellar and coleoptilar nodes; presence (designated by a "+" and characteristic of the Pooideae) or absence (designated by a "−," the panicoid state) of a small flap, the epiblast, opposite the scutellar node; presence (P) or absence (F) of a cleft between the scutellum and the coleorhiza; and transverse section of the first embryonic leaf showing few vascular bundles and nonoverlapping margins (F) or many vascular bundles and overlapping margins (P). Hence the Pooideae are F + F F (FIGURE 4n, o) and the Panicoideae P − P P (FIGURES 8n, o; 10l, m). The five subfamilies in this paper have unique combinations of these four characters (see characters 38–41 in

the APPENDIX). Five of the six embryological groups established by Reeder are the same as five of the six groups based on transverse leaf anatomy (Brown, 1958a; Carolin *et al.*).

The distribution of Avdulov's character states of chromosome size and base number divides the Gramineae into his three major subfamilial groups. His Sacchariferae have small chromosomes with base numbers of nine or ten. This group is basically the kranz subfamilies Panicoideae and Chloridoideae. His Poatae contain two "series": Festuciformes, with large chromosomes and base number usually seven, equivalent to the Pooideae; and Phragmitiformes, with small chromosomes in multiples of twelve, including the balance of the family.

While the works of Avdulov and Prat released grass systematics from the two-subfamily system, those of Reeder (1957, 1962) and Brown (1958a, 1977) have tended to stabilize formal classifications at five to eight subfamilies (Tateoka, 1957a; Prat, 1960; Parodi; Stebbins & Crampton; Clayton, 1978; Renvoize, 1981; Hilu & Wright; Gould & Shaw). Some agrostologists (Jacques-Félix, 1962; Clifford & Goodall; Hubbard, 1973b; Clifford & Watson), however, appreciating the taxonomic uncertainties at the highest subfamily levels, employ many more informal groupings.

The subfamilial classification used here consists of the Bambusoideae, Arundinoideae, Pooideae, Chloridoideae, and Panicoideae. Subfamily Bambusoideae is broadly conceived as encompassing the woody bamboos, the so-called herbaceous bambusoid grasses (e.g., the Phareae) (Tateoka, 1957a; Parodi; Clayton, 1978; Soderstrom & Calderón, 1979a; Renvoize, 1981; Hilu & Wright), and the oryzoid grasses (Jacques-Félix, 1955, 1962; Tateoka, 1957a; Clayton, 1981a; Renvoize, 1981). Since its conception as Avdulov's Phragmitiformes, subfam. Arundinoideae has encompassed a diverse assemblage of grasses united, not by the presence of specialized features, but by a general lack of specialization. As such, it presents both the greatest subfamilial taxonomic problem and the greatest potential source of insights regarding relationships at this level. Renvoize's (1981) concept of this subfamily, followed here, includes the Centotheceae (the Centothecoideae of Soderstrom (1981b)), the Aristideae, and the core tribe Arundineae, as well as other tribes not occurring in the southeastern United States. Subfamily Pooideae, a heterogeneous group even after the transfer of $C_4$ grasses to the Chloridoideae, has become more sharply defined by the removal of three traditionally pooid tribes, the Brachyelytreae, Diarrheneae, and Stipeae, by Macfarlane & Watson (1980, 1982). These three tribes do not fit well into any of the five subfamilies and are therefore treated here as unplaced. The composition of the Chloridoideae is similar to that of most systems of the past 30 years, but the tribal limits are broader here. The only major systematic question is the placement of tribe Aristideae. Some (Pilger; Parodi; Clayton, 1978; Hilu & Wright; Gould & Shaw) consider it to be chloridoid, but its closeness to *Danthonia* DC. and its relatives (Brown, 1977) argues for including it in the Arundinoideae, as Reeder (1957), Tateoka (1957a), Prat (1960), Stebbins & Crampton, Jacques-Félix (1962), and Renvoize (1981) did. Robert Brown's (1810, 1814) delimitation of the Panicoideae (as the Paniceae) persists with minor changes to the present.

The works of Butzin and of Clayton (1981c; in prep.) are important sources for answers to nomenclatural questions at the suprageneric level.

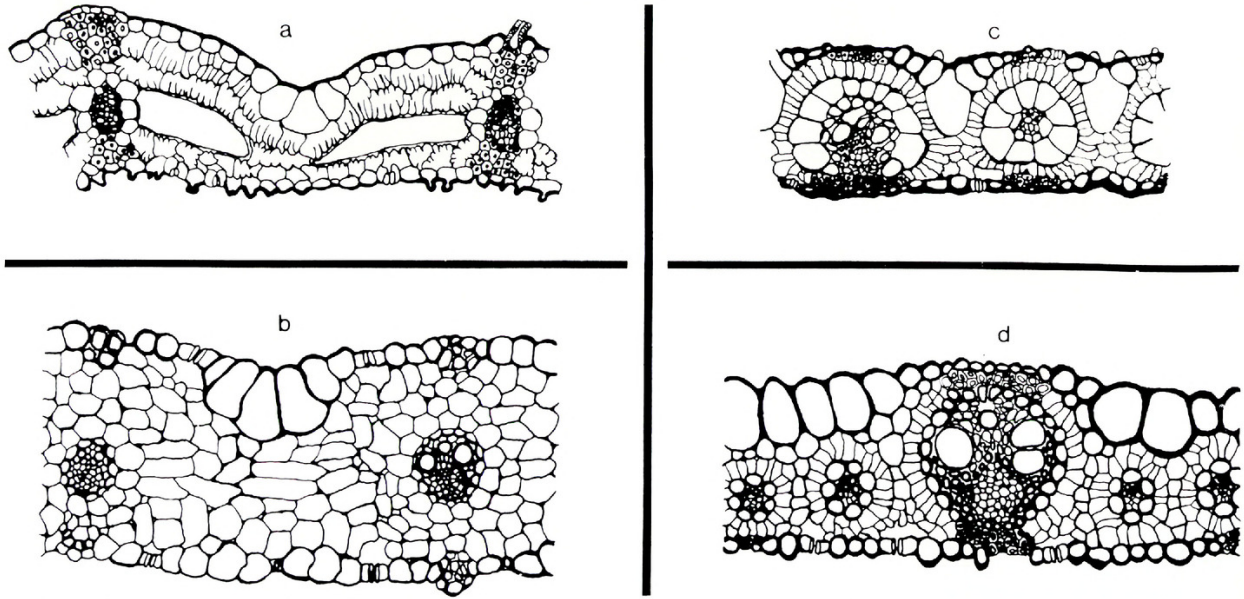


FIGURE 2. Drawings of portions of transverse sections of leaves. a, *Arundinaria variegata* (Bambusoideae, Arundinarieae; after Metcalfe (1960), *fig. XVIII, no. 3*): note numerous cells separating veins, indicating $C_3$ photosynthesis; large, elongated fusoid cells and arm or ratchet cells with invaginated cell walls; and sclerenchyma associated with vascular bundles. b, *Phalaris tuberosa* (Pooideae, Agrostideae; after Barnard, *fig. 4.22*): note numerous cells separating veins, indicating $C_3$ photosynthesis; 2 bundle sheaths; bulliform cells in upper epidermis; and stomata in both upper and lower epidermis. c, *Tragus racemosus* (Chloridoideae, Zoysieae; after Jacques-Félix (1962), *fig. 153B*): note short interveinal distance indicative of $C_4$ photosynthesis, large parenchyma sheath cells, bulliform cells, and thickened cuticle. d, *Andropogon Gerardii* (Panicoideae, Andropogoneae; after Barnard, *fig. 4.21*): note short interveinal distance indicative of $C_4$ photosynthesis, 2 bundle sheaths, sclerenchyma associated with vascular bundles, bulliform cells in upper epidermis, and stomata confined to lower epidermis.

## PHYLOGENETIC RELATIONSHIPS

The presence of numerous unique features makes the family Gramineae readily distinguishable from all other monocotyledons. Only two of its genera, *Anomochloa* Brongn. and *Ochlandra* Thw., are questionably graminaceous (Arber, 1934; Hubbard, 1948; Clifford, 1961). The distinctive bicellular microhairs of grasses may be derived from the multicellular hairs found in many monocotyledons (Stebbins, 1982). The complex development of the inflorescence characteristic of many grasses is not known outside the family (Stebbins, 1972), nor are structures strictly equivalent to the grass spikelet and its glumes, lemmas, and paleas. The anatomy of the grass stigma is unique (Y. Heslop-Harrison & Shivanna). Grasses are exceptional in having both gametophytic self-incompatibility and tricellular pollen (J. Heslop-Harrison). Finally, the coleoptile, epiblast, coleorhiza, and scutellar and coleoptilar nodes are peculiar to the grass embryo. Questions about the homologies of these unique features are still not fully answered.

Most agrostologists agree that grass perianths are derived from a trimerous, biseriate state but disagree about what has happened to the perianth in the evolution of the grass flower. Hackel (1881) thought that the palea was a modified prophyll because of its position and two nerves. Holttum, Bor, Hubbard (1973a), Clifford & Watson, Clayton (1978), Soderstrom (1981a), and many others also take this view, but Bourreill (1969) regarded the palea as homologous with a leaf sheath. A sepaloid origin of the palea was first hypothesized by Robert Brown (1814) and was supported by Bentham, Schuster, Stebbins (1972, 1982), and Cronquist. Virginia Page studied the unusual spikelets of the bambusoid genus *Streptochaeta* Schrader, which has two large, basally fused "palea bracts" (her term designating the position of the structures and not necessarily their equivalence to the palea of other grasses). Although she confirmed earlier reports of the separateness of the two palea bracts and the presence of a primordium of a third bract in the same whorl, she neither verified nor falsified the sepaloid homology of the palea. She suggested that the palea bracts of *Streptochaeta* might instead be sterile bracts or lemmas, a view also taken by Soderstrom (1981a). Hackel (1881) apparently thought the perianth to be totally absent from grass flowers, for he saw the position of the lodicules (between the lemma and the androecium in grasses with two lodicules) as evidence of their being two halves of a bract that continues the distichy of the spikelet. Arber (1934) pointed out that lodicules surely must be modified perianth parts because intermediates between stamens and lodicules can be found. According to Guédès & Dupuy, the fundamentally peltate nature of the lodicules confirms their petaloid origin.

With respect to the embryo, the nature of the scutellum is involved in interpretations of other parts. Brown (1960a), who also reviewed the extensive literature on homologies of the parts of the grass embryo, postulated that neither the scutellum nor the coleoptile is foliar because they do not arise from the shoot apex. He considered them to be parts of the cotyledon separated by an intercalated meristem, the mesocotyl. Cocucci & Astegiano suggested that the scutellum, coleoptile, and epiblast are lamina, ligule, and sheath, respectively,

of the foliar cotyledon. Shah & Sreekumari proposed that the scutellum, the coleoptile, and even the coleorhiza are parts of the cotyledon. The prevailing view holds that the scutellum and coleoptile are homologous with the cotyledon and first leaf of the shoot, respectively (Reeder, 1953, 1956; Guignard; Negbi & Koller; Guignard & Maestre). The formation of typical leaf hairs and chlorophyll in these structures supports this interpretation (Norstog). Because of the position of the epiblast opposite the scutellum, some (e.g., Negbi & Koller; see also Brown, 1960a) have seen it as a much-reduced second cotyledon. However, that the epiblast is actually an outgrowth of the coleorhiza is widely supported by observation (Brown, 1960a; Guignard; Soderstrom, 1981a) and experimentation (Foard & Haber). Apparently it is never vascularized (Reeder, pers. comm.). The predominant view of the coleorhiza is that it is homologous with the primary root or at least with the outer covering of the primary root (Guignard; Negbi & Koller; Guignard & Maestre).

In view of these specialized features, it is not surprising that the Gramineae are separated from other families by a large gap and that, as a result, their systematic relationships are poorly understood. The families most frequently considered as close relatives are the Cyperaceae, the Flagellariaceae, and the Palmae (Clifford, 1970; Dahlgren & Clifford). The resemblance in overall appearance and spikelet morphology of the Gramineae and the Cyperaceae has led to their union in various suprafamilial taxa. The two also have silica bodies in the leaf epidermis (Metcalfe, 1960, 1971), similar flavonoid patterns (Harborne & Williams), similar micropyles and ovules (Maze *et al.*), and nuclear endosperm formation (Dahlgren & Rasmussen). They are the only monocotyledonous families with $C_4$ species (Waller & Lewis). These similarities are, however, only superficial and may well represent parallel evolution (Metcalfe, 1971; Clayton, 1978). Many fundamental differences separate the two families. The bracts of the sedge spikelet are more often spirally than distichously arranged, and the similarity between sedge and grass spikelets is not close (Stebbins, 1982). Sedges also have differently shaped silica bodies (Metcalfe, 1971), pollen grains with more than one aperture (S. Chandra & Ghosh), simultaneous rather than successive microsporogenesis (Dahlgren & Rasmussen), embryos embedded in endosperm, several embryological features unlike those of grasses (Guignard; Clifford, 1970; Maze *et al.*; Maze & Bohm, 1973), lateral rather than terminal flowers, and diffuse centromeres. The Cyperaceae appear actually to lie closer to the Juncaceae (Takhtajan; Soo; Metcalfe, 1971; Stebbins, 1982; Dahlgren & Rasmussen), and the grasses share more features with the Flagellariaceae or the Joinvilleaceae, a segregate of the Flagellariaceae (Tomlinson & Smith). The Gramineae and Joinvilleaceae have both long and short epidermal cells that often have sinuous walls, similar stomata (Smithson), ulcerate pollen (S. Chandra & Ghosh), and some similar vegetative character states (Dahlgren & Clifford). Nevertheless, beyond its ties with this monogeneric family of Southeast Asia and the South Pacific, the Gramineae remain isolated.

By using the Joinvilleaceae (*sensu stricto*) or the monocotyledons in general as outgroups, it is possible to establish some evolutionary trends within characters of grasses and thereby some notions of evolution within the family. Stebbins (1982) used this outgroup criterion and four others to polarize the

states of 36 anatomical and morphological characters and two karyotype characters. Some of these characters—for example, habit (perennial vs. annual), ligule morphology, presence or absence of rhizomes, and several inflorescence characters—are not very useful taxonomically at the subfamilial and tribal levels and hence cannot help in phylogenetic hypothesis formation. The lack of knowledge about homologous structures for an outgroup makes polarization uncertain in seedling morphology (but see Hoshikawa's postulated trends), several inflorescence characters, and embryo anatomy. The use of starch grains (Stebbins, 1982) and karyotypes (Avdulov; Tsvelev; Brown & Smith, 1972; Mehra *et al.*; Sharma; Stebbins, 1982) is limited by lack of information about the outgroup character state. These qualifications leave leaf anatomy and floral morphology as useful.

The contention that the presence of microhairs in the leaf epidermis is primitive rests on their homology with the multicellular hairs of *Joinvillea* Gaudichaud and other monocots (see also Prat, 1936). There seems to be little doubt that the anatomical and physiological adaptations of the kranz syndrome are derived from the non-kranz conditions; Brown (1977) pointed out that there is no good evidence for reversals from $C_4$ to $C_3$. Among kranz grasses, long parenchyma-sheath cells are considered primitive and short ones derived (Brown, 1974). If it is assumed that grasses arose from ancestors with characteristically trimerous monocotyledonous flowers, it is safe to define as primitive in grasses perfect flowers with three highly vascularized lodicules, six stamens, and three styles. Hubbard (1948), Dedecca, Auquier, Sharma, and Ghorai & Sharma also called these floral states ancestral.

On the basis of these assertions about character-state evolution, the subfamily Bambusoideae, which has the greatest number of primitive floral character states among the subfamilies, is usually thought of as containing the most primitive extant grasses (Bews; Prat, 1936; Beetle, 1955; Stebbins, 1956b; Tateoka, 1957a; De Wet, 1958; Clayton, 1975, 1981a; Soderstrom & Calderón, 1979a). Floral evolution involves reduction in the number of each of these floral parts. The prominence of these floral reductions perhaps prompted Brown and colleagues (1957) to generalize that specialization in grasses means reduction. The absence of microhairs from the Pooideae and the kranz syndrome of the Chloridoideae and Panicoideae mark them as more advanced than the remaining subfamilies.

## Origin and Geographic Distributions

There is really no clear evidence for a place of origin of grasses. Some specialists (Bews; Stebbins, 1972; Clayton, 1975, 1981a) have suggested that they originated in tropical forests or at their margins. From these forest dwellers, an early offshoot similar to the Arundinoideae (Brown & Smith, 1972; Clayton, 1975, 1981a; Renvoize, 1981) extended into savannas and gave rise to—and was partially replaced by—the photosynthetically more efficient kranz subfamilies in the tropics and the pooids in the North Temperate Zone. The pooids migrated successfully along mountains into South America following the joining of North and South America in the Pliocene. An alternate hypothesis (Tsvelev)

calls for pooid-like prototypes bearing bambusoid flowers and originating in high mountains, with later movement to plains and temperate regions. This view finds some supporting evidence in the primitive nature of leaf and stem anatomy of pooids (Brown, 1958a; Auquier & Somers).

The meager fossil remains of grasses do little to resolve questions of the geologic age of the family, its relationships with other monocots, and evolution within the family. The oldest records of grass pollen are from the Paleocene (doubtful records from the Cretaceous) and, in North America, the uppermost Eocene (Muller). The first abundant grass pollen comes from Miocene deposits in Kansas and Nebraska. Caryopses of four species from England and oryzoid leaves from Germany, all from the Eocene, are among the first megafossil remains (Daghlian; Stebbins, 1981). Isolated florets (in which the flowers are not preserved) of the Stipeae and Paniceae from the Miocene in Kansas, and of the Oryzeae from the Miocene in Nebraska, provide the first extensive grass megafossils (Thomasson). The Miocene upsurge in grasses likely stems from their symbiotic relationship with the then newly evolved groups of grass-eating ungulates (Clayton, 1981a; Stebbins, 1981; De Wet, 1981).

Present distribution, in conjunction with past continental plate movement, can be used to infer the age of suprageneric grass taxa. Clayton (1975, 1981a) and Brown & Smith (1972) postulated that the subfamilies, tribes, and even some subtribes evolved by the end of the Cretaceous or the first half of the Tertiary before the continents were sufficiently separated to prevent dispersal between them. As a consequence, the continents now contain a full array of suprageneric taxa. The differentiation of many modern genera, however, followed the movement of continental plates beyond the dispersal range of most grasses, so that two-thirds of modern grass genera occur on single continents (Clayton, 1975, 1981a).

The subfamilies and larger tribes occupy all the world's tropical to temperate regions. Only the subfamily Pooideae has taken extensively to colder climates. Clayton (1975) recognized seven basic centers of distribution of grass genera (excluding those with worldwide ranges): Eurasia, North America, temperate South America, tropical America, Africa, India–Southeast Asia, and Australia. North America shares genera with only Eurasia (24 genera), temperate South America (ten), and Australia (one). Several disjunct distributions involve grass genera of the southeastern United States. Five genera—*Arundinaria, Brachyelytrum, Diarrhena, Schizachne,* and *Torreyochloa* (*Puccinellia*)—are found there, elsewhere in North America, and also in China or Japan (Koyama & Kawano). *Gymnopogon, Muhlenbergia,* and *Zizania* show a New World–Indian disjunction (Clayton, 1975). Temperature and rainfall strongly influence geographic distribution (Hartley, 1950, 1958a, 1958b, 1964, 1973; Hartley & Slater; Cross). These factors are discussed under the individual subfamilies and tribes.

Native grasslands develop where there are periodic droughts, level to gently rolling topography, frequent fires, and in some instances grazing and certain soil conditions (R. C. Anderson). Drought, fire, and grazing prevent invasion by woody plants, and the latter two may actually stimulate grassland productivity. Several factors may account for the competitive advantage of grasses in

the presence of fire and grazing: basal tillering; intercalary meristems at the base of the internodes, sheaths, and blades; short internodes of nonflowering stems; and caespitose habit. The general success of grasses may be further attributed to the protection of flower and fruit within the spikelet and to the great diversity of habit, photosynthetic pathways, breeding systems, and dispersal mechanisms.

## Reproductive Biology

The vagility of the fruits has promoted the ubiquity and ecological hegemony of grasses. Caryopses rarely leave the parent plant free from the spikelet or one or more of its parts, for these parts are multifariously adapted for dispersal by animals, wind, or water (Roshevits; Monod de Froideville; Hubbard, 1973a; Van der Pijl). Spiny involucres (as in *Cenchrus*), barbs, bristles, teeth, gluelike glandular secretions, hairs, awns, and awnlike glumes and lemmas catch on animal hair or even, in the case of the awns of some Triticeae, penetrate the skin around the mouth of herbivores (Stebbins, 1972). Many grasses bear fruits specially adapted to attract herbivores, which can then disperse the seeds. Some species have elaiosomes, encouraging ant dispersal (Monod de Froideville). Some bamboos produce fleshy berries, and the hard lemmas of some oryzoids are thought to have evolved as a protection from digestive enzymes (Stebbins, 1972). Wind dispersal depends upon winglike developments on spikelet parts or, more commonly, plumes on various spikelet or secondary-inflorescence parts. All or part of the inflorescence may break free from the plant and disperse by tumbling (Roshevits; Rabinowitz & Rapp). Grasses have at least two presumed adaptations for self-sowing of the dispersal unit. Hygroscopically sensitive awns may force the dispersal unit into the soil (Clayton, 1969; Stebbins, 1972; Clifford & Watson). Spikelet and floret calluses may serve the same purpose, sometimes operating together with awns (Hackel, 1890; Jain & Pal).

Grass flowers have obvious characteristics for wind pollination: reduced perianth (the lodicules), small and smooth pollen grains, high pollen-ovule ratio, and feathery stigmas. Pollination by pollen-collecting insects is infrequently of secondary importance (see Adams *et al.* and references therein), and it is primary only in certain herbaceous bambusoid grasses of relatively windless forests (Soderstrom & Calderón, 1971). Adaptations associated with animal pollination—large pollen (Adams *et al.*), numerous closely placed, bright-yellow anthers (Soderstrom & Calderón, 1971), and perhaps the striking sexine pattern of the insect-pollinated *Pariana* Aublet (J. S. Page)—are found in these partially or entirely entomophilous grasses.

Anthesis in grasses is of short duration (usually minutes), and in many species it regularly occurs at a certain time of day or night (Jones & Brown, Evans). The critical events of grass anthesis are the rapid swelling of the lodicules, which forces open the florets, the rapid extension growth of the staminal filaments, and the spreading of the stigmatic branches. Grass pollen is viable for less than five minutes in some species, and for up to 24 hours in others. Gregarious flowering of numerous genera of woody bamboos at sometimes very long intervals is an astounding phenomenon that is very rare in angio-

sperms (Soderstrom & Calderón, 1979a). Frequent protandry and rare protogyny (Hackel, 1890; Stapf; Monod de Froideville) promote outcrossing. A two-locus, multi-allelic control of self-incompatibility has been demonstrated in numerous grasses (J. Heslop-Harrison). On the other hand, self-compatibility and self-fertilization through cleistogamy are common in grasses (East; Connor, 1979, 1981). In the majority of cases of cleistogamy in grasses, two conditions prevail: leaf sheaths or bracts confine the spikelets so that the lodicules cannot open the spikelet for chasmogamy, and the pollen-ovule ratio of cleistogamous flowers is lower than that of chasmogamous flowers of the same individual or species (Hackel, 1906; Campbell *et al.*, 1983).

Knobloch listed over 2400 hybrids in grasses. Hybridization is often associated with polyploidy, the doubling of chromosomes in a sterile hybrid restoring chromosome pairing and fertility. Of the 4000 grass species for which chromosome counts have been made, 2200 show a multiple of the base number of the genus (Goldblatt). If the uncounted species of obviously polyploid genera are included, this estimate jumps from 55 to 64 percent. Hybridization and polyploidy have undoubtedly played significant roles in grass evolution (for examples, see Myers; Stebbins, 1956b, 1975; McWilliam; Dewey; Waines *et al.*).

Apomixis, usually arising following hybridization or polyploidization or both, has been demonstrated in 33 grass genera (Connor, 1979). Most apomictic grasses are pseudogamous. The genus *Poa* contains aposporous, diplosporous, pseudogamous, and nonpseudogamous biotypes (Nygren).

As judged by the frequency of cleistogamy (reported from 82 genera from a broad tribal spectrum by Campbell *et al.*, 1983) and the more extensive occurrence of self-compatibility (East), inbreeding is common in grasses. Like apomixis, inbreeding generates populational phenomena that pose major systematic problems. Inbreeding has also apparently been an important factor in the colonizing success of many weeds (Allard).

## Economic Importance

The economic importance of grasses lies in their paramount role as food: 70 percent of the world's farmland is planted in crop grasses, and over 50 percent of the world's calories come from grasses (Heiser). Man has cultivated the cereals for 10,000 years (De Wet, 1981). From the beginning of their domestication, wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and oats (*Avena sativa* L.) in the Near East, sorghum (*Sorghum bicolor* (L.) Moench) and pearl millet (*Pennisetum americanum* (L.) K. Schum.) in Africa, rice (*Oryza sativa* L.) in southeastern Asia, and maize (*Zea Mays* L.) in Meso-America have made possible the rise of civilizations. In terms of world production today, the first four crops are grasses: sugar cane (*Saccharum officinarum* L.), wheat, rice, and maize. Barley is seventh and sorghum eleventh. For an extensive review of the cultivation, breeding, and history of major grass crops, the reader is referred to volumes on sugar cane (Artschwager & Brandes), wheat (Quisenberry), rice (Grist), maize (Sprague), barley (Briggs), and sorghum (Hulse *et al.*).

Grasses are also used for livestock feed, erosion control, and turf production, and as a sugar source for the fermentation of many alcoholic beverages. Bamboos are an integral part of the economies of many tropical areas since they contribute young shoots for food, fiber for paper, pulp for rayon, strong stems for construction, and various items for numerous other uses (Soderstrom & Calderón, 1979a). In the southeastern United States the forage crop–ruminant livestock industry yields 40 percent as much in total sales as all row crops and close-grown field crops (Mays). Sugar cane, rice, maize, and sorghum are also grown commercially in this area.

The spread of civilization, commercial trade between the continents, and man's great nutritional dependence upon grasses have produced important, often weedy, adventive grass floras throughout the world (Hartley, 1964; De Wet, 1981). Species belonging to some 80 genera are cultivated as ornamentals in the United States (Bailey *et al.*).

## Key to the Subfamilies and Tribes of Grasses in the Southeastern United States

General characters: *Annual or perennial herbs, rarely shrubs; roots fibrous; leaves distichous, made up of sheath, ligule, and usually linear blade; leaf epidermis dominated by long cells and short cells, the latter often modified into hooks, prickles, or bicellular microhairs, or containing cork or variously shaped silica bodies; transverse-sectional anatomy of leaves either kranz and characterized by specialized bundle sheaths with large chloroplasts or non-kranz; primary inflorescence a spikelet consisting of an axis (the rachilla) and 3 kinds of distichously arranged bracts—glumes (basal, usually 2), lemmas, and paleas; secondary inflorescence paniculate, cymose, racemose, or spicate; florets 1–30 per spikelet and comprising a lemma subtending a flower and a palea between the flower and the rachilla; flowers perfect or imperfect, anemophilous; the outermost floral parts, the lodicules, 2 (rarely 3), fleshy; stamens 3, sometimes 1, 2, or 6; ovary superior, unilocular and uniovular; stigmas 2 or 3 (1); fruit a caryopsis or less often an achene or utricle; embryo basal and lateral, with a large cotyledon, the scutellum; endosperm usually abundant.*

A. Plants with $C_3$ photosynthesis and non-kranz leaf anatomy (2 or more mesophyll cells separating adjacent vascular bundles, chloroplasts uniform and all starch forming); hilum usually linear; embryos small, less than ⅓ the length of the caryopsis; stomatal subsidiary cells mostly parallel sided or dome shaped.
  B. Arm and fusoid cells usually present (Figure 2a) (fusoid cells absent in some Oryzeae); stamens often more than 3; stigmas usually 3 (2 in Oryzeae); first seedling leaf without a blade, except in Phareae. ..... Subfam. 1. BAMBUSOIDEAE.
    C. Stems woody; leaf blades disarticulating; fertile florets 6–12 per spikelet; glumes usually 2 per spikelet; flowers perfect; scutellar tail present. ..... Tribe 1a. Arundinarieae.
    C. Stems herbaceous; leaf blades not disarticulating; fertile floret 1 per spikelet; glumes usually absent (rarely 1 or 2 and vestigial); flowers often imperfect (plants monoecious); scutellar tail rarely present.
      D. Transverse veins absent in leaf blades; spikelets solitary; stigmas 2; first seedling leaf without a blade; microhairs present; silica bodies oryzoid; vascular bundles in stem internodes in 1 or 2 rings. ..... Tribe 1b. Oryzeae.
      D. Transverse veins present in leaf blades; spikelets paired; stigmas 3; first

seedling leaf with a blade; microhairs absent; silica bodies cross to dumbbell shaped to nodular; vascular bundles in stem internodes scattered... ..... Tribe 1c. PHAREAE.

B. Arm and fusoid cells absent (FIGURE 2b–d) (arm cells present in some Arundineae); stamens 3 or fewer; stigmas 2; first seedling leaf with a blade.

E. Scutellar tail absent (present in Diarrheneae); embryo mesocotyl short; microhairs absent (present in some Stipeae).

F. Rachilla not prolonged above uppermost floret; lodicules 2 or 3; microhairs sometimes present; silica bodies saddle shaped and crescentic. ..... ..... Tribe 6c. STIPEAE.

F. Rachilla prolonged above uppermost floret; lodicules generally 2; microhairs absent; silica bodies elongated, sinuous or crenate (absent from Brachyelytreae).

G. Embryonic leaf margins overlapping; silica bodies cross to dumbbell shaped to nodular.

H. Floret 1 per spikelet; lemmas awned, equally as firm as the glumes; lodicules glabrous; ovary apex hairy; pericarp adnate to seed; endosperm soft, the starch grains all simple; epidermis papillate; silica bodies not elongated, sinuous or crenate; sclerenchyma accompanying the smallest vascular bundles absent; base chromosome number 11. ..... Tribe 6a. BRACHYELYTREAE.

H. Florets 2–5 (rarely 1) per spikelet; lemmas awnless, firmer than the glumes; lodicules hairy; ovary apex glabrous; pericarp free from the seed; endosperm hard, at least some of the starch grains compound; epidermis not papillate; silica bodies elongated, sinuous or crenate; sclerenchyma accompanying at least some of the smallest vascular bundles present; base chromosome number 10. ..... .....Tribe 6b. DIARRHENEAE.

G. Embryonic leaf margins not overlapping; cross- to dumbbell-shaped silica bodies absent, tall and narrow silica bodies present. ..... ..... Subfam. 3. POOIDEAE.

I. Leaf auricles often present; ovary apex hairy; epiblast absent (present in some Triticeae); starch grains simple; seedling transitionary node roots present (supertribe Triticanae).

J. Inflorescence a panicle (rarely a raceme); lodicules glabrous; ovary appendage present; caryopsis compressed laterally. ..... ..... Tribe 3e. BROMEAE.

J. Inflorescence a solitary spike (rarely with spiciform branches); lodicules hairy (rarely glabrous); ovary appendage absent; caryopsis usually compressed dorsiventrally. ..... ..... Tribe 3f. TRITICEAE.

I. Leaf auricles absent; ovary apex glabrous (hairy in some Aveneae); epiblast present; at least some starch grains compound (rarely all simple in some Agrostideae); seedling transitionary node roots absent (supertribe Poanae).

K. Lodicules often truncate, connate, distally fleshy and palpably vascularized; base chromosome number 9 or 10. ..... ..... Tribe 3c. MELICEAE.

K. Lodicules acute, free, distally membranaceous and without evident veins; base chromosome number mostly 7.

L. Crescentic silica bodies present; vernation folded (rarely rolled). ..... Tribe 3d. POEAE.

L. Crescentic silica bodies absent; vernation rolled (rarely folded).

M. Florets usually 1 per spikelet; ovary apex glabrous (rarely hairy); hilum punctiform (rarely linear). ..... Tribe 3a. AGROSTIDEAE.

M. Florets usually more than 1 per spikelet; ovary apex mostly hairy (rarely glabrous); hilum linear. ..... Tribe 3b. AVENEAE.

E. Scutellar tail present; embryo mesocotyl long; microhairs present.

N. Spikelets usually dorsally compressed, disarticulating below the glumes, with 1 caryopsis-bearing floret; embryonic leaf margins overlapping (rarely not); base chromosome number generally 9 or 10. ..... Tribe 5b. PANICEAE.

N. Spikelets laterally compressed or not compressed, disarticulating above the glumes, with more than 1 caryopsis-bearing floret; embryonic leaf margins not overlapping; base chromosome number 12. ..... Subfam. 2. ARUNDINOIDEAE.

O. Rachilla prolonged above uppermost floret; hilum punctiform (rarely linear); epiblast absent; first seedling leaf curved; bulliform cell groups absent. ..... Tribe 2b. ARUNDINEAE.

O. Rachilla not prolonged above uppermost floret; hilum linear; epiblast present; first seedling leaf supine; bulliform cell groups present. ..... Tribe 2c. CENTOTHECEAE.

A. Plants with $C_4$ photosynthesis and kranz leaf anatomy (no more than 1 mesophyll cell separating adjacent vascular bundles, bundle sheaths starch forming); hilum mostly punctiform; embryos mostly large, more than ⅓ the length of the caryopsis; stomatal subsidiary cells dome shaped or triangular.

P. Stomatal subsidiary cells dome shaped. ..... Subfam. 2. ARUNDINOIDEAE.

Q. Floret 1 per spikelet; lemmas firmer than glumes; kranz bundle-sheaths 2; base chromosome number 11. ..... Tribe 2a. ARISTIDEAE.

Q. Florets 6–9 per spikelet; glumes and lemmas equally firm; kranz bundle sheath 1; base chromosome number 12. ..... Tribe 2b. ARUNDINEAE (*Neyraudia*).

P. Stomatal subsidiary cells triangular.

R. Spikelets compressed dorsally; staminate or neuter floret proximal to the lowermost carpel-bearing floret; epiblast absent; embryonic leaf margins overlapping; microhair distal cell narrow; tall and narrow silica bodies and saddle-shaped silica bodies absent (rarely present); parenchyma sheath cells elongate, their chloroplasts centrifugally positioned and containing either small grana or none; sclerenchyma accompanying the smallest vascular bundles absent. ..... Subfam. 5. PANICOIDEAE.

S. Glumes firmer than lemmas, the first glume longer than the spikelet; lemma nerves usually 3 or fewer. ..... Tribe 5a. ANDROPOGONEAE.

S. Glumes softer than lemmas, the first glume usually much shorter than the spikelet; lemma nerves usually 3 or more. ..... Tribe 5b. PANICEAE.

R. Spikelets compressed laterally (rarely dorsally) or not compressed; staminate or neuter florets usually distal to the lowermost carpel-bearing floret; epiblast present (rarely absent); embryonic leaf margins rarely overlapping; microhair distal cell inflated; tall and narrow silica bodies and saddle-shaped silica bodies present (rarely absent); parenchyma sheath cells short, their chloroplasts centripetally positioned and containing large grana; sclerenchyma accompanying the smallest vascular bundles present. .... Subfam. 4. CHLORIDOIDEAE.

T. Lemma nerves 7–11; silica bodies cross to dumbbell shaped; colorless cells traversing the leaf absent. ..... Tribe 4c. UNIOLEAE.

T. Lemma nerves 7 or fewer; silica bodies saddle shaped; colorless cells traversing the leaf usually present.

U. Leaf blade disarticulation present; flowers imperfect, plants dioecious. ..... Tribe 4a. AELUROPODEAE.

U. Leaf blade disarticulation usually absent; flowers usually perfect.
V. Rachilla usually prolonged above uppermost floret; lodicules usually distally fleshy; combined adaxial and abaxial girders with an "anchor," "I," or "T" shape usually absent. ..... Tribe 4b. CYNODONTEAE.
V. Rachilla not prolonged above uppermost floret; lodicules distally membranaceous; combined adaxial and abaxial girders with an "anchor," "I," or "T" shape present. ..... Tribe 4d. ZOYSIEAE.

Subfamily 1. BAMBUSOIDEAE Ascherson & Graebner, Synop. Mitteleurop. Fl. **2:** 769. 1902.

Aquatic to terrestrial, often rhizomatous annuals, perennial herbs, or woody plants. Lodicules 2 or 3; stamens 6, sometimes fewer; stigmas 2 or more often 3. Hilum linear; embryo small, with an epiblast but without a mesocotyl. Seedling mesocotyl usually short; first seedling leaf blade generally absent. Papillae and microhairs with narrow distal cells present in the leaf epidermis (FIGURE 1b). Arm and fusoid cells often present in the mesophyll; midrib with 2 or more vascular bundles that are usually superposed; photosynthesis of the $C_3$ type (FIGURE 2a). Base chromosome number usually 12. (Including Oryzoideae Parodi ex Caro, Dominguezia **4:** 10. 1982.) TYPE GENUS: *Bambusa* Schreber. FIGURES 1b, 2a, 3A–D.

A widely distributed, almost cosmopolitan subfamily, especially in the tropics. Each of the three groups making up the subfamily is represented by an indigenous tribe in the southeastern United States: the bamboos by the Arundinarieae, the herbaceous bambusoid grasses by the Phareae, and the oryzoids by the Oryzeae. There are about ten genera and 13 species in our area.

The concept of the Bambusoideae has been expanded from comprising only the woody bamboos to include a group of tribes called (Soderstrom & Calderón, 1979a) the herbaceous bambusoid grasses (Jacques-Félix, 1955; Tateoka, 1957a; De Wet, 1958; Parodi; Clayton, 1978; Renvoize, 1981; Soderstrom, 1981a; Soderstrom & Calderón, 1974, 1979a, 1979b; Hilu & Wright; Gould & Shaw). Important similarities between the bambusoids in general and the oryzoids (Brown, 1950; De Winter, 1951; Tateoka, 1957a; Reeder, 1962; Clifford, 1965; Christopher & Abraham, 1971; Clayton, 1978, 1981a; Renvoize, 1981) warrant inclusion of rice and its relatives in this subfamily as well. The bamboos, herbaceous bambusoids, and oryzoids share character states in the flowers, bundle-sheath anatomy (Brown, 1958a; Auquier & Somers), and amino-acid composition of the caryopses (Yeoh & Watson). Two mesophyll cell types, arm and fusoid cells (FIGURE 2a), are almost unique to this subfamily (arm cells occur in *Phragmites* and some other arundinoids). Although these cells differ somewhat in bambusoids and oryzoids (Calderón & Soderstrom, 1973), their presence supports a monophyletic origin of this subfamily. Terrell & Robinson and Soderstrom (1981a) suggest that these cells may be adaptations for life in moist forests or aquatic habitats.

Because of the number of lodicules, stamens, and stigmas of many members of the Bambusoideae, the subfamily is generally considered to contain the most primitive extant grasses. On the other hand, woodiness, complex vegetative

growth and inflorescence branching, various spikelet reductions, and perhaps the presence of arm and fusoid cells are presumably derived.

Tribe 1a. **Arundinarieae** Ascherson & Graebner, Synop. Mitteleurop. Fl. **2:** 770. 1902.

Stems woody. Leaf blades with transverse veins, disarticulating. Spikelets (FIGURE 3D) solitary, with 6–12 fertile florets and 2 glumes. Lemmas 11–17-nerved. Flowers perfect, with 3 lodicules, stamens, and stigmas. Embryos with a scutellar tail. Initial or first few seedling leaves without blades. Leaf epidermis (FIGURE 1b) with microhairs, cross- to dumbbell-shaped silica bodies, and saddle-shaped silica bodies, but without oryzoid silica bodies. TYPE GENUS: *Arundinaria* Michaux. FIGURES 1b, 2a, 3D.

A tribe of 61 genera extending from a center of distribution in tropical forests to 46°N and 47°S latitudes, to 4000 m elevation, and to regions with snowy winters (Soderstrom, 1981a). The major center of diversity of the group appears to be southeastern Asia. In the New World there are 17 genera. The one native bamboo in the southeastern United States, *Arundinaria gigantea* (Walter) Muhl., is the only New World member of this genus of over 100 species (McClure, 1973). This species, commonly called giant or switch cane, consists of three subspecies that grow in moist ground from southern Maryland and Ohio to Florida and Texas. Its rhizomatous growth produces extensive populations, sometimes called canebrakes, which are sought for cattle forage and as a source of materials for fishing rods, baskets, and other purposes (Hitchcock). Hall reported that various species of *Bambusa, Pseudosasa* Makino ex Nakai, and *Phyllostachys* Sieb. & Zucc. persist after cultivation in Florida.

Holttum's study of ovary anatomy and Grosser & Liese's study of rhizome and leaf anatomy generated four concordant groups. Nevertheless, tribal limits and interrelationships are not clear (McClure, 1966; Calderón & Soderstrom, 1980; Soderstrom & Calderón, 1979b), at least in part because bamboos grow primarily in the tropics where the flora is relatively poorly known, and more importantly, because it is difficult to make good herbarium specimens of the bulky stems and branches, the growth patterns of which are taxonomically important. Moreover, because the plants flower infrequently, they are often avoided by collectors and are not well represented in herbaria.

The infrequency of flowering is associated with flowering cycles of up to 120 years in many (perhaps the majority) of bamboos (Soderstrom & Calderón, 1979a). What makes the cyclical flowering all the more fascinating is that populations of a taxon tend to flower gregariously and, after fruiting, die. The functioning of the biological clock governing this rare phenomenon is unknown. Janzen hypothesized that this mast flowering oversaturates the food supply of fruit predators. The fruits of some bamboos may be as large as an avocado, and being poorly dispersed (at least by the wind), may accumulate in large numbers under the plants following a gregarious flowering (Soderstrom & Calderón, 1979a). Although *Arundinaria* may flower annually or remain sterile for many years, its aerial stems are monocarpic like those of most bamboos. Bamboos rely predominantly on vegetative reproduction by thick, extensively branched rhizomes (McClure, 1966, 1973). Reduced selection pressures for floral evolution may explain the primitiveness of bamboo flowers.

The bamboos are unique among grasses for their long-persistent aerial stems. Their woodiness comes not from cambial activity but from caps of fibers on both sides of the vascular bundles, thick-walled and lignified ground tissue, and to some extent, silicification of the epidermis (Soderstrom, 1981a). The two-stage growth pattern of bamboo stems is also unique. It consists of a relatively short period of apical dominance characterized by rapid internode elongation and suppression of lateral appendages, and then extensive lateral branching (Calderón & Soderstrom, 1980). Soderstrom (1981a) argued that competition with tropical trees for light brought about woodiness in bamboos, and that this woodiness and the polyploidy of bamboos are evidence for their derivation from the diploid herbaceous bambusoid grasses. Clayton (1981a, *fig. 1*) presented the same phylogeny.

Another unusual feature of bamboos, which is also found in herbaceous bambusoids, is leaf torsion or "sleep movement." Leaf-pulvinus activity serves either to orient all leaves of a branching system in one plane or to move leaves from a horizontal position during the day to a reflexed one at night (Calderón & Soderstrom, 1973). In addition to their unusual flowering cycles, growth pattern, and leaf torsion, the bamboos are parasitized by fungi generally distinct from those on other grasses (Savile).

Tribe 1b. **Oryzeae** Dumortier, Obs. Gram. Belg. 83. 1824.

Annual or perennial herbs. Stems and leaves more or less aerenchymatous. Leaf blades without transverse veins, not disarticulating. Spikelets (FIGURE 3A, B) solitary, with 1 fertile floret and glumes either small or absent. Lemmas 3–5(–7)-nerved. Flowers perfect, or more often plants monoecious; lodicules 2, stamens 6 (rarely as few as 1), stigmas 2. Embryos without a scutellar tail (except in *Zizania*). First seedling leaf without a blade. Leaf epidermis with microhairs and oryzoid silica bodies, but without cross- to dumbbell-shaped silica bodies or saddle-shaped silica bodies. TYPE GENUS: *Oryza* L. FIGURE 3A, B.

A tribe containing about ten genera (Hubbard, 1973a) and 100 species. It is best known for rice, both the Asian species, *Oryza sativa,* which occasionally escapes from cultivation in the southeastern United States, and the wild rice of North America, *Zizania aquatica* L. *Oryza,* and the four native genera that represent the tribe in our area, fall into three subtribes (Terrell & Robinson). The Oryzinae include the perfect-flowered *Oryza* and *Leersia* Sw. The monogeneric Zizaniinae Hitchc. are characterized by monoecy, the presence of a scutellar tail, the fusion of pericarp and seed coat, and a karyotype of relatively large chromosomes and base numbers of 15 or 17. *Luziola* Juss. (including *Hydrochloa caroliniensis* Beauv., of our area) and *Zizaniopsis* Doell & Ascherson, of the Luziolinae Terrell & Robinson, are also monoecious, but they lack a scutellar tail, the pericarp is free from the seed coat, and the chromosomes are small with a base number of 12.

The tribe Oryzeae has been regarded as an aquatic offshoot of the bambusoids (Ghorai & Sharma). The presence of stem and leaf aerenchyma, arm and fusoid cells (Terrell & Robinson), and the least specialized vessels of the family (Cheadle, 1960) may be associated with the predominantly moist or aquatic habitats


FIGURE 3. Spikelets or their parts, **Bambusoideae** and **Arundinoideae.** A, *Zizania aquatica* (Oryzeae): A1, 2 staminate spikelets slightly after anthesis, all anthers shed but 1 (note longitudinal dehiscence), no glumes, each spikelet 1-flowered, × 3; A2, carpellate spikelet at anthesis (note styles), with pedicel and portion of rachis (palea clasped by lemma), × 3; A3, base of carpellate spikelet disarticulated from pedicel to show callus,

of this tribe. The tribe is characterized by the oryzoid type of silica body, which is found elsewhere only sparingly in the genus *Aristida* (Watson & Dallwitz, 1981). The oryzoid silica body is basically dumbbell shaped, but unlike those of similarly shaped silica bodies of other grasses, its long axis is perpendicular to the long axis of the leaf. It seems best to recognize the affinities of this tribe by including it in the Bambusoideae rather than giving it subfamilial rank (Pilger; Parodi; Stebbins & Crampton; Hilu & Wright; Gould & Shaw) or treating it as a "series" (Jacques-Félix, 1962) or a "group" (Clifford & Watson).

Difficulty in assessing homology has beset the interpretation of the parts of the spikelets and florets of the Oryzeae. Hitchcock described the spikelet as one-flowered with reduced glumes, but most agrostologists consider Hitchcock's glumes to be actually the lemmas of sterile florets below the terminal, fertile floret (De Winter, 1951). The glumes form an inconspicuous cupular structure. In his review of the numerous ideas about the fertile floret, De Winter (1951) supported Pilger's concept of fusion of two florets, with the loss of paleas from both and of lodicules, androecium, and gynoecium from one. If this view is correct, then the three-or-more-nerved "palea" is actually a lemma and is the only remaining part of the terminal floret.

Tribe 1c. **Phareae** Stapf in Thiselton-Dyer, Fl. Capensis **7**: 319. 1898.

Perennial herbs. Leaf blades with obliquely oriented main veins connected by transverse veins, not disarticulating. Spikelets paired (1 carpellate and 1 staminate), with 1 fertile floret and no glumes. Lemmas few nerved. Stamens 6; stigmas 3. Embryos mostly without a scutellar tail. First seedling leaf with a blade. Leaf epidermis with cross- to dumbbell-shaped silica bodies, but without microhairs, saddle-shaped silica bodies, or oryzoid silica bodies. TYPE GENUS: *Pharus* P. Br. FIGURE 3C.

The Phareae are made up of the African genus *Leptaspis* R. Br. and *Pharus*, a New World genus of eight species. *Pharus* has survived where other herbaceous bambusoids presumably have not because it is successful in disturbed sites and disperses well (Soderstrom, 1981a). The sole member of the tribe in our area, *P. parvifolius* Nash, is rare in northern and central Florida (Hall).

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lemma (to right) and palea partly separated, styles protruding (spikelet rotated 90° from position in A2), × 6. B, *Leersia oryzoides* (Oryzeae), spikelet (lemma and palea separated, glumes absent), × 6. C, *Pharus parvifolius* (Phareae): C1, staminate (pedicellate) and carpellate spikelets (sessile; note dense pubescence [individual uncinate hairs not visible at this scale]), × 4; C2, staminate spikelet, showing 4 of 6 stamens, × 6; C3, lemma of carpellate floret completely enclosing palea (note 3 protruding styles), × 4. D, *Arundinaria gigantea* (Arundinarieae): D1, spikelet, × 2; D2, floret (lemma clasping palea), × 3. E, *Danthonia spicata* (Arundineae): E1, spikelet, × 3; E2, floret (lemma awned; note rachilla segment), × 5. F, *Chasmanthium latifolium* (Centotheceae): F1, spikelet, × 1.5; F2, floret, × 3; F3, caryopsis, × 5. G, *Phragmites australis* (Arundineae): G1, spikelet (parts spread out and hairs omitted for clarity), × 4; G2, floret with villous rachilla segment, × 5. H, *Arundo Donax* (Arundineae): H1, spikelet, × 3; H2, floret (from adaxial side; note hairs along edge of lemma and glabrous rachilla segment), × 3.

The herbaceous bambusoid grasses as a group consist of eight tribes and 24 genera (Soderstrom, 1981a). Only five genera are native to the Old World, while 21 occur from Mexico to Argentina, especially between 10°N and 9°S latitudes, mostly below 850 m, and in forest shade or more open places (Soderstrom & Calderón, 1979b). In addition to the characters of the APPENDIX that separate them from the more evolutionarily advanced bamboos, the herbaceous bambusoids differ in being mostly diploid, rather than mostly tetraploid or hexaploid (Hunziker *et al.*), and in their much simpler stem branching. Otherwise the boundary between the two groups is not well marked.

Animal pollination has developed in herbaceous bambusoids in response to the relative lack of wind in their habitats (Soderstrom & Calderón, 1971). In *Eremitis* Doell cleistogamy in subterranean spikelets (Soderstrom & Calderón, 1974) may also be a compensation for lack of wind. The strongly twisted awns of *Streptochaeta* (Soderstrom, 1981a) and the short, hooked hairs of the persistent lemma of *Leptaspis* (Bor) and perhaps those of *Pharus* are evidently adaptations for catching on animal fur.

The regularly produced spikelets of herbaceous bamboos may be inconspicuously situated within leaf sheaths, behind broad leaves, or even under leaf litter (Calderón & Soderstrom, 1980). Hence these plants may be as neglected by collectors as the bamboos are. The herbaceous bamboos are, however, better understood taxonomically. The flower of *Streptochaeta* is solitary and subtended by numerous spirally arranged bracts (V. M. Page; Soderstrom, 1981a). These specialized structures, called pseudospikelets (McClure, 1966, 1973), are also found in some bamboos (Soderstrom, 1981a). Leaf torsion is also common to both groups.

Subfamily 2. ARUNDINOIDEAE Tateoka, Jour. Jap. Bot. **32:** 377. 1957, "Arundoideae."

Perennial (rarely annual) herbs (in *Phragmites* somewhat woody). Ligules fringed or of hairs. Embryo with a scutellar tail and a long mesocotyl. First seedling leaf blade curved or supine. Microhairs with a narrow distal cell. Photosynthesis mostly $C_3$ ($C_4$ in about 7 genera, including *Aristida* and probably *Neyraudia* of our area). Base chromosome number (11) 12. (Centothecoideae Soderstrom, Taxon **30:** 614. 1981, as "Centostecoideae." Phragmitoideae Parodi ex Caro, Dominguezia **4:** 13. 1982. Aristidoideae Caro, *ibid.* 16.) TYPE GENUS: *Arundo* L. FIGURES 3E–H, 7B.

A subfamily treated by Renvoize (1981) as comprising eight tribes and 72 genera. It is represented in the southeastern United States by three tribes, four genera, and about 30 species.

Subfamily Arundinoideae is the least sharply defined and the most undoubtedly polyphyletic of the subfamilies. The APPENDIX shows the variability in numerous characters that are taxonomically discriminating for other subfamilies—for example, hilum shape (character 35), embryo size (36), seedling morphology (43, 45), and some leaf-epidermal (59–62) and transverse-sectional characters (63, 67, 75, and 82). Internal diversity in leaf ultrastructure (Carolin *et al.*) and in amino-acid profiles (Taira) surpasses that of other subfamilies.

It is not surprising, then, that discussions of the subfamily focus on phrases such as "miscellaneous group" (De Wet, 1958), "less homogeneous" (Stebbins & Crampton), "unspecialised subfamily" (Clayton, 1978), and "loosely related genera" (Renvoize, 1981), or that Clayton's *fig. 1* (1981a) shows this subfamily, as defined by Renvoize, to be paraphyletic.

The taxonomic concept of this group varies from one considerably broader than Renvoize's to one separating one to all three of the tribes of our area into different subfamilies (Pilger; Parodi; Clayton, 1978), "series" (Jacques-Félix, 1962), or groups (Clifford & Watson). Prat (1960) and Stebbins & Crampton agreed with Renvoize at least in including the Aristideae, Arundineae, Centotheceae, and Danthonieae in the subfamily. The results of Renvoize's multivariate analysis illustrate arundinoid taxonomic complexity well. Of the 72 genera he included, only 43 formed an "arundinoid nucleus," and 29 were peripheral. This nucleus, except for *Lygeum* L. and a few peripheral genera, makes up his Arundineae. The taxonomic relationships of *Lygeum, Danthonia,* and *Neyraudia* of Renvoize's Arundineae, as well as of four of Renvoize's peripheral tribes (Aristideae, Centotheceae, Ehrharteae Link, and Micraireae Pilger) need further study. This diverse assemblage holds together because its members have slightly more similarity to each other than to other grasses.

That only four genera of arundinoids are native to the southeastern United States reflects the Old World, Southern Hemisphere, subtropical, and Gondwanaland distribution of the subfamily (Clayton, 1975; Cross). The wide geographic distribution hints at considerable age.

Tribe 2a. **Aristideae** C. E. Hubbard in Bor, Grasses Burma, Ceylon, India, Pakistan, 685. 1960.

Annuals or perennials. Spikelets 1-flowered, with a 3-awned lemma. Embryo without an epiblast. Two kranz bundle-sheaths present. Base chromosome number 11. TYPE GENUS: *Aristida* L. FIGURE 7B.

A tribe considered by De Winter (1965) to comprise the large, cosmopolitan, often xerophytic *Aristida* (330 species) and two primarily African genera, *Stipagrostis* L. and *Sartidia* De Winter. In our area there are about 20 species of *Aristida* (Hitchcock).

Depending upon what aspect of the plant one considers, the Aristideae resemble several other groups. The overall similarity of spikelets, caryopses, and base chromosome number to those of the Stipeae are countered by a wealth of differences in ligules (character 7 of the APPENDIX), lemma-awn and nerve numbers (20, 22), lodicule number (24), embryos (38–40), silica bodies (52), and leaf anatomy (66, 67, and 78). The Aristideae have often been associated with chloridoids on the bases of leaf-mesophyll anatomy (characters 67, 78) (Brown, 1958a; De Winter, 1965; Carolin *et al.*; Sutton) and amino-acid patterns of the caryopses (Yeoh & Watson). But again, there are more differences: lemma-awn number (20), lodicule texture (25), epiblasts (38), microhair distal-cell shape (49), silica-body type (52), and base chromosome number (84). The presence of microhairs with narrow distal cells and cross- to dumbbell-shaped silica bodies in the leaf epidermis unites the Aristideae and the Panicoideae.

Furthermore, in longitudinal sections of leaves, the parenchyma-sheath cells are longer than wide in both the Aristideae and the Paniceae (Brown, 1974, 1975). These cells are usually isodiametric in chloridoids. Nevertheless, there are important differences between the Aristideae and the Paniceae in lodicule texture (25), embryonic leaf margins (41), silica-body types (52, 56, 57), colorless cells traversing the leaf (78), and base chromosome number (84).

In a consideration of the systematic position of the Aristideae, an important character is the unique double kranz sheath of *Aristida*. In all other $C_4$ grasses, the kranz bundle-sheath has evolved either from the parenchyma sheath (most chloridoids, danthonioids, and some panicoids) or the mestome sheath (some panicoids) (Brown, 1977). In *Aristida* both sheaths are kranz, giving the cross-sectional anatomy of the leaves a distinctive double sheath (Lommasson; Brown, 1958a).

Brown (1977) viewed the Aristideae as specialized, single-floreted Danthonieae and argued that the Aristideae arose from some danthonioid ancestor, possibly in southern Africa. Bourreill (1969) claimed that the wide distribution of *Aristida* indicates a Cretaceous beginning for the genus. His hypothesis (1968) about intratribal phylogeny disagrees with Brown's (1977) and does not give enough weight to the probably derived double sheath of *Aristida*.

Tribe 2b. **Arundineae** Dumortier, Obs. Gram. Belg. 82. 1824, "Arundinaceae."

Perennials. Spikelets 2- to many-flowered (except in axillary cleistogamous spikelets of *Danthonia*). Rachilla prolonged above uppermost floret. Stamens 3. Embryo without an epiblast. Parenchyma sheaths with large vacuoles and no chloroplasts. Bulliform cell groups absent from leaves. Base chromosome number 12. (Elytrophoreae Jacques-Félix, Jour. Agr. Trop. Bot. Appl. **5:** 304. 1958. Cortaderieae Zotov, New Zealand Jour. Bot. **1:** 83. 1963. Danthonieae Zotov, *ibid.* 86. Molineae Jirásek, Preslia **38:** 33. 1966.) TYPE GENUS: *Arundo* L. FIGURE 3E, G, H.

According to Renvoize's (1981) circumscription, a tribe of 57 genera. Five genera, all posing taxonomic problems, grow in the southeastern United States. Both *Arundo,* with one Old World species (*A. Donax* L., the reed, FIGURE 3H), and *Phragmites* Adanson, whose single species in our area (*P. australis* (Cav.) Steudel (*P. communis* Trin.), FIGURE 3G) has the widest geographic distribution of any angiosperm (L. G. Holm *et al.*), are peripheral in the tribe. Their stomata are narrower than the intervening epidermal cells and dominate the intercostal zones. *Phragmites* is unusual in the invaginated walls of the mesophyll cells (see Decker's *fig. 3*), which resemble bambusoid arm cells.

*Cortaderia* Stapf, pampas grass, a genus of the Southern Hemisphere represented in our area by the frequently planted ornamental *C. Selloana* (Schultes) Ascherson & Graebner, is unique in the subfamily in that its vascular bundles are linked by sclerenchyma to the adaxial leaf surface only. It was one of the ungrouped genera of Renvoize's Arundineae. Zotov put it in its own tribe, the Cortaderieae. *Neyraudia* Hooker f. is a small Old World genus of the Southern Hemisphere, represented by *N. Reynaudiana* (Kunth) King & Hitchc., an escape in Florida (Hall). It was placed in the Eragrostideae (the Cynodonteae in

this paper) because of its embryo anatomy (Decker) and its radially arranged mesophyll. Brown (1977) put it in the Tristegineae (Melinideae) of the Panicoideae because of its PS subtype of kranz leaf anatomy, but there is no biochemical evidence to verify its $C_4$ photosynthesis. Phillips suggested that the genus lies on the boundary between the Arundinoideae and the Chloridoideae. On the whole, morphological and anatomical data support placement of *Neyraudia* in the Arundinoideae (Tateoka, 1957a; Stebbins & Crampton; Jacques-Félix, 1962; Clifford & Watson; Renvoize, 1981).

Finally, *Danthonia* DC. in Lam. & DC. (FIGURE 3E), represented by only three species in the Southeast, is the largest genus of a primarily Southern Hemisphere group often recognized as the Danthonieae. Traditionally, it was grouped with the Aveneae because of its many-flowered, laterally compressed spikelets. However, Hubbard (1948), De Wet (1954, 1956), and Reeder (1957) pointed out numerous differences in spikelets, karyotypes, embryo anatomy, and leaf anatomy. Its intermediacy between the pooid and panicoid extremes of the family makes it a taxonomic problem. Since it fits quite well into Renvoize's arundinoid nucleus, he sank the Danthonieae into the older Arundineae. Nevertheless, the danthonioids remain a diverse group containing both $C_3$ genera, such as *Danthonia,* and $C_4$ genera, such as *Allochaete* Hubb., *Asthenatherum* Nevski, and *Pheidochloa* S. T. Blake. Further study of the group may elucidate some aspects of evolution in the family as a whole.

Many genera of the Arundineae are small and not dominant floristic elements—a situation that suggested to Renvoize (1979) that they are competitively inferior relative to the mainstream of grass evolution.

Tribe 2c. **Centotheceae** Ridley, Mater. Fl. Malay. Penin. **3:** 122. 1907.

Perennials. Spikelets awnless, few- to many-flowered (FIGURE 3F); rachilla not prolonged above uppermost floret. Stamen[s] 1 [generally 3 in other centothecoids]. Embryo without an epiblast. Parenchyma-sheath vacuoles not as large as those of the Arundineae. Bulliform cell groups prominent in leaves. Base chromosome number 12. TYPE GENUS: *Centotheca*[3] Desv. FIGURE 3F.

A group of nine genera and 26 species, represented in the southeastern United States by *Chasmanthium* Link. This endemic genus of five woodland species has its center of distribution in our area (Yates).

Many-flowered, laterally flattened spikelets made *Chasmanthium* an unquestioned member of the pooid alliance until Reeder (1957, 1962) demonstrated a unique embryo anatomy for this and related genera. Jacques-Félix (1962), Reeder (1962), and Decker established a centothecoid group on the basis of the transversely veined (tessellate) and pseudopetiolate leaves, truncate and heavily vascularized lodicules, distinctive embryo, narrow distal cell of the microhairs, dumbbell-shaped silica bodies, prominent bulliform cell groups in the leaves, and base chromosome number of 12. In addition, the plants of

[3]Reeder (Taxon **30:** 348, 349. 1981) has proposed the conservation of this spelling over *Centosteca,* an orthographic error.

this group grow in moist, often tropical forests, in contrast to the various habitats of the largely temperate pooids.

Jacques-Félix (1962) put his centothecoid series on an evolutionary line defined by embryo type between bamboos and chloridoids, but not far from the arundinoid series (see his *figs. 32* and *33*). Brown (1958a), Brown & Smith (1974), Clayton (1978), Ghorai & Sharma, and Renvoize (1981) mentioned ill-defined relationships with the bamboos. Soderstrom & Decker (1973), however, outlined numerous differences between the groups in leaf anatomy, lodicule morphology, caryopsis compression, and hilum shape. There are similarities to panicoids in amino-acid patterns (Taira) and smut pathogens (Watson), and to oryzoids in seedlings (Hoshikawa) and karyotypes (De Wet, 1960b). Tribe Centotheceae or its genera have either been placed in the Arundinoideae or its equivalent (Tateoka, 1957a; Prat, 1960; Parodi; Stebbins & Crampton; Yates; Renvoize, 1981) or been given the status of subfamily (Clayton, 1978; Soderstrom, 1981b; Gould & Shaw) or an informal, high-level group (Clifford & Watson). Whatever the rank, there is now a consensus about the composition of the group (Clayton, 1978; Renvoize, 1981; Soderstrom, 1981b). It fits into Renvoize's broad definition of the Arundinoideae, and differences from arundinoids in the palisade layer of the mesophyll, in nucleolus persistence (Brown & Emery, 1957), and in seedlings (Hoshikawa) do not warrant separation of the two groups at the level of subfamily.

The inclusion of *Chasmanthium* in *Uniola* L. by most authors prior to Yates's work reflects a striking example of convergent evolution in spikelet morphology. The Unioleae are a monogeneric tribe of the Chloridoideae (q.v.). *Chasmanthium* differs from other centothecoids in not having transversely veined and strongly pseudopetiolate leaves and in some aspects of leaf anatomy (Decker). In leaf cross-section it resembles some members of the Arundineae. In general, however, it is unquestionably centothecoid.

Subfamily 3. POOIDEAE [A. Braun in Ascherson, Fl. Prov. Brandenb. 32, 810. 1864, "Poëideae"].

Ligules membranaceous. Spikelet disarticulation usually above the glumes; rachilla prolonged above the uppermost floret. Staminate or neuter florets usually distal to lowermost carpel-bearing floret; lemmas usually with 3 or more nerves. Lodicules distally membranaceous, weakly vascularized. Hilum generally linear. Embryos small; epiblast present or absent, scutellar tail absent,

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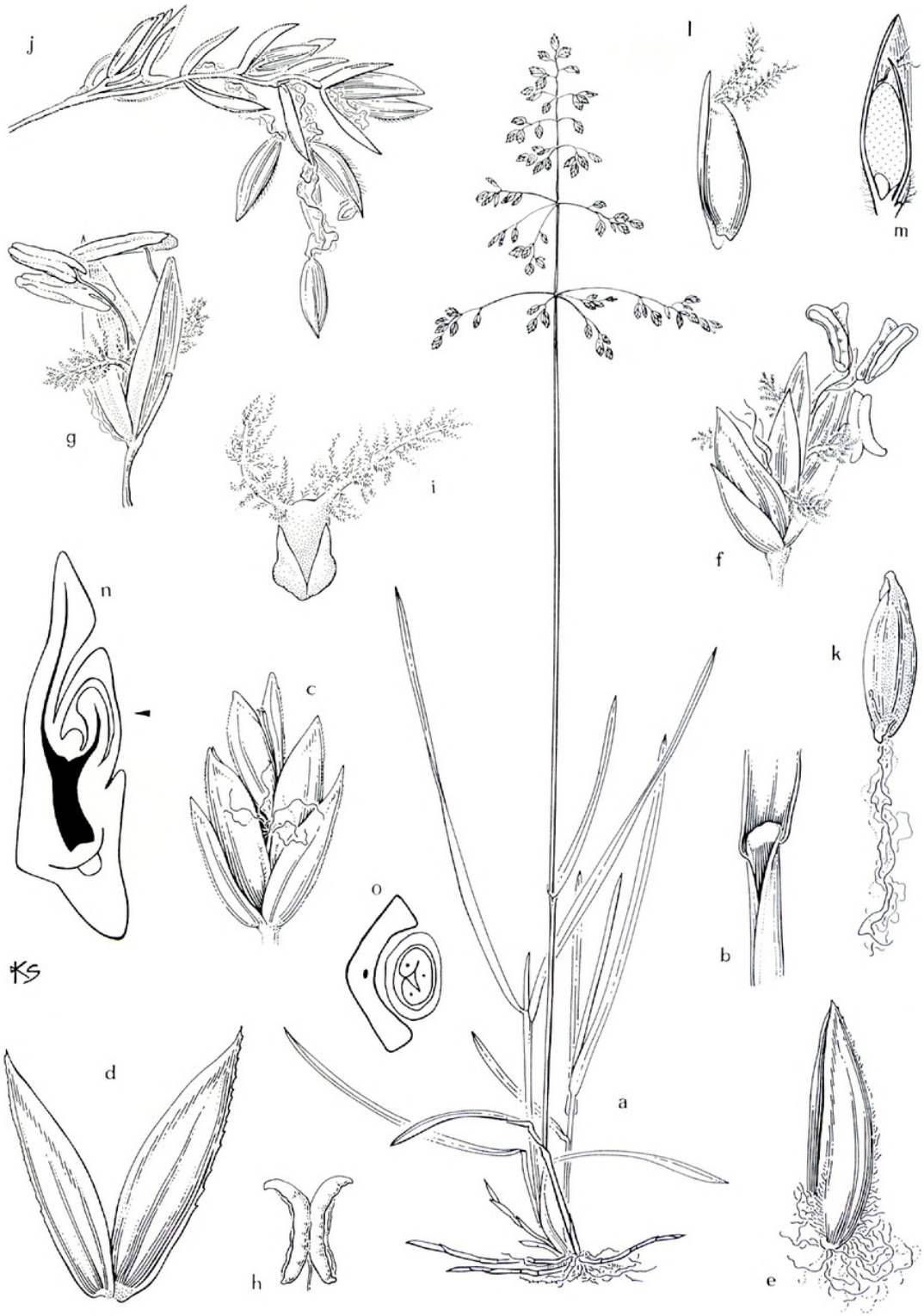
FIGURE 4. **Poa** (Pooideae, Poeae). a–o, *P. pratensis*: a, flowering plant with lateral stolons at base, × ½; b, apex of leaf sheath, ligule, and base of blade, × 3; c, spikelet, × 12; d, glumes, first glume to left, × 20; e, floret before anthesis, the lemma long-pubescent below, × 12; f, spikelet with lower flower open and stigmas receptive, the second floret open, anthers dehisced, × 12; g, floret at anthesis, lemma to left, palea and rachilla to right, × 12; h, dehisced anther with 2 locules, × 12; i, turgid lodicules and gynoecium with receptive stigmas, removed from open floret, × 15; j, portion of inflorescence with mature fruits, 2 florets falling from spikelets, disarticulation occurring above glumes and between florets, × 6; k, floret in fruit (note pubescent lemma), × 12; l, caryopsis, lemma removed, palea to left, × 12; m, caryopsis in diagrammatic longitudinal section, lemma to left, palea to right, endosperm stippled, embryo unshaded,




× 12; n, embryo in diagrammatic longitudinal section (scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black), showing no internode between scutellar and coleoptilar nodes, epiblast (small flaplike structure opposite scutellum), and no cleft between base of scutellum and coleorhiza; o, diagrammatic transverse section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in "n," showing few vascular bundles in leaf, margins of which meet but do not overlap ("n" and "o" redrawn after Reeder, 1957, *fig. 2*).

mesocotyl short, embryonic leaf margins not overlapping. First seedling leaf usually narrow and erect. Microhairs absent; elongated, sinuous or crenate silica bodies present; subsidiary cells parallel sided. Photosynthesis exclusively of the $C_3$ type. Base chromosome number most commonly 7. (Festucoideae Rouy, Fl. France **14:** 28. 1913.) TYPE GENUS: *Poa* L. FIGURES 1a; 2b; 4; 5A–C, E–I; 6.

A subfamily of about 155 genera in eight tribes and two subtribes (Macfarlane & Watson, 1982). Six tribes are represented in the southeastern United States by about 40 genera and 132 species.

The center of distribution of the Pooideae is the Mediterranean area (Cross). The not-nearly-as-diverse North American pooid component may represent immigrants from Europe before the separation of North America and Europe in the Eocene (Clayton, 1975). Today members of the Pooideae characteristically grow at high latitudes, especially in the Northern Hemisphere (Hartley, 1950, 1973; Cross). Past dispersal along tropical mountains presumably took members of the subfamily to the Southern Hemisphere.

Robert Brown's (1814) perceptions of spikelet morphology clearly defined the panicoids but left other grasses in one heterogeneous group, the pooids. The use of other character suites by Avdulov, Prat (1932, 1936), Reeder (1957, 1962), and Brown (1958a) led to the removal of major groups such as the bambusoids, arundinoids, and chloridoids from the Brownian Poeae. Decker and Macfarlane & Watson (1980, 1982) sharpened the limits of the subfamily even further and produced a reasonably homogeneous taxon, although there is no unique character state holding all pooids together. As a result of Macfarlane & Watson's thorough studies, three traditionally pooid tribes (Brachyelytreae, Diarrheneae, and Stipeae) have been removed from the subfamily. Until more is known about these tribes it seems best to leave them unplaced (see tribes 6a–c).

In supertribe Poanae there are five tribes: the Agrostideae, Aveneae, Meliceae, and Poeae, in our area; and the Seslerieae, a small tribe in the Mediterranean region. Supertribe Triticanae Macfarlane & Watson contains tribes Bromeae and Triticeae, which occur in our area, and the monogeneric Brachypodieae of tropical mountains. The two supertribes differ in numerous ways: presence or absence of auricles, number of nerves in the lemma awns, spikelet and caryopsis length (Macfarlane & Watson, 1982), lodicule and ovary-apex hairiness (characters 26 and 29 of the APPENDIX), presence of an epiblast (38), seedling mesocotyls (43; Harberd), and transitionary node roots (Hoshikawa). For most of these characters, considerable variability in one or more of the tribes produces overlap between the two supertribes. In addition, chemical differences exist in chain length of the starch fructosan (D. Smith, 1973), redundant DNA sequences (Bendich & McCarthy), enzyme kinetics of RuBP carboxylase (Yeoh *et al.*), pollen antigens (Watson & Knox), and the kinds of caryopsis glycosides (De Cugnac), globulins (P. Smith), and amino acids (Yeoh & Watson). Starch grains (character 42 of the APPENDIX) are simple or compound in the Poanae and always simple in the Triticanae. With the exception

of this difference in starch grains, these chemical features are like the morphological characters in not being entirely definitive. The great number of these divergent tendencies, however, supports recognition of the two groups.

Tribe 3a. **Agrostideae** Dumortier, Obs. Gram. Belg. 83. 1824.

Spikelets usually 1-flowered. Ovary apex usually glabrous. Hilum usually punctiform. Embryo with an epiblast. At least some starch grains compound. (Phalarideae Dumort. Anal. Fam. Pl. 64. 1829. Milieae Endl. Fl. Posoniensis, 109. 1830. Anthoxantheae Endl. *ibid.* 113.) TYPE GENUS: *Agrostis* L. FIGURES 2b, 5G.

The Agrostideae, as delimited by Macfarlane & Watson (1982), are the largest tribe in the Pooideae. Its 55 genera are most abundant relative to other grasses north of a line between 52° and 62°N latitude, with southern extensions in eastern and western North America (Hartley, 1973). Nineteen genera and about 50 species occur in the southeastern United States. Thirteen of the genera (*Agrostis, Alopecurus* L., *Ammophila* Host, *Calamagrostis* Adanson, *Cinna* L., *Deschampsia* Beauv., *Hierochloë* R. Br., *Koeleria* Pers., *Limnodea* L. H. Dewey, *Milium* L., *Phalaris* L., *Sphenopholis* Scribner, and *Trisetum* Pers.) have indigenous species. Six genera (*Aira* L., *Anthoxanthum* L., *Holcus* L., *Lagurus* L., *Phleum* L., and *Polypogon* Desv.) indigenous mostly to Europe are represented in our area by one or more adventive species.

The Agrostideae are most closely related to the Aveneae; the relationship between the two tribes is discussed under the latter. Both tribes also appear to be close to the Poeae serologically (P. Smith), in enzyme kinetics of RuBP carboxylase (Yeoh *et al.*), and in being the only tribes of grasses in which the endosperm is liquid in some species (Terrell; Macfarlane & Watson, 1982). These three tribes may form a "reticulate biological unit" (Hilu & Wright).

The tribe Phalarideae has been recognized on the basis of the presence of reduced structures between the glumes and the single, perfect terminal floret of spikelets in its three genera (*Anthoxanthum, Hierochloë,* and *Phalaris*). These reduced structures, often thought to be sterile lemmas (Hitchcock), are not necessarily homologous between genera. Barnard considered the spikelet of *Anthoxanthum* to consist of four sterile glumes and two lemmas, each of which subtends a single stamen. The gynoecium forms directly from the apex of the spikelet axis. Since nothing else sets these genera off from agrostoid or avenoid grasses, the Phalarideae have been lumped either with the Agrostideae (Macfarlane & Watson, 1982) or the Aveneae (Clayton, 1978), or with the combined Agrostideae and Aveneae (Tateoka, 1957a; Stebbins & Crampton; Hilu & Wright).

Tribe 3b. **Aveneae** Dumortier, Obs. Gram. Belg. 82. 1824, "Avenaceae."

Spikelets usually 2–7-flowered. Ovary apex usually hairy. Hilum linear. Embryo with an epiblast. At least some starch grains compound. TYPE GENUS: *Avena* L.

Macfarlane & Watson (1982) included eight genera in the Aveneae. Four are confined to the Old World, one to the New, with three occurring in both. In our area the tribe is represented by three adventive species in three genera, *Avena* (*A. fatua* L.), *Amphibromus* Nees (*A. scabrivalvis* (Trin.) Swallen), and *Arrhenatherum* Beauv. (*A. elatius* (L.) Mert. & Koch).

This tribe is so similar to the Agrostideae that many workers (Pilger; Tateoka, 1957a; Stebbins & Crampton; Watson; Hilu & Wright) have united the two. On the basis of rather small samples, it seems that the two tribes are not distinct serologically (P. Smith), embryologically (Maze & Bohm, 1974), or in terms of enzyme kinetics of RuBP carboxylase (Yeoh *et al.*). In contrast, immunology (Watson & Knox) and amino-acid complements (Yeoh & Watson) appear to separate the two tribes, but sample sizes here were also small. Macfarlane & Watson (1982), who have made the most recent and thorough study of the two groups, maintain them as tribes. In addition to noting differences in the number of florets per spikelet, hairiness of the ovary apex, and hilum shape (see characters 15, 29, and 35 in the APPENDIX), they pointed out tendencies for the Aveneae to bear longer spikelets, awns from terminal notches (rather than abaxially), and lower glumes with more than one vein (rather than usually a single vein).

Tribe 3c. **Meliceae** Reichenbach, Consp. Reg. Veg. 53. 1828, "Melicaceae."

Lodicules usually connate, truncate, and distally fleshy. Ovary apex glabrous. Leaf-sheath margins more or less connate. Embryo with an epiblast. Base chromosome number 9 or 10. TYPE GENUS: *Melica* L. FIGURE 5A–C.

A tribe of nine genera that do not form a closely interrelated group (Hilu & Wright; Macfarlane & Watson, 1982). Three genera, *Glyceria* R. Br., *Melica*, and *Schizachne* Hackel, with about 12 species, occur in our area.

The Meliceae are distinguished from other pooids by unusual lodicules and relatively small chromosomes with base numbers atypical for the subfamily.

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FIGURE 5. Spikelets and their parts, **Pooideae, Stipeae,** and **Brachyelytreae.** A, *Glyceria striata* (Meliceae), × 12: A1, spikelet; A2, floret with portion of rachilla. B, *Glyceria septentrionalis:* B1, spikelet, × 3; B2, floret with portion of rachilla, × 6. C, *Melica mutica* (Meliceae), × 5: C1, spikelet; C2, fertile floret with segment of rachilla; C3, upper fertile floret with knoblike cluster of empty lemmas. D, *Brachyelytrum erectum* (Brachyelytreae): D1, spikelet with long-awned lemma, × ½; D2, spikelet, showing second glume (first glume absent), fertile floret with lemma and palea (lemma awn not shown), and rachilla extending upward as bristle against palea, segment of rachis to right of spikelet, × 5. E, *Lolium perenne* (Poeae): E1, spikelet with portion of rachis, × 3; E2, second floret from base of spikelet, lemma without awn, palea toward viewer, × 5; E3, awned lemma of fertile floret, palea hidden from view, × 5. F, *Briza minor* (Poeae): F1, spikelet, × 6; F2, floret with rachilla segment, palea not visible, × 12; F3, same, seen from axis, palea visible within lemma, × 12. G, *Agrostis hiemalis* (Agrostideae), × 12: G1, spikelet, showing glumes and single floret; G2, floret (lemma) enclosing caryopsis, palea absent. H, *Elymus repens* (*Agropyron repens*) (Triticeae), × 3: H1, spikelet with part of rachis behind it (contrast with E1); H2, floret from near base of spikelet, showing back of awned lemma; H3, same, showing palea. I, *Elymus canadensis* (Triticeae), × 2: I1, section of rachis with a pair of spikelets, each with 2 glumes and 1 floret; I2, upper florets of a


spikelet, lateral view showing awned lemma. J, *Piptochaetium avenaceum* (*Stipa avenacea*) (Stipeae): J1, spikelet with single floret (only base of lemma awn shown), × 2; J2, floret, to show relative length of hygroscopic lemma awn, × ½; J3, floret, note hairy base of lemma and rachilla forming bearded, sharp-pointed callus, lemma clasping pointed palea (only base of lemma awn shown), × 5; J4, palea, × 5.

The tribe is also serologically distinct (on the basis of *Melica* alone—Fairbrothers & Johnson, P. Smith) and is unusual among pooids for its sometimes abundantly papillose leaf epidermis, uniformly thickened walls of the inner bundle sheath (Decker), and scarcity of silica bodies in the leaf epidermis (Stebbins & Crampton). Although in most characters the tribe certainly belongs in the supertribe Poanae, its similarity to the supertribe Triticanae in disaccharides and oligosaccharides in the seeds (MacLeod & McCorquodale), amino-acid patterns of the caryopses (Yeoh & Watson), and enzyme kinetics of RuBP carboxylase (Yeoh *et al.*) hints that it may be intermediate between the two supertribes.

Tribe 3d. **Poeae** [R. Brown in Flinders, Voy. Terra Austral. **2:** 583. 1814].

Leaf vernation often folded. Ovary apex glabrous. (Festuceae Dumortier, Obs. Gram. Belg. 82. 1824. Including Monermeae C. E. Hubb. in Hutchinson, Brit. Fl. Pl. 332. 1948.) TYPE GENUS: *Poa* L. FIGURES 4; 5E, F.

A tribe of 50 genera (Macfarlane & Watson, 1982), primarily north-temperate in distribution. According to Hartley (1950), they are most abundant relative to other grasses north of the 50°F isotherm for mean temperature of the mid-winter month. Four (*Festuca* L., *Poa, Puccinellia* Parl., and *Vulpia* K. C. Gmelin) of the ten genera found in the southeastern United States are represented by native species. The other genera, *Briza* L., *Catapodium* Link, *Cynosurus* L., *Dactylis* L., *Lolium* L., and *Parapholis* C. E. Hubb., are mostly natives of Europe. In all, there are approximately 37 species of this tribe in our area. The Monermeae, containing the genus *Parapholis* of our area, have been included in the Poeae by Macfarlane & Watson (1982).

The group is rather heterogeneous morphologically, serologically (P. Smith), and in the composition of seed carbohydrates (MacLeod & McCorquodale) and fructosans (D. Smith, 1968, 1973). The only pooid tribe with more multistate characters in the APPENDIX is also the only larger tribe, the Agrostideae. The Poeae are morphologically very close to both the Agrostideae and the Aveneae (see discussion under Agrostideae). The Poeae differ from the other two tribes in having folded, rather than rolled, vernation (character 6 of the APPENDIX) and in the presence of crescentic silica bodies in the leaf epidermis (56). They differ further from the Agrostideae in the number of florets per spikelet (15), and from the Aveneae in the lodicule apex (27) and ovary apex (29).

Tribe 3e. **Bromeae** Dumortier, Obs. Gram. Belg. 82. 1824, "Bromaceae."

Stem leaf sheaths united into a tube. Lemma awns abaxial or from a terminal notch. Ovary appendage hairy, terminal; styles laterally positioned. Embryo without an epiblast. Starch grains all simple. TYPE GENUS: *Bromus* L.

The genus *Bromus* (about 50 species) is distributed in cooler regions throughout the world. It is usually either isolated as a monogeneric tribe (Clayton, 1978; Hilu & Wright; Macfarlane & Watson, 1982) or grouped with *Boissiera* Hochst. & Steudel (Bor). About 15 species of *Bromus,* two-thirds of them adventive, occur in the southeastern United States.

Inflorescence and spikelet morphology alone dictate placement of *Bromus* in the Poeae, and it has often been placed there (e.g., Hitchcock; Pilger; Prat, 1960; Parodi; Jacques-Félix, 1962; Decker; Hubbard, 1973a; Gould & Shaw). Hubbard (1948) and Stebbins & Crampton, while maintaining *Bromus* in the Poeae, pointed out that its starch grains are all simple (first noted by Harz) and never compound like those of members of the Poeae.

Both Avdulov and Hubbard (1948) noted the similarity of *Bromus* and the Triticeae in their starch grains and hairy ovary apices. In addition, the Bromeae and Triticeae share numerous morphological, anatomical, and other character states (see discussion of subfam. Pooideae). The two tribes are clearly distinct from one another, however, in secondary-inflorescence form (character 10 of the APPENDIX), lemma-awn position (21), lodicule hairiness (26), and ovary appendage (30). The Bromeae also differ from the Triticeae in amino-acid composition of the caryopses (Yeoh & Watson). The Bromeae have been considered to be a linking group between the Triticeae and other pooids (P. Smith; Clayton, 1978).

Tribe 3f. **Triticeae** Dumortier, Obs. Gram. Belg. 82. 1824.

Inflorescence a solitary spike. Lemma awns apical. Lodicules hairy. Ovary apex hairy. Embryo with or without an epiblast. Starch grains all simple. (Hordeae Spenner, Fl. Friburg. **1:** 155. 1825. Secaleae Reichenb. Consp. Reg. Veg. 48. 1828. Brachypodieae Harz, Linnaea **43:** 15. 1880. Frumenteae Krause, Verh. Nat. Ver. Preuss. Rheinl. **59:** 172. 1903.) TYPE GENUS: *Triticum* L. FIGURES 1a; 5H, I; 6.

The Triticeae are not a prominent tribe in our area, for there are only about nine indigenous species in three genera (*Agropyron* Gaertner, *Elymus* L. [including *Hystrix* Moench], and *Hordeum* L.). About seven species in five genera (*Aegilops* L., *Agropyron, Hordeum, Secale* L., and *Triticum*) are adventive, mostly from Eurasia. In North America the tribe is more common at latitudes north of 35°N (Dewey). Worldwide, it is most frequent relative to other grasses in low-lying areas in and near Asia Minor, Iraq, the Caspian Sea, and to a lesser extent, the western United States (Hartley, 1973).

The Triticeae, easily recognized by the spicate inflorescences, form a close-knit group (Macfarlane & Watson, 1982) most closely related to the Bromeae (see discussion under the latter tribe). Within the tribe, however, there have been widely differing opinions about generic limits, ranging from a monogeneric concept (Stebbins, 1956a) to the most generally accepted circumscription of 15 to 30 genera (Baum, 1982a, 1982b, 1983; Dewey). Taxonomic problems persist in the group, although the economic importance of some of its members as cereals (wheat, barley, and rye [*Secale cereale* L.]) and as forage and range grasses (*Agropyron* and *Elymus*) has motivated extensive research.

The Triticeae are remarkable for the great extent of intergeneric hybridization. For the 28 genera Baum (1982a) recognizes, he records 65 intergeneric crosses or about 17 percent of all possible intergeneric hybrids. Only five genera do not hybridize with others, while *Agropyron* and *Hordeum* each cross with 14 other triticoid genera. It is therefore not surprising that the taxonomy of this tribe at both generic and specific levels is difficult and that polyploidy

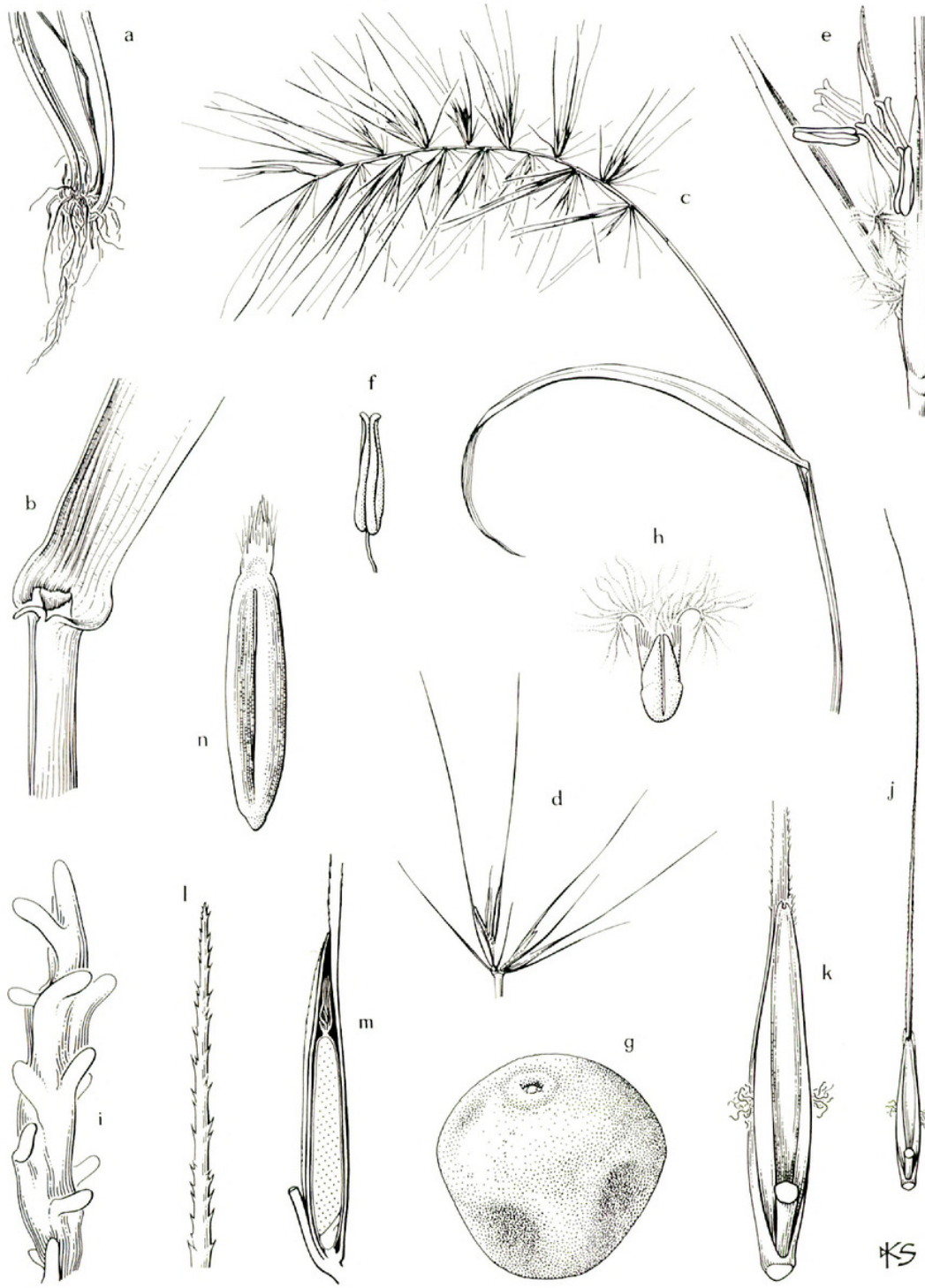


FIGURE 6. **Elymus** (*Hystrix*) (Pooideae, Triticeae). a–n, *E. Hystrix* (*H. patula*): a, base of plant, × ½; b, junction of leaf sheath and leaf blade (note ligule), × 6; c, inflorescence, × 1; d, paired spikelets from near base of inflorescence (note 2 glumes subtending each spikelet), × 1; e, spikelet with 1 floret at anthesis (lemma awn not shown), × 4; f, longitudinally dehiscent basifixed anther, × 6; g, pollen with single germination pore, × 750; h, gynoecium and turgid lodicules, × 6; i, tip of stigmatic branch, × 500; j, floret in fruit, × 2; k, base of same to show palea and rachilla, × 5; l, tip of lemma awn, × 25; m, base of floret in fruit, vertical section (rotated 90° from floret in "k"), endosperm stippled, embryo unshaded, × 5; n, adaxial side of caryopsis, × 6.

predominates: only two of the approximately 50 species occurring in North America are diploid. Hybridization has been important in the development of agriculturally desirable taxa such as triticale (*Triticum* × *Secale*) and the bread wheats.

Subfamily 4. CHLORIDOIDEAE Rouy, Fl. France **14:** 2. 1913, "Chloridineae."

Ligules often fringed. Spikelets often laterally flattened; staminate or neuter florets usually distal to the lowermost carpel-bearing floret; lemma nerves often 3 or fewer. Lodicules usually fleshy distally. Hilum punctiform. Embryo with an epiblast and a long mesocotyl, usually with a scutellar tail; embryonic leaf margins not overlapping. First seedling leaf usually broad. Microhair distal cell usually inflated; both tall and narrow silica bodies and saddle-shaped silica bodies usually present; subsidiary cells generally triangular. Photosynthesis of the $C_4$ type; mesophyll cells radially arranged. Sclerenchyma accompanying the smallest vascular bundles usually present. Base chromosome number usually 10. (Eragrostoideae Pilger, Nat. Pflanzenfam. ed. 2. **14d:** 167. 1956.) TYPE GENUS: *Chloris* Sw. FIGURES 1d; 2c; 7A, C–I.

A subfamily of about five tribes, 90 genera, and 900 species. In the southeastern United States, the 26 genera, six of which are represented only by adventive species, are divided into four tribes. The boundaries between some of the traditionally recognized tribes (e.g., Eragrostideae and Cynodonteae (Chlorideae); Eragrostideae and Sporoboleae) are arbitrary (Hubbard, 1973a; Christopher & Abraham, 1974; Clayton, 1978; Hilu & Wright; Phillips). A broad tribal concept is therefore used here.

The Chloridoideae, perhaps the most homogeneous grass subfamily, are clearly defined by leaf anatomy. The distal cell of the microhairs is inflated (character 49 of the APPENDIX); the parenchyma sheath is kranz, and its chloroplasts are in most cases centripetally positioned (Brown, 1960b, 1975, 1977; Sutton); and salt glands are known in 17 chloridoid genera but in none outside this subfamily (Lipschitz & Waisel).

The subfamily is apparently most closely related to the Arundinoideae (Clifford *et al.*; Clayton, 1981a; Phillips) and may be evolutionarily derived from ancestral stock of that subfamily. Some affinities with the Paniceae have also been suggested (Watson), and the two groups do share a center of distribution in Africa (Clayton, 1981a). They differ, however, in numerous ways (see discussion under the Panicoideae).

The abundance (in terms of number of taxa and endemics) of chloridoids in tropical Africa led Hartley & Slater to propose an African origin for the group. Their association of high speciation with arid climates was challenged by Cross, who characterized chloridoids as savanna grasses primarily of Africa and Australia. Clayton (1981a), noting the conspicuously large number of chloridoids in North America, suggested that they are filling a gap created by the "evolutionary lethargy" of the pooids there.

Tribe 4a. **Aeluropodeae** Nevski ex Bor, Oesterr. Bot. Zeitschr. **112:** 184. 1965.


FIGURE 7. Spikelets and their parts, **Chloridoideae** and **Aristideae.** A, *Monanthochloë littoralis* (Aeluropodeae), × 5: A1, staminate spikelet at anthesis, 3 stamens visible; A2, carpellate spikelet at tip of branch with 4 leaves; A3, carpellate floret (glumes absent). B, *Aristida longispica* (Aristideae): B1, spikelet with glumes spread apart, × 6; B2, floret with mature caryopsis, 3-awned lemma completely enclosing palea and caryopsis, × 6; B3, caryopsis, × 6; B4, palea, × 12 (note palea drawn twice as large as lemma in B2).

Rhizomatous or stoloniferous. Leaf blades disarticulating. Plants usually dioecious. Lemma nerves 7 or more. Embryo without a scutellar tail. Starch grains all simple. Short cells over the veins solitary or in short rows. TYPE GENUS: *Aeluropus* Trin. FIGURE 7A.

A small tribe of about seven genera including 25–30 species. They are rhizomatous or stoloniferous, often dioecious halophytes, mostly with narrow distributions in the New World. The largest genus, *Distichlis* Raf., is represented by *D. spicata* (L.) Greene in the southeastern United States. The only other species in our area comes from the monotypic genus *Monanthochloë* Engelm. (*M. littoralis* Engelm.), which is found elsewhere only in the West Indies.

The Aeluropodeae are close to the Cynodonteae but are distinguished by several features uncommon in the subfamily: short, pungent leaves; abundant epidermal papillae; small, rounded, often sunken microhairs; and many-nerved lemmas (Stebbins & Crampton; Decker; Soderstrom & Decker, 1964).

Tribe 4b. **Cynodonteae** Dumortier, Obs. Gram. Belg. 83. 1824, "Cynodoneae."

Inflorescence usually paniculate or of spiciform branches. Spikelets disarticulating above the glumes. Cross- to dumbbell-shaped silica bodies present. (Chlorideae Reichenb. Consp. Reg. Veg. 48. 1848. Spartineae Gren. & Godron, Fl. France **3:** 434. 1855. Sporoboleae Stapf in Thiselton-Dyer, Fl. Capensis **7:** 315. 1898. Eragrostideae Stapf, *ibid.* 316. Perotideae C. E. Hubb. in Bor, Grasses Burma, Ceylon, India, Pakistan, 686. 1960.) TYPE GENUS: *Cynodon* Rich. FIGURES 1d; 7C–E, G–I.

A broadly defined tribe, here including four traditionally recognized tribes: Cynodonteae (Chlorideae), Eragrostideae, Spartineae, and Sporoboleae. The first two contain many genera; the third, only *Spartina* Schreber; and the last, only *Calamovilfa* (A. Gray) Scribner, *Muhlenbergia* Schreber and *Sporobolus* R. Br. Twenty-one genera of this enlarged tribe occur in the southeastern United States: *Bouteloua* Lag., *Buchloë* Engelm., *Calamovilfa, Chloris, Crypsis* Aiton,

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C, *Ctenium aromaticum* (Cynodonteae), × 6: C1, transverse section of rachis (unshaded) with 2 spikelets (spikelets in 2 rows), the first spikelet shaded (note small first glume, stoutly awned second glume; first 2 florets sterile and with long awns, third floret fertile); C2, fertile (third) floret, showing hairy lemma, palea, and hairy callus. D, *Cynodon dactylon* (Cynodonteae): D1, portion of rachis, showing sessile spikelets in 2 rows, each spikelet 1-flowered, × 6; D2, floret, lemma to left, rachilla prolonged behind palea, × 12. E, *Eustachys* (*Chloris*) *petraea* (Cynodonteae): E1, portion of rachis, showing spikelets in 2 rows, × 10; E2, spikelet, × 12; E3, spikelet with glumes removed, fertile floret to left, rudimentary floret to right (stippled), × 12; E4, fertile floret, turned to show part of palea within lemma, × 12. F, *Uniola paniculata* (Unioleae): F1, spikelet, lower florets sterile, × 1.5; F2, fertile floret, palea to left, × 12. G, *Muhlenbergia Schreberi* (Cynodonteae), × 12: G1, spikelet, from side, showing glumes, lemma (to right), and palea; G2, lemma from back. H, *Muhlenbergia capillaris* (Cynodonteae): H1, spikelet at anthesis, stigmas protruding, 1 anther visible, × 6; H2, spikelet, showing long pedicel of this species, × 3. I, *Eragrostis Elliottii* (Cynodonteae): I1, spikelet, × 5; I2, floret with segment of rachilla, × 12; I3, caryopsis, palea persistent on rachilla, and mature floret, × 12.

*Ctenium* Panzer, *Cynodon, Dactyloctenium* Willd., *Diplachne* Beauv., *Eleusine* Gaertner, *Eragrostis* Wolf, *Eustachys* Desv., *Gymnopogon* Beauv., *Leptochloa* Beauv., *Muhlenbergia, Opizia* Raf., *Schedonnardus* Steudel, *Spartina, Sporobolus, Tridens* Roemer & Schultes, and *Triplasis* Beauv. Clayton (1967), D. E. Anderson, and Phillips have discussed numerous problems in defining generic limits in the Cynodonteae.

The four tribes combined here are based upon inconsistent inflorescence characters: the Cynodonteae and Spartineae bear one-sided, spiciform secondary inflorescences of one-flowered spikelets; the Eragrostideae, panicles of several-flowered spikelets; and the Sporoboleae, panicles of one-flowered spikelets. Hilu & Wright pointed out that certain genera (e.g., *Dactyloctenium, Eleusine,* and *Leptochloa*) bear the spiciform inflorescences of the Cynodonteae, but their spikelets are eragrostoid in having several florets. The Eragrostideae may rarely have one-flowered spikelets like the Sporoboleae (Phillips). Furthermore, at least for the Cynodonteae and Eragrostideae, there are no other significant distinguishing characters, and the two groups should either be given subtribal status (Hilu & Wright) or merged entirely. The Sporoboleae, on the other hand, differ from eragrostoids in lacking a culm pulvinus (Brown *et al.,* 1959b) and in the centrifugal position of the parenchyma-sheath plastids of some of the species of *Muhlenbergia* and *Sporobolus* (Brown, 1960b). That these differences do not hold all the time, however, underscores the artificiality of the Sporoboleae. Phillips considered the tribe to be "clearly no more than an offshoot of the Eragrostideae," and Stebbins & Crampton, Sutton, and Gould & Shaw lumped it with the Eragrostideae. *Spartina* does not differ from the Cynodonteae sufficiently to warrant tribal status (Mobberley; Hitchcock; Reeder & Singh; Hubbard, 1973a).

The broadly circumscribed Cynodonteae make up most of the Chloridoideae, and hence the discussion of the distribution of the subfamily applies well to this dominant tribe.

Tribe 4c. **Unioleae** (Clayton) Roshevits ex C. S. Campbell, stat. nov.

Lemma nerves 7–11. Microhair distal cell narrowly dome shaped; cross- to dumbbell-shaped silica bodies absent; cork-silica pairs absent; short cells over the veins in rows of 5 or more. Midrib bundles more than 1 and arranged in an arc. (Subtribe Uniolinae Clayton, Kew Bull. **37**: 417. 1982. Tribe Unioleae Roshevits, Zlaki, 244. 1937, nomen invalidum sine descriptione latine.) TYPE GENUS: *Uniola* L. FIGURE 7F.

The tribe contains only *Uniola,* comprising two species of sea beach grasses. *Uniola Pittieri* Hackel ranges from Mexico to Ecuador, and *U. paniculata* L., commonly called sea oats, occurs from Virginia to Texas and in the Caribbean and Mexico. Spikelets of *Uniola* strongly resemble the many-flowered, laterally compressed spikelets of many non-chloridoid grasses, but Yates clearly demonstrated that leaf and embryo anatomy and chromosome number show *Uniola* to be chloridoid. It differs from other chloridoids in the lemma nerves and in several characters of the leaf epidermis (see diagnosis above).

Tribe 4d. **Zoysieae** Bentham, Jour. Linn. Soc. Bot. **19:** 29. 1881.

Floret 1 per spikelet; disarticulation below the glumes; rachillas not prolonged above the floret. Tall and narrow silica bodies absent. (Nazieae Hitchc. Gen. Grasses U. S. 15. 1920. Trageae Hitchc. Contr. U. S. Natl. Herb. **24:** 599. 1927.) TYPE GENUS: *Zoysia* Willd. FIGURE 2c.

Clayton & Richardson considered this tribe of 12 genera to be entirely Old World in distribution and closely related to the Cynodonteae. One species of *Tragus* Haller, *T. racemosus* (L.) All., is occasionally adventive in our area, and a few species of *Zoysia* used in lawns escape from cultivation (Hitchcock).

Subfamily 5. PANICOIDEAE A. Braun in Ascherson, Fl. Prov. Brandenb. 32, 799. 1864.

Spikelets (FIGURES 8–11) compressed dorsally, with 1 carpel-bearing floret per spikelet, the staminate or neuter florets proximal to the carpel-bearing one. Lodicules distally fleshy (FIGURES 8h, 10h). Embryo with a scutellar tail, without an epiblast, the mesocotyl long (FIGURES 8n, 10l), embryonic leaf margins overlapping (FIGURES 8o, 10m). First seedling leaf blade broad. Microhair distal cell narrow; cross- to dumbbell-shaped silica bodies present (FIGURE 1c); guard cells overlapped by interstomatals. $C_3$- or $C_4$-type photosynthesis (FIGURE 2d); sclerenchyma not accompanying the smallest vascular bundles. Base chromosome number mostly 9 and 10. (Saccharoideae Reichenb. Repert. Herb. 37. 1841. Andropogonoideae Ridley, Mat. Fl. Malay. Penin. **3:** 120. 1907.) TYPE GENUS: *Panicum* L. FIGURES 1c, 2d, 8–11.

Because of its distinctive spikelets, the subfamily Panicoideae was circumscribed early (R. Brown, 1810, 1814). This is the largest subfamily in terms of genera (about 200) and species (about 2800), most of which fall into two large tribes, the Andropogoneae and Paniceae. Up to ten other tribes, all with fewer than seven genera, are recognized by some agrostologists, but the three small panicoid tribes represented in the southeastern United States—Anthephoreae, Maydeae, and Tristegineae (Melinideae)—are here included in the two large tribes. In our area there are about 46 genera and 275 species.

Clayton (1981a) considered subfamily Arundinoideae to have provided the ancestral stock for the Panicoideae. Of the other subfamilies it resembles the Chloridoideae in $C_4$ photosynthesis, chromosome base number (mostly 10), and broadly tropical distribution. These two subfamilies differ in numerous ways, however: spikelets (APPENDIX, characters 12, 15, and 18), embryos (38, 41), microhair distal-cell shape (49), and silica bodies (53–55). In photosynthetic pathway (67), 20 percent of the genera of Panicoideae are non-kranz; of the kranz genera, 89 percent are of the mestome-sheath (MS) subtype of kranz anatomy (Brown, 1977). Chloridoids, on the other hand, uniformly have the parenchyma-sheath (PS) subtype. The caryopses of the Panicoideae contain lower levels of glutamine and methionine and higher levels of proline, alanine, and leucine than the Chloridoideae (Yeoh & Watson). The levels of proline and glycine in the Paniceae are intermediate between the levels in subfam. Chloridoideae and in tribe Andropogoneae.


FIGURE 8. **Schizachyrium** (Panicoideae, Andropogoneae). a–r, *S. scoparium* (*Andropogon scoparius*): a, solitary inflorescence with 1 spikelet at anthesis, × 2; b, apex of leaf sheath, ligule, and base of blade, × 3; c, spikelet pair, sterile spikelet to upper left and behind, fertile spikelet at anthesis, × 6; d, first glume (abaxial side), × 6; e, second glume (abaxial side), × 6; f, sterile lemma, × 6; g, fertile lemma with long awn (palea absent),

More chromosome base numbers have been reported in the Panicoideae than in any other subfamily (character 84 of the APPENDIX). Base numbers are mostly nine or ten, but five (Christopher & Abraham, 1976) and four (Celarier & Paliwal) have also been reported.

Tribe 5a. **Andropogoneae** Dumortier, Obs. Gram. Belg. 84. 1824, "Andropogineae."

Spikelets often paired, with 1 sessile, perfect or carpellate, and 1 pedicellate, staminate or neuter (FIGURES 8, 9); glumes usually firmer than the lemmas and with 3 or fewer nerves; lemmas of fertile floret awned (FIGURE 8g) or unawned. Photosynthesis type kranz, subtype MS. (Saccharineae Dumortier, *op. cit.* 83, 141. Maydeae Dumortier, *op. cit.* 84, 142. Zeae Reichenb. Consp. Reg. Veg. 55. 1828. Ophiureae Dumortier, Anal. Fam. 64. 1829. Imperateae Gren. & Godron, Fl. France **3:** 471. 1855. Coiceae Nakai, Ord. Fam. etc. Append. 223. 1943. Euchlaeneae Nakai, *ibid.* Tripsaceae Nakai, *ibid.*) TYPE GENUS: *Andropogon* L. FIGURES 1c, 2d, 8, 9.

The approximately 85 genera of the Andropogoneae form one of the most easily recognized and clearly monophyletic large taxa in the family. Clayton (1972, 1973, 1981b, and in prep.) recognized about 12 subtribes, eight of which occur in our area: Andropogoninae Presl (*Andropogon* and *Schizachyrium* Nees); Anthistirriinae Presl (*Heteropogon* Pers., *Hyparrhenia* Fourn., and *Themeda* Forskål); Coicinae Reichenb. (*Coix* L.); Dimeriinae Hackel (*Arthraxon* Beauv.); Rottboelliinae Presl (*Coelorachis* Brongn. [*Manisuris* L., in part], *Elionurus* Willd., *Eremochloa* Buese, *Hackelochloa* Kuntze, and *Hemarthia* R. Br. [*Manisuris,* in part]); Saccharinae Griseb. (*Erianthus* Michaux, *Imperata* Cyr., and *Microstegium* Nees); Sorghinae Stapf (*Bothriochloa* Kuntze, *Chrysopogon* Trin., *Sorghastrum* Nash, *Sorghum* Moench, and *Vetiveria* Bory); and Tripsacinae Dumort. (*Tripsacum* L.). The last was long recognized as the tribe Maydeae, but this group is closely tied to the Andropogoneae through the Rottboelliinae. These 21 genera contain about 57 species in our area.

All species studied so far are $C_4$ and have the MS subtype of kranz anatomy (Carolin *et al.*; Johnson & Brown; Brown, 1977). Epidermal and transverse-sectional anatomy of leaves (Renvoize, 1982), base chromosome number (Celarier), host distribution of smuts (Watson), overall morphology (Hackel, 1889; Keng), and perhaps the nature of the spikelets (Grassl) emphasize the uniformity of the tribe and its distinctness from other tribes.

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× 6; h, floret (lemma removed), showing turgid lodicules, receptive stigmas, and staminal filaments (anthers fallen), × 12; i, dehisced anther with apical slits, × 6; j, pollen with 1 germination pore, × 500; k, solitary inflorescence, × 2; l, spikelet pair in fruit, vestigial sterile spikelet recurved to right, × 6; m, caryopsis, × 6; n, embryo in diagrammatic longitudinal section (scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black), showing internode between scutellar and coleoptilar nodes, no epiblast, and cleft between base of scutellum and coleorhiza; o, diagrammatic transverse section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in "n," showing numerous vascular bundles and overlapping margins of leaf ("n" and "o" after Reeder, 1957, *fig. 16*).


FIGURE 9. Inflorescences, spikelets, and their parts, **Andropogoneae (Panicoideae)**. A, *Coix Lacryma-Jobi*: A1, inflorescence, staminate spikelets above, carpellate spikelet enclosed in bony involucre below, style of fertile spikelet and tips of 2 sterile spikelets protruding, × 2; A2, glumes of staminate spikelet, × 3; A3, fertile staminate floret, palea facing viewer, lemma behind, × 3; A4, sterile staminate floret, × 3; A5, carpellate spikelet removed from involucre, glumes separated to show fertile floret, sterile florets removed from both sides of central ridge on fertile floret, × 2; A6, fertile floret seen from side opposite that in A5, delicate lemma overlapping thin palea, × 3; A7, sterile carpellate floret, × 2. B, *Tripsacum dactyloides*: B1, portion of inflorescence with staminate spikelets, × 2; B2, staminate spikelet seen from side, showing glumes, × 3; B3, staminate floret, anthers partly visible (before anthesis), × 3; B4, portion of carpellate inflorescence at anthesis, styles omitted from third floret from bottom, × 2; B5, carpellate spikelet removed from rachis, outer glume to left, × 3; B6, carpellate floret, gynoecium removed, × 3. C, *Coelorachis rugosa* (*Manisuris rugosa*): C1, portion of inflorescence, showing 2 fertile spikelets (outer glume rugose) and their pedicellate sterile spikelets, × 3; C2, joint

The andropogonoid spikelet pairs are often grouped into a linear structure (FIGURES 8a, k; 9B1, B4) traditionally called a raceme but perhaps deserving a separate term such as rame (Pohl). At maturity this linear structure breaks up into dispersal units (FIGURES 8l, 9D1) consisting of an internode, a sessile spikelet, a pedicel, and the pedicelled spikelet if it has not already senesced and fallen.

The Andropogoneae presumably arose in the Old World (Hartley, 1950, 1958a; but see Cross) from a kranz panicoid ancestor (Brown & Smith, 1972; Johnson & Brown) probably resembling members of the small tribe Arundinelleae (Clayton, 1981a). The andropogonoids reached North America by way of southern Europe before the separation of the continents beyond dispersal range in the Tertiary (Brown & Smith, 1972). Now they range broadly in the tropics and subtropics, with centers of diversity in savannas of Indochina and southwestern Africa (Hartley, 1950, 1958; Cross).

In addition to the differences between the Andropogoneae and Paniceae given in the diagnoses, the Andropogoneae have higher levels of proline and glycine in their caryopses (Yeoh & Watson) and more numerous and longer mesocotylar roots in their seedlings (Hoshikawa). They may also be a younger group (Brown, 1958b).

Tribe 5b. **Paniceae** R. Brown in Flinders, Voy. Terra Austral. **2:** 582. 1814.

Spikelets usually solitary; glumes usually less firm than lemmas and with 3 or more nerves; lemmas usually awned. Photosynthesis types non-kranz and kranz, subtypes MS and PS (both NAD-me and PCK). (Tristegineae Link ex Nees in Hooker & Arnott, Bot. Voy. Beechey, 237. 1836. Melinideae Link, Hort. Bot. Berol. **1:** 270. 1827, nomen invalidum; see Clayton, 1981c. Anthephoreae Pilger ex Potztal, Willdenowia **1:** 771. 1957.) TYPE GENUS: *Panicum.* FIGURES 10, 11.

A large, widely distributed tribe represented in the southeastern United States by about 26 genera and 230 species. Cross documented the wide distribution of the Paniceae in the tropics and their prominence in the grass flora of the East African savanna. Hartley (1950, 1958b) pointed out the prominence of the tribe in the moist New World tropics, especially northeastern South America. The tribe does appear to be better developed in the New World than the andropogonoids. Brown (1958b) recorded a geographic distribution of panicoid apomictic taxa more widespread and uniform than that of andropogonoid apomicts. If, as he assumed, apomicts are more poorly dispersed than sexually reproducing taxa, then the distributional difference between panicoid and andropogonoid apomicts might indicate a greater age for the former group. The relatively frequent occurrence of apomicts in the Paniceae may be linked to

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of rachis, with fertile spikelet to right and pedicellate sterile spikelet above and behind fertile spikelet, × 5; C3, joint of rachis, × 5; C4, sterile spikelet and pedicel, × 5; C5, fertile floret, lemma to left, × 5. D, *Andropogon Gerardii,* × 4: D1, spikelet pair, joint of rachis to right behind fertile spikelet, pedicellate spikelet above and behind awn, with slight notch at left marking limit of spikelet (sterile); D2, fertile floret.

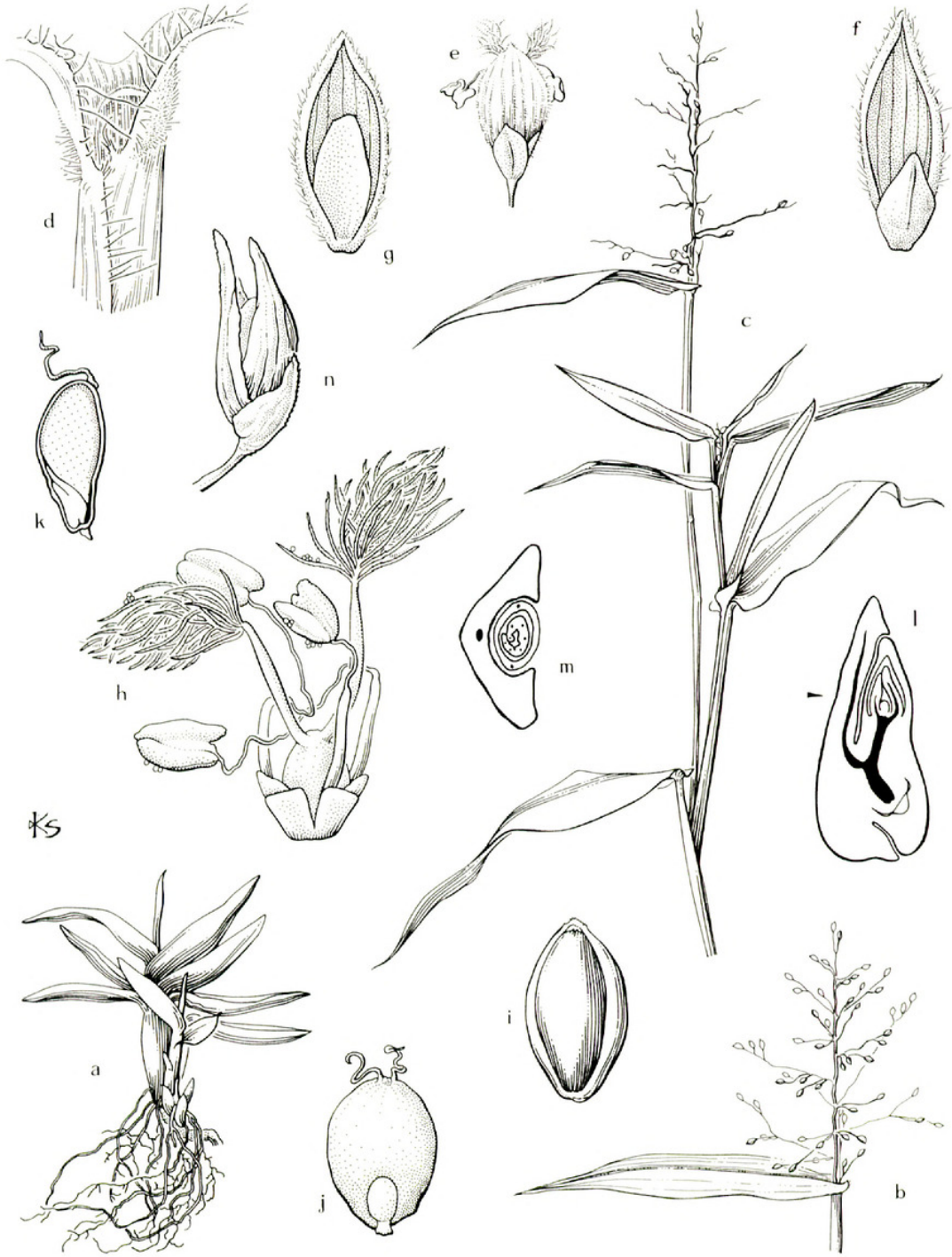


FIGURE 10. **Panicum** (Panicoideae, Paniceae). a–m, *P. clandestinum* (*Dichanthelium clandestinum*): a, part of winter rosette of leaves, × ½; b, inflorescence of chasmogamous spikelets, × ½; , c, upper part of plant, chasmogamous spikelets in fruit or shed from inflorescence, inflorescence of cleistogamous spikelets below, × ½; d, detail of upper part of leaf sheath, base of blade, and ligule, × 6; e, chasmogamous spikelet at anthesis, pollen already shed from anthers, 1 stamen not visible, × 6; f, small first and larger second glume, × 10; g, sterile lemma (pubescent) and sterile palea, × 10; h, flower of cleistogamous spikelet (note shriveled staminal filaments, pollen on stigmas, and lodicules), × 20; i, fertile lemma (behind) and palea enclosing mature caryopsis, × 10; j, mature caryopsis, adaxial surface (note shriveled styles and hilum), × 12; k, diagrammatic longitudinal

the high frequency (77 percent) of polyploidy estimated by Christopher & Abraham (1976) for this tribe.

Unlike the Andropogoneae, the Paniceae are not sharply defined in leaf anatomy (Carolin *et al.*) or photosynthetic pathway (Brown, 1977). Thirty-one genera are characterized by $C_3$ photosynthesis; 44 have the MS subtype of kranz anatomy, 13 the PS subtype; and two (*Panicum* and *Alloteropsis* Presl) contain both $C_3$ and $C_4$ taxa. Both PCK and NAD-me types have been reported among the PS taxa. Brown (1975) postulated two origins of kranz anatomy in the Paniceae, one involving the mestome sheath for most of the kranz taxa, and the other the parenchyma sheath.

Up to about eight small tribes are more or less closely related to the Paniceae. Two of these, the Anthephoreae and the Tristegineae (Melinideae), are represented in our area by adventive taxa. They are close enough to the Paniceae to be included (Stebbins & Crampton), although they are also arguably separable (Pilger; Brown, 1977). The Anthephoreae include *Anthephora* Schreber (about 20 species), which resembles the Paniceae in all respects except two. First, while the genus as a whole shows the MS subtype of kranz anatomy, some species also have "distinctive cells"—kranz cells not associated with a vascular bundle. That these unusual cells uniquely characterize the Anthephoreae and three other small panicoid tribes (Arthropogoneae Pilger, Garnotieae Tateoka, Arundinelleae Stapf) has suggested to some (Johnson & Brown; Brown, 1977) that these taxa should be amalgamated. Second, the spikelets of *Anthephora* are partially fused into groups of four. The Tristegineae are mostly African, with two species from two genera, *Melinis* (*M. minutiflora* Beauv.) and *Rhynchelytrum* Nees (*R. repens* (Willd.) Hubb.), adventive in the southeastern United States. This tribe is characterized by the PS subtype of kranz anatomy, known elsewhere in the Paniceae only in the subtribe Brachiariinae Butzin (see below) and in *Panicum* subgenus *Panicum*. The small panicoid tribes are important to an understanding of phylogeny within the subfamily. The Anthephoreae may share a common ancestor with the Andropogoneae, since both have MS anatomy, delicate and often awned fertile lemmas, and a base chromosome number of 10. Clayton (1981a) considered the Arundinelleae to be ancestral to the Andropogoneae; both he and Brown (1977) considered another small tribe, the Isachneae Bentham, to have been ancestral to the Paniceae.

Brown (1977) divided the Paniceae (*sensu stricto*) into four groups. All genera with the MS subtype of kranz anatomy fall into his informal group, subtribe 1. Thirteen of these genera occur in our area: *Athaenantia* Beauv., *Axonopus*

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section of caryopsis, embryo to left, adaxial side to right, hilum to right of embryo, aleurone layers densely stippled, endosperm lightly stippled, × 12; l, embryo in diagrammatic longitudinal section (scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black), showing internode between scutellar and coleoptilar nodes, no epiblast, and cleft between base of scutellum and coleorhiza; m, diagrammatic transverse section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in "l," showing numerous vascular bundles and overlapping margins of leaf. n, *P. anceps*: spikelet in fruit, first glume to lower right, second glume to left, sterile lemma and tip of fertile lemma visible, × 10. (Diagrammatic sections "l" and "m" after Reeder, 1957, *fig. 12.*)

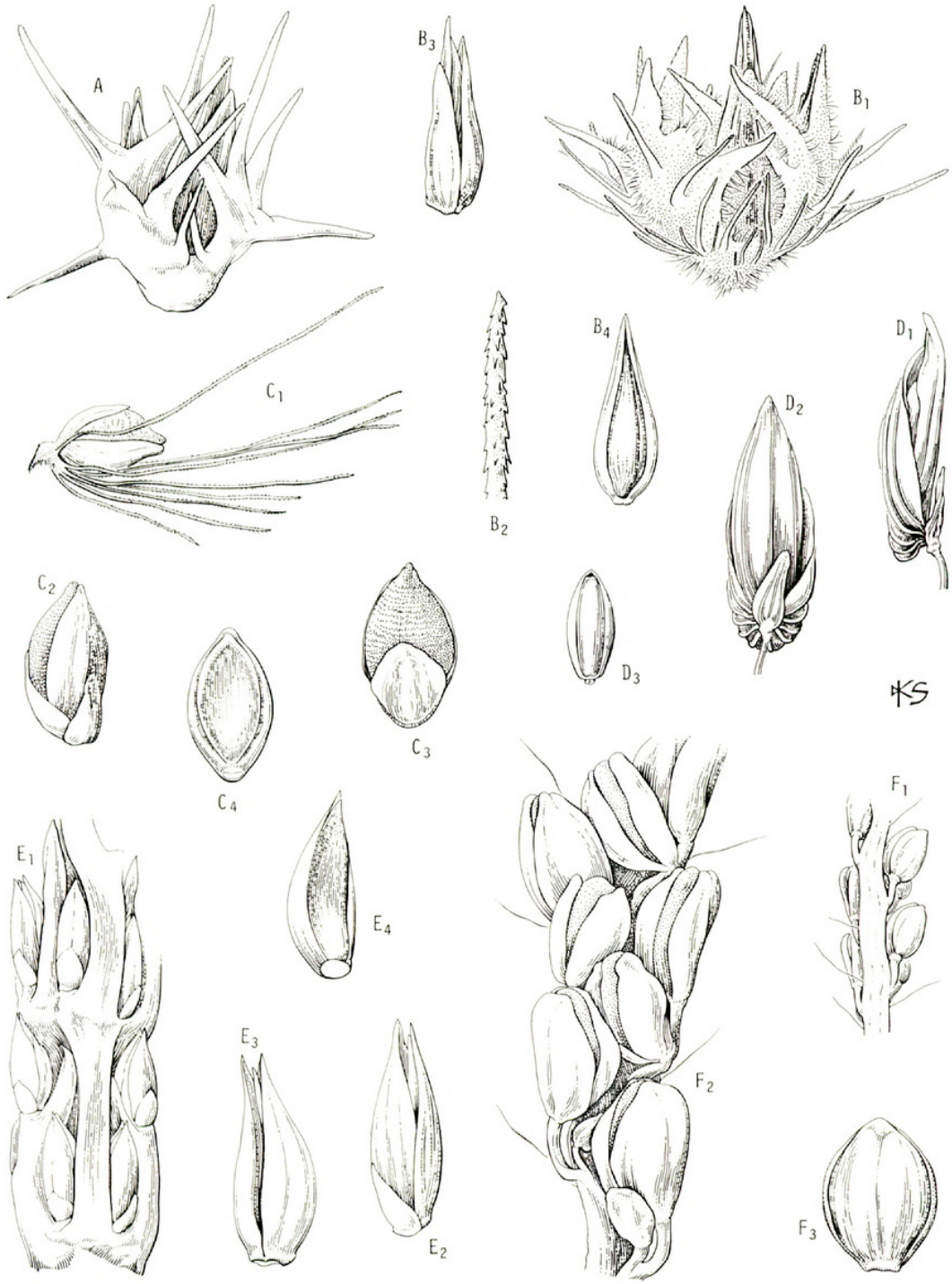


FIGURE 11. Inflorescences, spikelets, and their parts, **Paniceae (Panicoideae)**. A, *Cenchrus gracillimus*: involucre with spikelets, × 5. B, *Cenchrus echinata*: B1, involucre with spikelets, × 5; B2, tip of spine from involucre, × 25; B3, spikelet, × 5; B4, floret, palea to front, lemma behind, × 5. C, *Setaria geniculata*: C1, spikelet with subtending bristles, × 5; C2, spikelet, showing 2 glumes, sterile lemma to right, fertile lemma to left (slightly rugose), × 10; C3, spikelet, showing second glume and slightly rugose indurated lemma of fertile floret, × 10; C4, fertile floret, lemma clasping palea, × 10. D, *Sacciolepis striata,* × 10: D1, spikelet, showing 2 glumes and lemma of sterile floret; D2, same, turned 90° to show shape of sterile lemma and glumes; D3, fertile floret, showing lemma

Beauv., *Cenchrus* L., *Digitaria* Heister, *Echinochloa* Beauv., *Leptoloma* Chase, *Paspalidium* Stapf, *Paspalum* L., *Pennisetum* L., *Reimaria* Fluegge, *Setaria* Beauv., *Stenotaphrum* Trin., and *Trichachne* Nees. Brown's subtribe 2 contains the non-kranz genera, which both his (1977) and Hsu's data support as the most primitive in the tribe. Seven genera are found in our area: *Amphicarpum* Kunth, *Hymenachne* Beauv., *Lasiacis* (Griseb.) Hitchc., *Panicum* subgenus *Dichanthelium* Hitchc. & Chase, *Oplismenus* Beauv., *Sacciolepis* Nash, and *Steinchisma* Raf. Brown's third group, the Brachiariinae, has the PS, PCK subtype of kranz anatomy. It contains three genera in the Southeast: *Brachiaria* Griseb., *Coridochloa* Nees, and *Eriochloa* Kunth. The last group, the Panicinae Stapf, consists of *Panicum* species related to the type species, *P. miliaceum* L., the broomcorn millet. Some common species of this subtribe found in the southeastern United States are *P. capillare* L., *P. flexile* (Gatt.) Scribner, and *P. virgatum* L.

## UNPLACED TRIBES

Three small tribes, all with $C_3$ photosynthesis and mostly temperate in distribution and therefore traditionally assigned to the Pooideae, are not well accommodated in that subfamily (Macfarlane & Watson, 1980). All three share several character states with the Bambusoideae as defined here, but none of them fits well in either that subfamily or any other. Hence they are left unplaced pending further study.

### Tribe 6a. **Brachyelytreae** Ohwi, Bot. Mag. Tokyo **55:** 361. 1941.

Stem internodes solid. Transverse veins sometimes present in the leaves. Rachillas prolonged; spikelets (FIGURE 6D) 1-flowered; glumes very small; ovary with a short-hairy apex below the styles, forming a persistent beak on the caryopsis. Embryo with or without a scutellar tail; embryonic leaf margins overlapping. Microhairs absent; papillae present; dumbbell-shaped silica bodies present but elongated, sinuous or crenate silica bodies and tall and narrow silica bodies absent. Sclerenchyma not accompanying the smallest vascular bundles; vascular bundles without both adaxial and abaxial girders. Base chromosome number 11. TYPE GENUS: *Brachyelytrum* Beauv. FIGURE 5D.

A monogeneric tribe; *Brachyelytrum* contains one species (*B. erectum* (Schreber) Beauv.) found in moist woodlands of eastern Canada, the United States, Japan, Korea, and China. The Asian populations have been considered distinct at the varietal or specific level. The genus has most often been placed in the Pooideae, either in the Agrostideae (Bentham; Hitchcock; Prat, 1960; Stebbins

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clasping palea. E, *Stenotaphrum secundatum*: E1, section of flattened, thickened rachis, showing partially embedded spikelets, × 3; E2, spikelet, first glume to left, × 6; E3, spikelet with glumes removed, fertile (upper) floret to right, sterile floret to left, × 6; E4, fertile floret, showing lemma to left, × 12. F, *Paspalum floridanum*: F1, section of rachis, × 2; F2, section of rachis from other side, showing spikelets in pairs, 1 spikelet of each of 2 lowest pairs aborted, × 5; F3, fertile floret, lemma behind, inrolled margins clasping palea, × 5.

& Crampton), the Poeae (Pilger), or the Stipeae (Hackel, 1887; Brown, 1950; Clifford, 1965) or in its own tribe and near the Stipeae (Tateoka, 1957b) or the Bromeae (Ohwi).

Reeder (1957) and Macfarlane & Watson (1980) noted the similarity of the embryos of *Brachyelytrum* to those of *Oryza* and *Leersia*. There are other character states shared by *Brachyelytrum* and the Bambusoideae. Brown (1958a) put *Brachyelytrum* and the bambusoids together because of their somewhat specialized, thick-walled parenchyma sheath cells, and because transverse veins (character 4 of the APPENDIX), papillae (51), and cross- to dumbbell-shaped to nodular silica bodies (53) are found in both taxa. Among $C_3$ grasses, a base chromosome number of 11 is known in the Stipeae and some herbaceous bambusoids (Calderón & Soderstrom, 1980). Campbell and colleagues (in preparation) present evidence for bambusoid affinities of *Brachyelytrum* in seedling morphology and leaf ultrastructure. Like the seedlings of herbaceous and woody bamboos (Hoshikawa; Soderstrom, 1981a), that of *Brachyelytrum* has a very short mesocotyl and no adventitious roots at the first two seedling nodes or in the internode connecting them. In terms of leaf ultrastructure, *Brachyelytrum* and the few bamboos studied by Carolin and co-workers, unlike pooids, have few or no osmophilic granules in the mestome sheath and numerous thylakoids and large grana in the mesophyll plastids.

There are, however, numerous fundamental differences between *Brachyelytrum* and the Bambusoideae in number of floral parts (characters 24, 28, and 31 of the APPENDIX), ovary apex (29, 30), first seedling leaf blade (44), microhairs (47), stomatal subsidiary-cell shape (60), and leaf anatomy (69, 70). The inclusion of *Brachyelytrum* in the Bambusoideae would greatly loosen the circumscription of the subfamily.

Tribe 6b. **Diarrheneae** (Ohwi) Tateoka ex C. S. Campbell, stat. nov.[2]

Rachis prolonged above uppermost floret; spikelets with 2–5 florets. Lodicules hairy; ovary appendage yellowish or whitish, hard and glossy. Pericarp free from the seed coat. Embryo with a scutellar tail; embryonic leaf margins overlapping. Microhairs absent; elongated, sinuous or crenate silica bodies and cross- to dumbbell-shaped to nodular silica bodies present; tall and narrow silica bodies absent. Some vascular bundles with both adaxial and abaxial girders. Base chromosome number 11. TYPE GENUS: *Diarrhena* Beauv.

Like *Brachyelytrum, Diarrhena* is a small genus of broad-leaved, rhizomatous, woodland herbs with appendaged ovaries and a distributional disjunction between the eastern United States (*D. americana* Beauv.) and eastern Asia (several species). None of the subfamily positions suggested in the past—Pooideae (Stebbins & Crampton; Decker; Gould & Shaw), Arundinoideae (Tateoka, 1957a, 1957c), and Eragrostoideae (Schwab)—is defensible (Macfarlane & Watson, 1980). Hilu & Wright recommended a possible new subfamily, the Nardoideae, composed of *Diarrhena, Nardus* L., and *Lygeum* and intermediate between oryzoids and pooids. From embryo anatomy, Macfarlane & Watson (1980) concluded that this odd genus might have some connection with oryzoids or bambusoids.

[2]See note on page 188.

Tribe 6c. **Stipeae** Dumortier, Obs. Gram. Belg. 83. 1824, "Stipaceae."

Rachillas not prolonged above uppermost floret; spikelets with 1 floret; lemma awns terminal, often basally twisted. Lodicules 2 or 3 per flower. Microhairs present or absent; epidermal papilla 1 per cell; elongated, sinuous or crenate silica bodies absent, saddle-shaped silica bodies and crescentic silica bodies present. Some vascular bundles with both adaxial and abaxial girders. Base chromosome numbers 9, 10, 11, 12. TYPE GENUS: *Stipa* L. FIGURE 5J.

The Stipeae comprise about nine genera and 380 species, most of which belong to the genus *Stipa*. The tribe occurs primarily in dry grasslands of temperate latitudes and especially in the Caspian Sea region, Australia, and the Andes (Hartley, 1973). It is noteworthy for its rather extensive fossil record (Thomasson, Muller). In the southeastern United States the tribe is represented only by *Stipa leucotricha* Trin. & Rupr. and two species of *Piptochaetium* Presl: *P. avenaceum* (L.) Parodi (*Stipa avenacea* L.) and *P. avenacioides* (Nash) Valencia & Costas (*S. avenacioides* Nash).

There is abundant and eclectic evidence that the Stipeae are not closely related to pooid grasses (Macfarlane & Watson; Barkworth). Rachillas are not prolonged and lodicules are two or three in stipoids. Pooids and stipoids also differ in silica-body complements (APPENDIX, characters 52, 53, 55, 56). Johnston & Watson (1977) reported microhairs from the adaxial leaf surface of several species of *Stipa*. The two groups differ serologically (P. Smith), in terms of amino-acid complements (Semikhov; Yeoh & Watson), in the rusts and smuts parasitizing them (Watson, Savile), and in their germination response to IPC (Al-Aish & Brown). The stipoid embryo bears a distinctively long epiblast and a sharply bent primary root (Reeder, 1957). Finally, the extensive aneuploid series of chromosome numbers based on 11 and 12 (Reeder & Reeder) is quite unlike pooid karyotypes.

Suggested taxonomic affinities with the Aristideae (see discussion under this tribe), the Arundinoideae (Tateoka, 1957a; Johnston & Watson, 1977; Savile), or the Bambusoideae (Brown, 1958a; Auquier & Somers; Yeoh & Watson) do not appear to be convincingly strong.

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## NOTE ADDED IN PROOF

In 1941 Ohwi established subtribe Diarrheninae to accommodate *Diarrhena,* and much later Tateoka (Canad. Jour. Bot. **38:** 963. 1960) suggested that the establishment of a separate tribe might be "the best way to arrange *Diarrhena* into the grass system." However, because further studies seemed desirable, Tateoka confined himself to pointing out the peculiarities of the genus. It seems appropriate at this point to raise the subtribe formally to the rank of tribe and to attribute the new status to Tateoka. The tribal name is then Diarrheneae (Ohwi) Tateoka ex C. S. Campbell and is based upon subtribe Diarrheninae Ohwi (Acta Phytotax. Geobot. **10:** 134. 1941), with the type genus *Diarrhena* Beauv.

APPENDIX. **Data matrix of grass subfamilies and tribes.**

| TAXON \ CHARACTER | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | a(b) | var | var | pr(ab) | (pr)ab | (a) | a(b) | a/b | b | d/e | a(b) |
| ARUNDINARIEAE | b | b | var | pr | pr | NC | var | a | b | d/e | a |
| ORYZEAE | a | (a)b | var | ab | ab | (a) | a | (a)b | b | d/e | a |
| PHAREAE | a | a | pr | pr | ab | NC | a | b | b | e | b |
| ARUNDINOIDEAE | a(b) | var | ab | ab | (pr)ab | var | b | a(c) | b | (a/b)e | a |
| ARISTIDEAE | a | var | ab | ab | ab | a | b | a | b | a/e | a |
| ARUNDINEAE | a(b) | var | ab | ab | var | var | b | a(c) | b | e | a |
| CENTOTHECEAE | a | b | ab | ab | ab | NC | b | a | b | b | a |
| POOIDEAE | a | (a)b | ab | (pr)ab | ab | a(b) | a | a | b | (a/b/d)e | a(c) |
| AGROSTIDEAE | a | b | ab | ab | ab | a(b) | a | a | b | e | a |
| AVENEAE | a | b | ab | ab | ab | a | a | a | b | e | a |
| MELICEAE | a | b | ab | (pr)ab | ab | var | a | a | b | (d)e | a |
| POEAE | a | (a)b | ab | ab | ab | (a)b | a | a | b | (a)e | a |
| BROMEAE | a | b | ab | ab | ab | a | a | a | b | (d)e | a |
| TRITICEAE | a | (a)b | ab | ab | ab | a | a | a | b | a(b) | a(c) |
| CHLORIDOIDEAE | a | var | (pr)ab | ab | var | a(b) | (a)b | a(b/c) | (a)b | (a/b/c/d)e(f) | a |
| AELUROPODEAE | a | a | ab | ab | pr | a | b | (a/b)c | b | d/e/f | a |
| CYNODONTEAE | a | var | (pr)ab | ab | (pr)ab | var | (a)b | a(b/c) | (a)b | (a)b(c/d)e | a |
| UNIOLEAE | a | b | ab | ab | NC | NC | b? | a | b | e | a |
| ZOYSIEAE | a | a | ab | ab | ab | a | b | a | b | a/c/d | a |
| PANICOIDEAE | a(b) | var | (pr)ab | (pr)ab | (pr)ab | var | var | a(b) | var | (a)b(c)e(f) | var |
| ANDROPOGONEAE | a(b) | a(b) | (pr)ab | ab | ab | var | (a)b | a(b) | var | (a)b/e(f) | a/b(c) |
| PANICEAE | a(b) | var | (pr)ab | (pr)ab | (pr)ab | a(b) | var | a | (a)b | b(c)e | var |
| UNPLACED | | | | | | | | | | | |
| BRACHYELYTREAE | a | a | ab | var | ab | a | a | a | b | e | a |
| DIARRHENEAE | a | NC | ab | ab | ab | NC | a(b) | a | b | e | a |
| STIPEAE | a(b) | var | ab | ab | ab | var | a(b) | a | b | e | a |

APPENDIX (*continued*).

| TAXON \ CHARACTER | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | a/c | var | b | 1(6-12) | 0(1/2/3) | ab/NA | b/NA | b/NA | a/b |
| ARUNDINARIEAE | a | a | b | 6-12 | (1)2(3) | ab | b | b | a/b |
| ORYZEAE | a/c | var | b | 1 | 0(2) | NA | NA | NA | a/b |
| PHAREAE | c | NA | b | 1 | 0 | NA | NA | b | a |
| ARUNDINOIDEAE | a(b/c) | a | a(b) | 1-20 | 2 | (pr)ab | a(b)NA | (a/b)c | var |
| ARISTIDEAE | a(b) | a | a | 1 | 2 | var | NA | b | b/c |
| ARUNDINEAE | a/c | a | a | 2-20 | 2 | ab | var | a/c | var |
| CENTOTHECEAE | a | a | b | 3-12 | 2 | ab | a | c | a |
| POOIDEAE | a(b)c | a(b) | a(b) | 1-30 | (0/1)2 | (pr)ab | (a)b/NA | var | a/b(c) |
| AGROSTIDEAE | a(b)c | a(b) | a(b) | 1(2-12) | 2 | (pr)ab | a/b/NA | var | a/b(c) |
| AVENEAE | a/c | a | a | (1)2-7(10) | 2 | ab | a/b/NA | b(c) | b |
| MELICEAE | a/c | a(b) | a | (1)3-7(16) | 2 | ab | b | b | a/b |
| POEAE | a/c | a | a | (1)2-10(22) | 2 | var | b | var | a/b |
| BROMEAE | a/c | a | a | (1/2)3-30 | 2 | ab | b | c | a/b |
| TRITICEAE | a/c | a/b | a | (1)2-7(12) | (0/1)2 | var | b/NA | var | (a)b(c) |
| CHLORIDOIDEAE | a(b)/c | a(b)NA | var | 1-45 | (0)2 | (pr)ab | (a)b(c) | var | a(b/c) |
| AELUROPODEAE | a/c | a/NA | a | (2)3-12(20) | 0/2 | ab | b | NC | a |
| CYNODONTEAE | a(b)/c | a(b)NA | a(b) | 1-5(45) | (0)2 | var | b/NA | (var) | a(b/c) |
| UNIOLEAE | a/c | a | a | 3-13 | 2 | ab | a/c | a/c | a |
| ZOYSIEAE | var | b/NA | b | 1 | 2 | ab | NA | a | a |
| PANICOIDEAE | (a)b(c) | (a)b/NA | (a)b | 1 | (0/1)2 | (pr)ab | a/NA | a/b(c) | a/b |
| ANDROPOGONEAE | (a)b(c) | b | b | 1 | 2 | (pr)ab | a/NA | a | a/b |
| PANICEAE | (a)b(c) | (a)b/NA | (a)b | 1 | (0/1)2 | (pr)ab | a | (a)b(c) | a |
| UNPLACED | | | | | | | | | |
| BRACHYELYTREAE | b/c | a | a | 1 | 1/2 | ab | NA | c | b |
| DIARRHENEAE | a/c | a | a | (1)2-5 | 2 | ab | b | b | a |
| STIPEAE | a/c | a | b | 1 | 2 | ab | NA | b/c | b |

| TAXON \ CHARACTER | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | a/NA | 3-17 | 2 or more | 2/3 | (b) | var | var | (1-)3/6 | b | ab |
| ARUNDINARIEAE | a | 11-17 | 2 | 3 | NC | var | b | 3 | b | ab |
| ORYZEAE | a/NA | 3-5(7) | (2)3 or more | 2 | b | b | var | (1-)6 | b | ab |
| PHAREAE | NA | NC | NC | NC | NC | NC | NC | 6 | NC | NC |
| ARUNDINOIDEAE | a(b)NA | 1-15 | 0-2 | (0)2 | var | (a)b | (a)b | 1(2)3 | b | ab |
| ARISTIDEAE | a | 1-3 | 0-2 | 0/2 | b | b | b | 1-3 | b | ab |
| ARUNDINEAE | a/b | 1-15 | 2(var) | 2 | a(b) | var | NC | 3 | b | ab |
| CENTOTHECEAE | NA | 5-15 | 2 | 2 | a | b | var | 1 | b | ab |
| POOIDEAE | (a)b/c | (1)3-15 | (0/1)2(4) | 2 | (a)b | (a)b | var | (1/2)3 | var | (pr)ab |
| AGROSTIDEAE | b/c | (1)3-5(7) | (0/1)2(4) | 2 | b | (a)b | var | (1-)3 | (a)b | ab |
| AVENEAE | c | 3-15 | 2 | 2 | b | b | (a)b | 3 | a(b) | ab |
| MELICEAE | b/c | 5-15 | 2 | 2 | a | b | (var) | 3 | b | ab |
| POEAE | var | 3-15 | 2 | 2 | b | b | a(b) | (1-)3 | (a)b | ab |
| BROMEAE | b/c | 5-15 | 2 | 2 | var | b | b | 2/3 | a | pr |
| TRITICEAE | a(b) | (3)5-7(11) | 2 | 2 | b | a(b) | var | 3 | a | ab |
| CHLORIDOIDEAE | var/NA | 1-11 | (0/1)2 | (0)2 | a(b) | b | (a/b) | (1-)3 | b | ab |
| AELUROPODEAE | NA | 3-7 | 2 | 2 | var | b | a | 3 | b | ab |
| CYNODONTEAE | a/b | 1-7 | 2 | 2 | a(b) | b | (var) | 3 | b | ab |
| UNIOLEAE | NA | 7-11 | 2 | 2 | a | NC | NC | 1/3 | b | ab |
| ZOYSIEAE | NA | 1/3 | 0/1/2 | 2 | b | b | a | 2/3 | b | ab |
| PANICOIDEAE | a/b(c)NA | (0)1-6(11) | 0/2/NA | (0/1)2 | a(b) | (a)b | b | (1-)3 | b | ab |
| ANDROPOGONEAE | a/b(c) | (0)1-3(5) | 0/2/NA | (0)2 | a(b) | (a)b | b | (1-)3 | b | ab |
| PANICEAE | NA | (0)3-6(11) | 2 | (0/1)2 | a(b) | b | b | 3 | b | ab |
| UNPLACED | | | | | | | | | | |
| BRACHYELYTREAE | a | 5 | 2 | 2 | b | b | b | 3 | a | pr |
| DIARRHENEAE | NA | 3-5 | 2 | 2 | b | a | var | (1)2/3 | b | ab |
| STIPEAE | a/b | 3-7 | 1/2 | 2/3 | var | b | b | (1)3 | b | ab |

APPENDIX (*continued*).

| TAXON \ CHARACTER | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | (2)3 | (a/b) | pr(ab) | b/c | a | b | b | pr | var | b | a(b) |
| ARUNDINARIEAE | 3 | NC | pr | c | a | b | b | pr | pr | b | a |
| ORYZEAE | 2 | a/b | (ab) | b/c | a | b | b | pr | (pr)ab | b | a/b |
| PHAREAE | 3 | NC | NC | NC | NC | NC | NC | pr | (pr)ab | b | a |
| ARUNDINOIDEAE | 2 | b | (pr)ab | var | var | var | b | (pr)ab | pr | a | b |
| ARISTIDEAE | 2 | b | ab | b | a/b | a | b | ab | pr | a | b |
| ARUNDINEAE | 2 | b | var | a/b | (a)b | var | b | (pr)ab | pr | a | b |
| CENTOTHECEAE | 2 | b | ab | b | b | b | b | pr | pr | a | b |
| POOIDEAE | 2 | b | var | var | a(b) | (a)b | (a)b | pr(ab) | ab | b | b |
| AGROSTIDEAE | 2 | b | var | var | (a)b | (a)b | var | pr | ab | b | b |
| AVENEAE | 2 | b | var | var | a | b | (a)b | pr | ab | b | b |
| MELICEAE | 2 | b | pr | a/c | a | b | b | pr | ab | b | b |
| POEAE | 2 | b | var | a(b) | var | b | (a)b | pr | ab | b | b |
| BROMEAE | 2 | b | pr | b | a | b | b | ab | ab | b | b |
| TRITICEAE | 2 | b | pr | a(b/c) | a | b | b | var | ab | b | b |
| CHLORIDOIDEAE | 2 | (a)b | ab | var | b | a(b) | b | pr(ab) | pr(ab) | a(b) | (a)b |
| AELUROPODEAE | 2 | NC | NC | NC | b | NC | b | pr | ab | a | b |
| CYNODONTEAE | 2 | (a)b | ab | var | b | a(b) | b | pr | var | a(b) | (a)b |
| UNIOLEAE | 2 | b | NC | NC | b | a | NC | pr | pr | a | b |
| ZOYSIEAE | 2 | b | ab | var | b | a | b | pr | pr | a | b |
| PANICOIDEAE | 2 | b | ab | var | (a)b | a(b) | b | ab | pr | a | a(b) |
| ANDROPOGONEAE | 2 | b | ab | var | b | a(b) | b | ab | pr | a | a(b) |
| PANICEAE | 2 | b | ab | a(b/c) | (a)b | a(b) | b | ab | pr | a | a |
| UNPLACED | | | | | | | | | | | |
| BRACHYELYTREAE | 2 | b | pr | a/c | a | b | b | pr | pr/ab | b | a |
| DIARRHENEAE | 2 | a | NC | c | var | b | b | pr | pr | b | a |
| STIPEAE | 2 | b | ab | a/c | a | b | b | pr | ab | b | b |

| TAXON \ CHARACTER | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | (b) | b | ab(pr) | a(b) | (a)c | pr(ab) | 2 | a/NA | a | pr | ab | pr(ab) |
| ARUNDINARIEAE | NC | b | ab | NA | NA | pr | 2 | a | a | pr | ab | pr |
| ORYZEAE | b | var | ab | NA | NA | pr | 2 | a | a | pr | ab | ab |
| PHAREAE | NC | b | pr | a | c | ab | NA | NA | a | NC | ab | pr |
| ARUNDINOIDEAE | b | var | pr | var | b(c) | pr(ab) | 2 | a | a | ab | (pr)ab | pr |
| ARISTIDEAE | b | b | pr | b | b | pr | 2 | a | a | ab | pr | pr |
| ARUNDINEAE | b | var | pr | var | b | pr(ab) | 2 | a | a | ab | ab | pr |
| CENTOTHECEAE | NC | a | pr | a | c | pr | 2 | a | a | NC | ab | pr |
| POOIDEAE | (a)b | var | pr | var | a | ab | NA | NA | var | (pr)ab | pr | (pr)ab |
| AGROSTIDEAE | (a)b | a(b) | pr | (a)b | a | ab | NA | NA | var | ab | pr | (pr) |
| AVENEAE | b | a | pr | (var) | (a) | ab | NA | NA | (a)b | ab | pr | ab |
| MELICEAE | b | a | (pr) | (var) | (a) | ab | NA | NA | var | pr/ab | pr | (pr) |
| POEAE | b | a(b) | pr | (a)b | a | ab | NA | NA | var | (pr)ab | pr | ab |
| BROMEAE | a | var | pr | b | a | ab | NA | NA | b | ab | pr | ab |
| TRITICEAE | a | (a)b | pr | b | a | ab | NA | NA | var | ab | pr | ab |
| CHLORIDOIDEAE | (a)b | a(b) | pr | a(b) | (var) | pr(ab) | 1/2 | (a)b | a(b) | var | (pr)ab | var |
| AELUROPODEAE | a | NC | NC | NC | NC | var | 1/2 | b | a | var | ab | ab |
| CYNODONTEAE | b | (a) | (pr) | (a/b) | (a/b) | pr | 1/2 | (a)b | a(b) | var | (pr) | (pr/ab) |
| UNIOLEAE | NC | NC | NC | NC | NC | pr | 2 | a | a | ab | ab | pr |
| ZOYSIEAE | b | a/b | pr | a | a/c | pr(ab) | 2 | b | a | var | ab | ab |
| PANICOIDEAE | var | a(b) | pr | a | var | pr | (1)2 | a(b) | a(b) | var | ab | pr |
| ANDROPOGONEAE | var | a | (pr) | (a) | (var) | pr | 2 | a(b) | a(b) | var | ab | pr |
| PANICEAE | a(b) | a(b) | pr | a | (a)b(c) | pr | (1)2 | a(b) | a(b) | (pr)ab | ab | pr |
| UNPLACED | | | | | | | | | | | | |
| BRACHYELYTREAE | a | b | pr | b | var | ab | NA | NA | a | pr | ab | pr |
| DIARRHENEAE | b | NC | NC | NC | NC | ab | NA | NA | a | ab | pr | pr |
| STIPEAE | var | var | pr | b | a | var | 2 | a | a | var | ab | pr |

APPENDIX (*continued*).

| TAXON \ CHARACTER | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 |
|---|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | ab | (pr)ab | (pr)ab | (pr)ab | ab | (b) | (a)c | (var) | var | b |
| ARUNDINARIEAE | ab | pr | ab | ab | ab | NC | c | NC | b(a) | b |
| ORYZEAE | ab | ab | (pr) | pr | ab | b | a | var | var | b |
| PHAREAE | ab | ab | ab | ab | ab | NC | c | NC | a | b |
| ARUNDINOIDEAE | pr(ab) | pr(ab) | pr(ab) | (pr)ab | ab | var | var | var | var | (a)b |
| ARISTIDEAE | pr | pr | pr | var | ab | var | a(b) | var | a/c | a |
| ARUNDINEAE | (pr) | (pr) | (pr) | ab | ab | var | var | var | var | (a)b |
| CENTOTHECEAE | ab | ab | ab | ab | ab | NC | a | pr | var | b |
| POOIDEAE | pr(ab) | (pr)ab | (pr)ab | ab | (pr)ab | a(b) | b | var | (a)b/c | b |
| AGROSTIDEAE | (pr) | (pr) | ab | ab | (pr) | a(b) | b | var | (a/b)c | b |
| AVENEAE | ab | ab | ab | ab | ab | a(b) | b | ab | b/c | b |
| MELICEAE | ab | ab | ab | ab | ab | NC | b | var | (a/b)c | b |
| POEAE | (pr) | ab | pr | ab | ab | a(b) | b | var | (a/b)c | b |
| BROMEAE | pr | ab | pr | ab | ab | a | b | ab | var | b |
| TRITICEAE | pr | (pr) | pr | ab | ab | a | b | var | b/c | b |
| CHLORIDOIDEAE | pr(ab) | pr(ab) | var | ab | ab | (a)b | a(b/c) | pr(ab) | var | a |
| AELUROPODEAE | pr | pr | ab | ab | ab | var | a | pr | c | a |
| CYNODONTEAE | (pr) | pr(ab) | (pr/ab) | ab | ab | var | a(b/c) | var | a(b/c) | a |
| UNIOLEAE | ab | ab | ab | ab | ab | NC | a | ab | a | a |
| ZOYSIEAE | ab | pr | pr | ab | ab | var | a | pr | var | a |
| PANICOIDEAE | (pr)ab | (pr)ab | ab | ab | (pr)ab | (a)b | a | var | a(b/c) | a(b) |
| ANDROPOGONEAE | ab | ab | ab | ab | ab | b | a | var | a(b/c) | a |
| PANICEAE | (pr) | (pr) | ab | ab | (pr) | (a)b | a | var | a(b/c) | a(b) |
| UNPLACED | | | | | | | | | | |
| BRACHYELYTREAE | ab | ab | ab | ab | ab | var | b | ab | a | b |
| DIARRHENEAE | ab | ab | ab | ab | ab | a | var | ab | a/c | b |
| STIPEAE | pr | pr | pr | ab | ab | var | var | ab | var | b |

| TAXON \ CHARACTER | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | ab | (ab) | ab | a | (a)b | pr | pr(ab) | (a)b | pr | var | (var) |
| ARUNDINARIEAE | ab | NC | ab | a | b | pr | pr | b | NC | pr | NC |
| ORYZEAE | ab | ab | ab | a | b | pr | var | (a)b | (pr) | var | var |
| PHAREAE | NC | NC | ab | NC | a | pr | pr | b | pr | NC | NC |
| ARUNDINOIDEAE | (ab) | ab | var | a(b) | b | (pr)ab | ab | a(c) | (pr)ab | var | var |
| ARISTIDEAE | ab | ab | pr | b | b | ab | ab | a | ab | var | var |
| ARUNDINEAE | NC | ab | var | a | b | (pr)ab | ab | a/c | ab | var | ab |
| CENTOTHECEAE | NC | NC | ab | a | b | ab | ab | NC | pr | NC | NC |
| POOIDEAE | (ab) | ab | (pr)ab | a | b | ab | ab | a(c) | (pr) | var | var |
| AGROSTIDEAE | (ab) | ab | (pr)ab | a | b | ab | ab | a(c) | (pr) | var | (pr)ab |
| AVENEAE | NC | ab | ab | a | NC | ab | ab | a | NC | (pr)ab | var |
| MELICEAE | ab | ab | ab | a | NC | ab | ab | a | (pr) | (pr)ab | (pr)ab |
| POEAE | NC | ab | ab | a | b | ab | ab | a | NC | var | (pr)ab |
| BROMEAE | NC | ab | ab | a | b | ab | ab | a | NC | var | ab |
| TRITICEAE | NC | ab | ab | a | b | ab | ab | a(c) | NC | var | (pr)ab |
| CHLORIDOIDEAE | (ab) | ab | pr(ab) | a | (a)b | ab | ab | a/c | (pr) | var | var |
| AELUROPODEAE | NC | ab | pr | a | b | ab | ab | a | NC | ab | ab |
| CYNODONTEAE | (ab) | ab | pr(ab) | a | (b) | ab | ab | a(c) | (pr) | (pr)ab | pr(ab) |
| UNIOLEAE | ab | ab | pr | a | NC | ab | ab | c | pr | pr | NC |
| ZOYSIEAE | NC | ab | pr | a | var | ab | ab | a | NC | var | var |
| PANICOIDEAE | (pr)ab | (pr)ab | pr(ab) | var | var | ab | ab | a/c | (var) | var | var |
| ANDROPOGONEAE | (ab) | ab | pr(ab) | b | a(b) | ab | ab | (a)c | NC | var | var |
| PANICEAE | (pr)ab | (pr)ab | pr(ab) | var | var | ab | ab | a/c | (var) | var | var |
| UNPLACED | | | | | | | | | | | |
| BRACHYELYTREAE | ab | ab | ab | a | b | ab | ab | a | pr | pr | ab |
| DIARRHENEAE | ab | ab | ab | a | NC | ab | ab | a | pr | pr | ab |
| STIPEAE | NC | ab | ab | a | b | ab | ab | a/c | pr | pr | ab |

APPENDIX (*continued*).

| TAXON \ CHARACTER | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 |
|---|---|---|---|---|---|---|---|---|---|---|
| BAMBUSOIDEAE | (ab) | (ab) | (var) | (var) | (pr) | pr | pr | (ab) | a/c | 12 |
| ARUNDINARIEAE | NC | NC | NC | NC | NC | pr | pr | NC | NC | 12 |
| ORYZEAE | ab | ab | var | var | pr | pr | (pr) | ab | a | 12(15/17) |
| PHAREAE | NC | NC | NC | NC | NC | pr | NC | NC | c | 12 |
| ARUNDINOIDEAE | var | ab | ab | var | pr | pr | var | var | a/b(c) | (11)12 |
| ARISTIDEAE | ab | ab | ab | pr | pr | pr | ab | pr | b/c | 11 |
| ARUNDINEAE | var | ab | ab | ab | pr | pr | var | var | a/b | 12 |
| CENTOTHECEAE | NC | NC | NC | NC | NC | pr | NC | NC | a/b | 12 |
| POOIDEAE | ab | ab | ab | (pr)ab | pr(ab) | var | var | (pr)ab | a/b | (var) |
| AGROSTIDEAE | ab | ab | ab | ab | pr(ab) | pr(ab) | (pr)ab | (pr)ab | a(b) | (4/5)7(9/13) |
| AVENEAE | ab | ab | ab | (pr)ab | pr | pr(ab) | ab | (pr)ab | a | 7 |
| MELICEAE | ab | ab | ab | ab | pr | pr(ab) | var | ab | (a) | 9/10 |
| POEAE | ab | ab | ab | ab | pr(ab) | var | (pr)ab | (pr)ab | (a) | (5)7(13/19) |
| BROMEAE | ab | ab | ab | ab | var | pr | var | ab | a | 7 |
| TRITICEAE | ab | ab | ab | ab | pr(ab) | pr(ab) | (pr)ab | ab | a | 7 |
| CHLORIDOIDEAE | ab | ab | (pr)ab | var | pr(ab) | pr(ab) | var | ab | a(b) | (7/9)10(12) |
| AELUROPODEAE | ab | ab | ab | pr | pr | pr | pr | ab | NC | 10 |
| CYNODONTEAE | ab | ab | (pr)ab | pr(ab) | pr(ab) | pr(ab) | (pr)ab | ab | var | (7)10(9/12) |
| UNIOLEAE | ab | ab | NC | ab | pr | NC | NC | ab | a | 10 |
| ZOYSIEAE | ab | ab | ab | var | pr | pr | pr | ab | a | 10 |
| PANICOIDEAE | ab | (pr)ab | var | (pr)ab | (pr)ab | pr(ab) | var | (pr)ab | var | 5/9/10(var) |
| ANDROPOGONEAE | ab | (pr)ab | var | (pr)ab | (pr)ab | pr(ab) | var | (pr)ab | var | 5/10(var) |
| PANICEAE | ab | (pr)ab | var | (pr)ab | (pr)ab | pr(ab) | (pr)ab | ab | var | 9/10(var) |
| UNPLACED | | | | | | | | | | |
| BRACHYELYTREAE | ab | ab | ab | ab | ab | ab | ab | ab | NC | 11 |
| DIARRHENEAE | ab | ab | ab | ab | pr | pr | var | ab | NC | 10 |
| STIPEAE | ab | ab | ab | ab | pr | pr | pr | var | a | 9-12 |

Data for this table are based on the character states found in the genera of the southeastern United States that make up the tribes and subfamilies. Data come both from the literature (Hitchcock; Johnston & Watson, 1977; McClure, 1973; Reeder, 1957, 1962; Metcalfe, 1960; Yates, 1966; Terrell; Macfarlane & Watson, 1980, 1982; Soderstrom, 1981a; Watson & Dallwitz, 1981, 1982) and from examination of living material or herbarium specimens (A, GH, NY, and US). The characters and their states in this table are defined below. Two or more characters occurring with roughly equal frequency are separated by a slash, while "var," meaning variable, indicates that all character states occur with roughly equal frequency. Character states enclosed in parentheses are rare, occurring in a third or fewer of the taxa (genera of tribes or tribes of subfamilies). When data are available for a minority of the genera of a tribe or tribes of a subfamily, the recorded character state or states are also enclosed in parentheses. "NA" indicates not applicable and "NC" no data available. The presence or absence of a character is indicated by "pr" or "ab," respectively.

CHARACTERS AND THEIR STATES AS USED ABOVE

1. Stems: (a) herbaceous, (b) woody
2. Stem internodes: (a) solid, (b) hollow
3. Pseudopetioles: pr/ab
4. Transverse veins: pr/ab
5. Leaf blade disarticulation: pr/ab
6. Vernation: (a) rolled, (b) folded
7. Ligules: (a) membranaceous, (b) of hairs or fringed
8. Sex distribution: (a) some perfect flowers present, (b) plants monoecious, (c) plants dioecious
9. Inflorescences: (a) leafy, (b) not leafy
10. Inflorescence form: (a) solitary spike, (b) spiciform branches, (c) glomerule, (d) raceme, (e) panicle, (f) other
11. Spikelets: (a ) solitary, (b) paired, (c) in 3's
12. Spikelet compression: (a) lateral, (b) dorsal, (c) absent
13. Spikelet disarticulation: (a) above glumes, (b) below glumes (NA indicates disarticulation of axis at some point below the spikelet)
14. Rachilla: (a) prolonged above uppermost floret, (b) not prolonged above uppermost floret
15. Carpellate and/or perfect florets/spikelet
16. Glumes/spikelet
17. Glume awns: pr/ab
18. Staminate or neuter florets: (a) proximal to lowermost carpel-bearing floret, (b) distal to lowermost carpel-bearing floret, (c) both proximal and distal to lowermost carpel-bearing floret
19. Relative glume/lemma firmness: (a) glumes firmer, (b) lemmas firmer, (c) equal
20. Lemma-awn number: (a) 0, (b) 1, (c) more than 1
21. Lemma-awn position: (a) apical, (b) apical notch, (c) dorsal
22. Lemma-nerve number
23. Palea-nerve number

24. Lodicules/flower
25. Lodicules: (a) distally fleshy, (b) distally membranaceous
26. Lodicules: (a) hairy, (b) glabrous
27. Lodicules: (a) toothed, (b) entire
28. Stamens/flower
29. Ovary apex: (a) hairy, (b) glabrous
30. Ovary appendage: pr/ab
31. Stigmas/gynoecium
32. Pericarp: (a) free, (b) adnate to seed
33. Caryopsis groove: pr/ab
34. Caryopsis compression: (a) dorsiventral, (b) lateral, (c) none
35. Hilum: (a) linear, (b) punctiform
36. Embryo length: (a) more than one third of caryopsis, (b) less than one third of caryopsis
37. Endosperm: (a) liquid or soft, (b) hard
38. Epiblast: pr/ab
39. Scutellar tail: pr/ab
40. Embryo mesocotyl: (a) long, (b) short
41. Embryonic leaf margins: (a) overlapping, (b) not overlapping
42. Starch grains: (a) all simple, (b) at least some compound
43. Seedling mesocotyl: (a) long, (b) short
44. First seedling leaf blade: pr/ab
45. First seedling leaf blade; (a) broad, (b) narrow
46. First seedling leaf blade: (a) erect, (b) curved, (c) supine
47. Microhairs: pr/ab
48. Microhair cell number
49. Microhair distal cell: (a) narrow, (b) inflated
50. Long cell wall: (a) sinuous, (b) more or less straight
51. Papillae: pr/ab
52. Elongated, sinuous or crenate silica bodies: pr/ab
53. Cross- to dumbbell-shaped to nodular silica bodies: pr/ab
54. Tall and narrow silica bodies: pr/ab
55. Saddle-shaped silica bodies: pr/ab
56. Crescentic silica bodies: pr/ab
57. Oryzoid silica bodies: pr/ab
58. Acutely angled silica bodies: pr/ab