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A MOLECULAR PHYLOGENY OF *PANICUM* (POACEAE: PANICEAE): TESTS OF MONOPHYLY AND PHYLOGENETIC PLACEMENT WITHIN THE PANICOIDEAE[1]

SANDRA S. ALISCIONI,[2,3] LILIANA M. GIUSSANI,[2,3]
FERNANDO O. ZULOAGA,[2] AND ELIZABETH A. KELLOGG[3,4]

[2]Instituto de Botánica Darwinion, Labardén 200, Casilla de Correo 22, San Isidro B1642HYD, Buenos Aires, Argentina; and
[3]Department of Biology, University of Missouri–St. Louis, 8001 Natural Bridge Rd., St. Louis, Missouri 63121 USA

Panicum L. is a cosmopolitan genus with approximately 450 species. Although the genus has been considerably reduced in species number with the segregation of many taxa to independent genera in the last two centuries, *Panicum* remains a heterogeneous assemblage, as has been demonstrated in recent years. The genus is remarkably uniform in its floral characters but exhibits considerable variation in anatomical, physiological, and cytological features. As a result, several classifications, and criteria of what the genus should really include, have been postulated in modern literature. The purpose of this research, based on molecular data of the chloroplast *ndhF* gene, is to test the monophyly of *Panicum*, to evaluate infrageneric classifications, and to propose a robust phylogenetic hypothesis. Based on the present results, previous morphological and molecular phylogenetic studies, and inferred diagnostic morphological characters, we restrict *Panicum* sensu stricto (s.s.) to the former subgenus *Panicum* and support recognition of *Dichanthelium*, *Phanopyrum*, and *Steinchisma* as distinct genera. We have transfered other species of *Panicum* to other genera of the Paniceae. Most of the necessary combinations have been made previously, so few nomenclatural changes have been required. The remaining species of *Panicum* sensu lato (s.l.) are included within *Panicum* incertae sedis representing isolated species or species grouped within monophyletic clades. Additionally, we explore the performance of the three codon position characters in producing the supported phylogeny.

Key words: codon position; *Dichanthelium*; *Hymenachne*; molecular phylogeny; *ndh*F; Paniceae; Panicoideae; *Panicum*; *Phanopyrum*; Poaceae.

Subfamily Panicoideae of the Poaceae, as conventionally delimited, includes approximately 208 genera (Clayton and Renvoize, 1986; Watson and Dallwitz, 1992). The subfamily comprises two main tribes: Paniceae, with approximately 101 genera, and Andropogoneae, with approximately 85 genera. Smaller tribes are Arundinelleae (11 genera), Isachneae (five genera), Neurachneae (three genera), and the monotypic tribes Hubbardieae and Steyermarkochloeae, the latter placed in Arundinoideae by Watson and Dallwitz (1992). Eriachneae, with two genera, is conventionally included in the subfamily, but was placed in Arundinoideae by Watson and Dallwitz (1992); recent molecular data have shown convincingly that Eriachneae does not belong in the Panicoideae (GPWG, 2001).

Monophyly of the subfamily is supported by the presence of bifloral spikelets with the lower flower staminate or neuter (Brown, 1810, 1814), and distinctive, simple starch grains (Tateoka, 1962; Kellogg and Campbell, 1987), as well as by extensive molecular data from both chloroplast and nuclear genes (Gómez Maríınez, 1998; Kellogg, 1998; Soreng and Davis, 1998; Gómez-Maríınez and Culham, 2000; Giussani et al., 2001; J. Barber, L. Giussani, F. Zuloaga, and E. Kellogg, unpublished data).

The tribe Paniceae contains almost half of the genera and 60% of the species of the Panicoideae with several genera having worldwide distribution; its greatest diversity is concentrated in the tropics. Members of the tribe differ extensively in morphological, physiological, anatomical, and karyological characters. This has resulted in different evolutionary schemes of the tribe and its genera.

Panicum, the type genus of Paniceae and Panicoideae, is a large and taxonomically difficult group of species. Taxonomists have held different opinions on the delimitation of this genus, which we will summarize below. For the purposes of this discussion, we will use the name *Panicum* sensu lato (s.l.) to refer to the classification proposed by Zuloaga (1987a) and subsequent modifications (Zuloaga et al., 1989, 1992, 1993b; Zuloaga and Morrone, 1996; F. Zuloaga and O. Morrone, unpublished data; see details below and Table 1). *Panicum* sensu stricto (s.s.) refers to the more narrowly circumscribed group recognized herein. The genus was described by Linnaeus (1753), who recognized 20 species for *Panicum*. Fifteen of these species have been transferred to other genera (e.g., *Dichanthelium*, *Digitaria*, *Echinochloa*, *Paspalum*, *Pennisetum*, *Stenotaphrum*), and only three of Linnaeus's species are still recognized within *Panicum* subg. *Panicum*; the other two correspond to the same species, *P. brevifolium* L., which is in sect. *Parvifolia* subg. *Phanopyrum*.

Panicum s.l. is one of the largest genera of Poaceae, with about 450 species. The species conventionally assigned to the genus are widely distributed, from wet or dry woodlands, grasslands, shores, and marshes to disturbed areas and cultivated fields. Many species grow in subtropical regions, but the genus is also well represented in temperate regions (Zuloaga, 1987a). *Panicum* s.l. is fairly uniform in spikelet morphology but quite diverse in vegetative features (Crins, 1991). The genus shows a wide range of variation, and no single character defines it. Brown (1977), in a study based on anatomical and

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[4] Author for reprint requests (e-mail: tkellogg@umsl.edu).

physiological data, postulated that a C_3 *Panicum* could be the ancestor of all remaining Paniceae. Later, Clayton and Renvoize (1986), in an intuitive classification of the tribe, placed *Panicum* as the core genus, from which all other genera were derived. The lack of an obvious synapomorphy, the broad range of morphological and physiological variation, and the suggestion of being a group from which all others are derived, indicate the likely para- or polyphyletic nature of *Panicum*.

Panicum s.l. includes, among its species, all photosynthetic types known to occur in the Poaceae. The genus has C_3 and C_4 photosynthetic systems (Brown, 1977), and also some C_3/C_4 intermediate species (Brown and Smith, 1975; Ku and Edwards, 1978; Morgan and Brown, 1979; Brown et al., 1985; Hattersley et al., 1986; Zuloaga et al., 1998). The C_4 species include representatives of the PEP-ck, NAD-me and NADP-me subtypes (Downton, 1975; Hatch et al., 1975). This variation is uncommon among genera of Poaceae; photosynthetic pathway is usually uniform among closely related species.

Basic chromosome numbers also vary within *Panicum* s.l. Multiples of 8, 9, 10, 11, and 15 are reported, suggesting up to five basic numbers for *Panicum* (Darlington and Wylie, 1955; Gould, 1960; Bolkhovskikh et al., 1969; Christopher and Abraham, 1976; Bouton et al., 1981; Kumatsu and Suzuki, 1987; Urbani, 1990; Hamoud et al., 1994). Of these, the most common basic chromosome numbers are 9 and 10, while other numbers, those not in multiples of 9 or 10, may have evolved by cytological aberrations (Jauhar and Joshi, 1965; Tateoka, 1965; Jauhar, 1969). Of the proposed subgenera of *Panicum* s.l., *Steinchisma*, *Panicum*, and *Dichanthelium* are uniform regarding basic chromosome number, while *Agrostoides* and *Phanopyrum* are heterogeneous (Dubcovsky and Zuloaga, 1991).

The taxonomy, anatomy, and physiology of *Panicum* have received considerable attention in recent years. A small sample of *Panicum* has been analyzed in recent morphological and molecular studies, using chloroplast and nuclear gene sequences (Gómez-Martínez and Culham, 2000; Zuloaga et al., 2000; Duvall et al., 2001; Giussani et al., 2001; J. Barber, L. Giussani, F. Zuloaga, and E. Kellogg, unpublished data); all these treatments concluded that the genus is polyphyletic and that more comprehensive studies, analyzing more taxa, are needed.

Several taxonomic studies have been conducted in the genus, but none has studied it in its entirety (Zuloaga and Soderstrom, 1985). Hitchcock and Chase (1910, 1915) analyzed the North American species and placed them in informal groups or subgenera, suggesting natural relationships between the species (Table 1). Later, several of these groups were removed from *Panicum*, such as subg. *Paurochaetium* (transferred to *Setaria*), Fasciculata group (*Urochloa*), Geminata group (*Paspalidium*), and Maxima group (*Urochloa*). Pilger (1931, 1940) divided the genus into eight subgenera and 23 sections. Hsu (1965), who made a complete study of the tribe Paniceae considering new characters (e.g., lodicule morphology, epidermal characters), recognized five subgenera and 25 sections within *Panicum* (Table 1). Crins (1991), in a review of Paniceae for the southern United States, considered that several taxa currently placed in *Panicum* deserve generic status; according to him this goal can be achieved only when tribal, subtribal, and generic classification schemes are based on phylogenetic considerations and the infratribal groups are based on true apomorphies.

Zuloaga (1987a) proposed an intuitive classification of the genus for America, based on exomorphological, anatomical, and karyological characters. In this classification and subsequent modifications, six subgenera and 24 sections were recognized. We based our study on Zuloaga's classification (Table 1) with the following minor changes. Zuloaga (1987a) considered *Repentia* a section of subg. *Panicum*, with approximately 12 species. Afterwards, F. O. Zuloaga (unpublished data) considered that several species of this sect. should be included in section *Virgata*, and *Panicum gouinii*, *P. repens*, and *P. pedersenii* were assigned to section *Dichotomiflora*. *Panicum validum* was first considered by Zuloaga (1987a) as an ungrouped species within subg. *Agrostoides*, but later, Zuloaga et al. (1989) created section *Valida* based on this unique species. *Panicum penicillatum*, placed by Zuloaga (1987a) within subg. *Phanopyrum*, was later classified in section *Dichanthelium* subgenus *Dichanthelium* (Zuloaga et al., 1993b). *Panicum stramineum* was considered by Zuloaga (1987a) as a synonym of *P. hirticaule*, but *P. stramineum* was revalidated by Zuloaga and Morrone (1996).

Because Zuloaga's classification is the starting point for the present study (Table 1), we summarize the six subgenera and their major characters below.

Subgenus *Panicum*, with five sections, includes Kranz species, which are characterized by having two sheaths around the vascular bundles, with the outer parenchymatous sheath usually having centripetal specialized chloroplasts (Fig. 1A). This subgenus was considered by W. V. Brown (1977) as homogeneously C_4, NAD-me subtype; nevertheless, some species (e.g., *P. elephantipes*) were described as having PEP-ck type anatomy by Zuloaga (1987a). The basic chromosome number of the subgenus is $x = 9$. Most of its species are cespitose with erect culms, usually growing in dry and open places. The species are distinguished by having pyramidal inflorescences, lax and diffuse, with ellipsoid to lanceolate spikelets (Fig. 2E–F), with the upper glume 7–9-nerved, and the upper anthecium smooth and shining with compound or simple papillae toward the apex of the palea (Fig. 1B).

Subgenus *Dichanthelium* was considered by Zuloaga (1987a) to include sect. *Dichanthelium*, with species growing from Canada and the United States to southern America, and sect. *Cordovensia*, with five species ranging from Mexico and Central America to Argentina. Subgenus *Dichanthelium* includes non-Kranz, C_3 species; all species have lax panicles with spreading or occasionally contracted branches, spikelets obovoid to ellipsoid, the upper glume and lower lemma usually 7–9-nerved, with the lower palea absent in species of sect. *Cordovensia*, and the upper anthecium apiculate, the lemma and palea covered by simple papillae regularly distributed (Fig. 1G). The basic chromosome number for subg. *Dichanthelium* is $x = 9$.

Hitchcock and Chase (1910) considered *Dichanthelium* as a subgenus of *Panicum*; later, Hitchcock and Chase (1915) recognized the Cordovensia group within subg. *Dichanthelium*, indicating that the morphology of this group was intermediate between *Dichanthelium* and *Panicum* (Table 1). Gould (1974) raised *Dichanthelium* to the generic level. Later, Clark and Gould (1975), Brown and Smith (1975), Gould and Clark (1978), and Gould (1980), while studying North American species of the subgenus, confirmed this taxonomic decision on the basis of exomorphological characters, photosynthetic type, and upper anthecium ornamentation. In North America, *Dichanthelium* can be recognized easily by the presence of a basal rosette of leaves during the winter and a clear foliar dimorphism (Fig. 2H). This character is not seen in the Central

TABLE 1. Review of the major infrageneric classifications for the genus *Panicum*. Zuloaga's classification (1987a) and subsequent modifications (Zuloaga et al., 1989, 1993b; Zuloaga and Morrone, 1996; and F. O. Zuloaga and O. Morrone, unpublished data) is shown in the first column of the table. A comparative view of different sectional treatments can be followed in each row. Subgeneric treatment varies among authors (column), and abbreviations are listed after sections: subg. *Dichanthelium* Hitchc. & Chase = DIC; subg. *Megathyrsus* Pilg. = MEG; subg. *Panicum* = PAN; subg. *Phanopyrum* (Raf.) Pilg. = PHA; subg. *Sarmentosum* Pilg. = SAR; subg. *Eupanicum* Pilg., PAN. (Nomen invalidum for subg. *Panicum* Pilg.).

Zuloaga's classification for species of *Panicum* and current accepted names for other genera	Hsu, 1965	Pilger, 1931, 1940	Hitchchock and Chase, 1910, 1915; Hitchchock, 1951
Subgenus *Agrostoides* (Hitchc. & Chase ex Hsu) Zuloaga			
Section *Agrostoidea* Hitchc. & Chase ex Hsu	Sect. *Agrostoidea* Hitchc. & Chase ex Hsu, SAR		Group Agrostoidea Hitchc. & Chase, PAN
Sect. *Bulbosa* Zuloaga	Sect. *Maxima* Hitchc. & Chase ex Pilg., MEG	Sect. *Maxima* Hitchc. & Chase ex Pilg., MEG	Group Maxima Hitchc. Chase, PAN
Sect. *Discrepantia* Zuloaga			
Sect. *Obtusa* Pilg.	Sect. *Obtusa* Pilg., PHA	Sect. *Obtusa* Pilg., PAN*	*P. obtusum* Kunth, ungrouped PAN
Sect. *Prionitia* Zuloaga			
Sect. *Tenera* Hitchc. & Chase ex Pilg.	Sect. *Tenera* Hitchc. & Chase ex Pilg., SAR	Sect. *Tenera* Hitchc. & Chase ex Pilg., PAN*	Group Tenera Hitchc. & Chase, PAN
Sect. *Tuerckheimiana* Zuloaga			
Sect. *Valida* Zuloaga & Morrone			
Subg. *Dichanthelium* Hitchc. & Chase			
Sect. *Cordovensia* (Hitchc. & Chase) Parodi			Group Cordovensia Hitchc. & Chase, DIC
Sect. *Dichanthelium*	Sect. *Dichotoma* Hitchc. & Chase ex Hsu, DIC Sect. *Latifolia* Hitchc. & Chase, DIC Sect. *Turfosa* Pilg., DIC	Sect. *Turfosa* Pilg. PAN*	17 informal groups, DIC
Subg. *Megathyrsus* Pilg.	Sect. *Maxima* Hitchc. & Chase ex Pilg., MEG	Sect. *Maxima* Hitchc. & Chase ex Pilg. 1931, MEG	Group Maxima Hitchc. & Chase, PAN
Subg. *Panicum* Hithchc. & Chase			
Sect. *Dichotomiflora* (Hitchc. and Chase) Honda	Sect. *Dichotomiflora* (Hitchc. and Chase), Honda, PAN	Sect. *Dichotomiflora* (Hitchc. and Chase) Honda, PAN*	Group Dichotomiflora Hitchc. & Chase, PAN *P. gouinii* E. Fourn. in group Virgata Hitchc. & Chase, PAN
Sect. *Panicum*	Sect. *Panicum*, PAN	Sect. *Eupanicum*, PAN*	Group Capillaria Hitchc. & Chase, PAN Group Diffusa Hitchc. & Chase, PAN
Sect. *Rudgeana* Zuloaga			*P. rudgei* ungrouped, PAN
Sect. *Urvilleana* Hitchc. & Chase ex Pilg.	Sect. *Dura* Stapf, PHA	Sect. *Urvilleana* Hitchc. & Chase ex Pilg. Sect. *Dura* Stapf, PAN*	Group Urvilleana Hitchc. & Chase, PAN
Sect. *Repentia* Stapf	Sect. *Repentia* Stapf., PAN	Sect. *Repentia* Stapf, PAN* Sect. *Virgata* Hitchc. & Chase ex Pilg., PAN*	Group Virgata Hitchc. & Chase, PAN
Subg. *Phanopyrum* (Raf.) Pilg.			
Sect. *Laxa* Hitchc. & Chase ex Pilg.	Sect. *Laxa* Hitchc. & Chase ex Pilg., MEG	Sect. *Laxa* Hitchc. & Chase ex Pilg., PAN*	Group Laxa Hitchc. & Chase, PAN
Sect. *Lorea* Zuloaga			
Sect. *Megista* Pilg.	Sect. *Megista* Pilg., PHA	Sect. *Megista* Pilg., PAN*	*Panicum megiston* Roth (= *P. mertensii*), ungrouped, PAN
Sect. *Monticola* Stapf	Sect. *Monticola* Stapf, MEG	Sect. *Monticola* Stapf, PAN*	Group Trichoidea Hitchc. & Chase, PAN
	Sect. *Sarmentosa* Pilg., SAR	Sect. *Sarmentosa* Pilg., PAN*	
	Sect. *Trichoidea* Hitchc. & Chase ex Pilg., MEG	Sect. *Trichoidea* Hitchc. & Chase ex Pilg., PAN*	*P. millegrana* Poir; ungrouped, PAN
Sect. *Parvifolia* Hitchc. & Chase ex Pilg.	Sect. *Parvifolia* Hitchc. & Chase ex Pilg., SAR	Sect. *Parvifolia* Hitchc. & Chase ex Pilg., PAN*	Group Parvifolia Hitchc. & Chase, PAN
Sect. *Parviglumia* Hitchc. & Chase ex Pilg.	Sect. *Parviglumia* Hitchc. & Chase ex Pilg., SAR	Sect. *Parviglumia* Hitchc. & Chase ex Pilg., PAN*	Group Parviglumia Hitchc. & Chase, PAN
Sect. *Phanopyrum* Raf.	Sect. *Gymnocarpa* Hitchc., PHA	Subg. *Phanopyrum* Raf.	Group Gymnocarpa Hitchc., PAN
Sect. *Stolonifera* Hitchc. & Chase ex Pilg.	Sect. *Stolonifera* Hitchc. & Chase ex Pilg., SAR	Sect. *Stolonifera* Hitchc. & Chase ex Pilg., PAN*	*P. stoloniferum* Poir.; ungrouped, PAN
Sect. *Verrucosa* Hitchc. & Chase ex Hsu	Sect. *Verrucosa* Hitchc. & Chase ex Hsu, MEG		Group Verrucosa Hitchc. & Chase, PAN

TABLE 1. Continued.

Zuloaga's classification for species of *Panicum* and current accepted names for other genera	Hsu, 1965	Pilger, 1931, 1940	Hitchchock and Chase, 1910, 1915; Hitchchock, 1951
Subg. *Steinchisma* Raf.	*P. hians* Elliott in sect. *Laxa* Hitchc. & Chase ex Pilg., MEG	*P. hians* in sect. *Laxa* Hitchc. & Chase ex Pilg., PAN*	*P. hians* in group Laxa Hitchc. & Chase, PAN
	Sect. *Clavelligera* Stapf, MEG	Sect. *Clavelligera* Stapf, PAN*	
	Sect. *Depauperata* Pilg., MEG	Sect. *Depauperata* Pilg., PAN*	
	Sect. *Pectinata* Stapf, MEG	Sect. *Pectinata* Stapf, PAN*	
	Sect. *Verruculosa* Stapf, MEG	Sect. *Verruculosa* Stapf, PAN*	
Acroceras Stapf		Subg. *Acroceras* (Stapf) Pilger	*P. zizanioides* Kunth; ungrouped
Acroceras Stapf		Subg. *Commelinidium* (Stapf) Pilger	
Acroceras Stapf		Subg. *Neohusnotia* (A. Camus) Pilg.	
Pseudolasiacis (A. Camus) A. Camus		Sect. *Pseudolasiacis* A. Camus, PAN*	
Paspalidium Stapf			Group Geminata Hitchc., PAN
Setaria P. Beauv.		*Setaria* sect. *Paurochaetium* (Hitchc. & Chase) Pilg.	Subg. *Paurochaetium* Hitchc. & Chase
Urochloa P. Beauv.		Subg. *Urochloides* Pilg. 1931	
Urochloa P. Beauv.		Group Fasciculata Hitchc. & Chase, URO	Group Fasciculata Hitchc. & Chase, PAN
Urochloa P. Beauv.			Group Purpurascentia Hitchc., PAN

and South American taxa, which led Lelong (1984) to treat *Dichanthelium* as a subgenus within *Panicum*, as did Zuloaga et al. (1986, 1993b), Clayton and Renvoize (1986), Zuloaga (1987a), and Webster (1988).

Subgenus *Steinchisma* includes C_3/C_4 intermediate species (Fig. 1C), with a basic chromosome number of $x = 10$. The species grow in open and humid places. Spikelets are arranged in open or contracted panicles, the upper anthecium is covered with compound papillae over the entire surface (Fig. 1D), and the lower palea is conspicuously expanded at spikelet maturity (Fig. 2A). *Steinchisma* was established as a genus by Rafinesque (1830). Later, several authors included *Steinchisma* in sect. *Laxa* of *Panicum* (Hitchcock and Chase, 1910, 1915; Pilger, 1931, 1940; Hsu, 1965; see Table 1). Brown (1977) mentioned that habitat, ornamentation of the upper anthecium, lower palea features, and inflorescence type are strong characters to segregate *Steinchisma* from *Panicum*. Brown et al. (1985) stressed that several artificial hybrids were produced between species of *Steinchisma* and species of *Panicum* sect. *Laxa*; these authors therefore concluded that *Steinchisma* should be retained within *Panicum* and not as an independent genus. More recently, *Steinchisma* has been considered either a subgenus of *Panicum* (Zuloaga, 1987a; Webster, 1988) or as a distinct genus (Clayton and Renvoize, 1986; Renvoize, 1998; Zuloaga et al., 1998).

Subgenus *Megathyrsus*, as delimited by Zuloaga (1987a), contains a single species, *Panicum maximum* Jacq. Webster (1987), in a revision of Paniceae of Australia, transferred this species to the genus *Urochloa*. *Panicum maximum* is C_4, of the PEP-ck photosynthetic subtype (Fig. 1E); exomorphologically it is characterized by its lax and pyramidal, many-flowered panicles, ellipsoid spikelets with the upper anthecium transversely rugose, with single papillae on the wrinkles (Fig. 1F). The basic chromosome number of this species is polymorphic $x = 8$ or 9.

When establishing subg. *Agrostoides*, Zuloaga (1987a) included in it a few isolated species of *Panicum*, which are all C_4, of the mestome sheath (MS) subtype, e.g., with a single mestome sheath with specialized chloroplasts around the vascular bundles (exceptionally with an outer parenchymatous bundle sheath in *P. prionitis* and *P. petersonii*, species of sect. *Prionitia*); additionally, most species have spikelets with the upper glume and lower lemma 3–5-nerved. Sections (mostly monotypic or oligotypic) assembled in this subgenus are American and each has a restricted distribution, with the exception of an Asian species, *P. antidotale*. Basic chromosome number can be $x = 9$ (in sects. *Agrostoidea* and *Bulbosa* and in *P. antidotale*) or $x = 10$ (in sects. *Obtusa*, *Prionitia*, *Tenera*, and *Valida*); no chromosome counts have been reported for sects. *Tuerckheimiana* and *Discrepantia*. Brown (1977) previously placed these taxa in his ''Miscellaneous Assemblage,'' indicating they were not closely related to each other. Later, Zuloaga et al. (1989, p. 228) emphasized that most species placed in *Agrostoides* are diploids and may represent ''an adaptative line differentiated from C_4, PS species.''

Subgenus *Phanopyrum* (Zuloaga, 1987a) includes non-Kranz species of *Panicum*, with spikelets with the upper glume and lower lemma usually five-nerved (except in *P. mertensii*, of sect. *Megista*, with the upper glume and lower lemma 7–9-nerved). Some sections have spikelets arranged on unilateral branches (e.g., *Phanopyrum*, *Stolonifera* or *Laxa*), and other taxa have lax and open inflorescences. The upper anthecium may be covered with simple papillae and bicellular microhairs (e.g., *Parvifolia*, *Monticola*, *Verrucosa*), whereas in sects. *Parvifolia* and *Lorea* the upper anthecium is smooth, and in *Monticola* and *Verrucosa* it is slightly transversely rugose. Consistency of the upper anthecium ranges from hard and indurate to membranous, with the margins of the upper lemma not enclosing the upper palea completely. Chromosome counts also vary within this subgenus, with both $x = 9$ sections (*Parvifolia*, *Monticola*, *Verrucosa*, and *Parviglumia*), and $x = 10$ sections (*Stolonifera*, *Laxa*, *Lorea*, and *Phanopyrum*).

A broad molecular study of subfamily Panicoideae suggested the polyphyly of *Panicum* (Giussani et al., 2001), al-

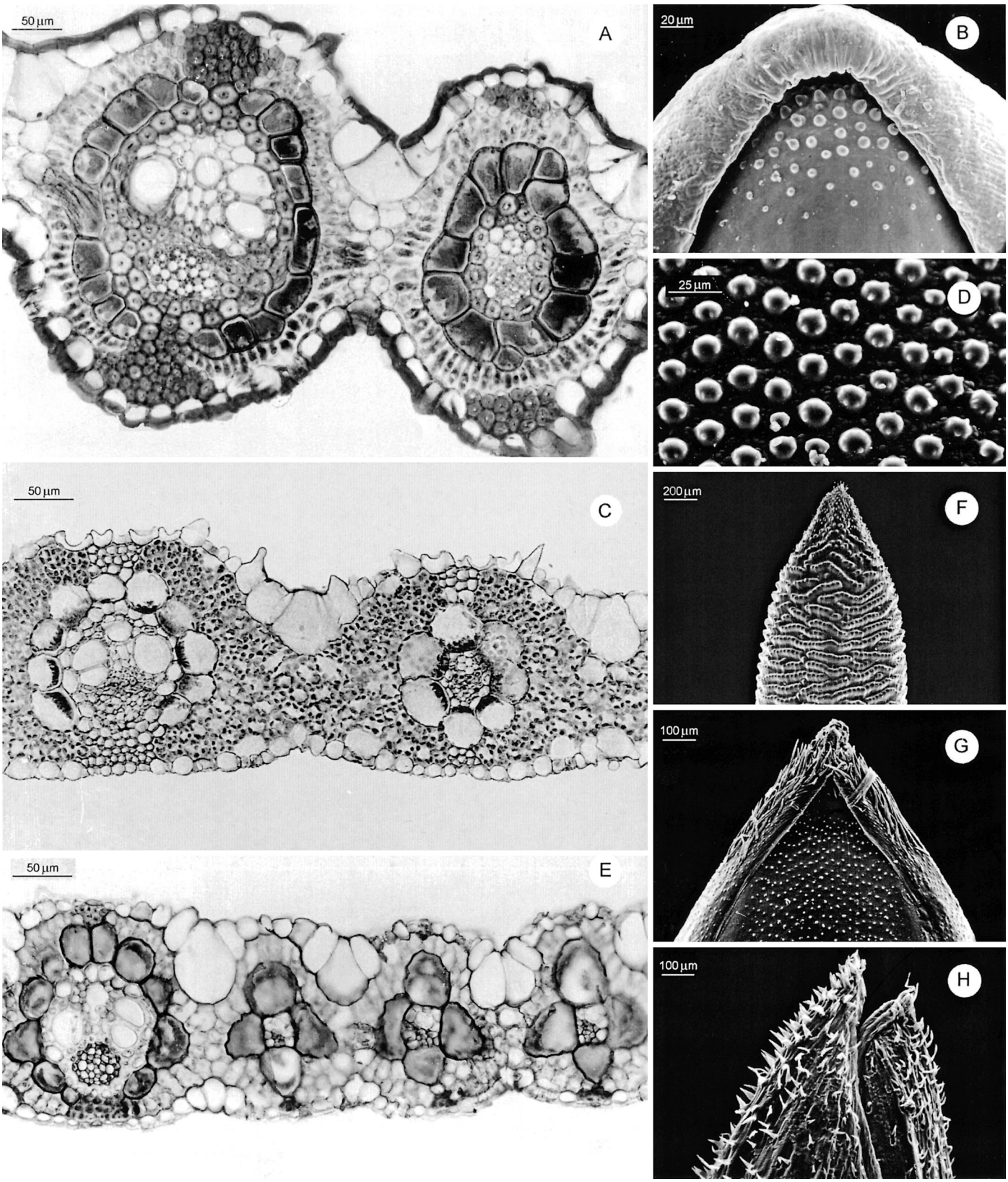


Fig. 1. (A–B). *Panicum* sensu stricto. (A) *Panicum cervicatum* Chase. Cross section of leaf, showing Kranz anatomy, subtype NAD-me. (B) *Panicum furvum* Swallen. Upper anthecium in ventral view showing papillae at the apex of palea. (C–D) *Steinchisma*. (C) *Steinchisma decipiens* (Nees ex Trin.) W.V. Br. Cross section of the leaf showing intermediate C_3/C_4, anatomy. (D) *Steinchisma hians* (Elliot) Nash. Detail of the upper anthecium in dorsal view showing compound papillae regularly distributed over the lemma. (E–F) *Urochloa maxima* (Jacq.) R.D. Webster. (E) Cross section of the leaf showing Kranz anatomy, C_4 PEP-ck subtype. (F) Transversely rugose upper anthecium in dorsal view with simple papillae on the wrinkles. (G) *Dichanthelium assurgens* (Renvoize) Zuloaga. Upper

though sampling of the genus was incomplete. In particular, it was shown that the six subgenera described above do not form a monophyletic group. Subgenus *Panicum* is monophyletic, but not related to the other five subgenera. Subgenus *Dichanthelium* is apparently polyphyletic, with sect. *Dichanthelium* falling in a different clade from sect. *Cordovensia*. Subgenus *Steinchisma* is monophyletic. Subgenus *Megathyrsus* (*Panicum maximum*) is indeed within the *Urochloa* group, supporting its transfer to that genus. The subgenera *Agrostoidea* and *Phanopyrum* were apparently polyphyletic, but too poorly sampled for definite conclusions.

The goal of this paper is to elucidate the phylogenetic placement of almost all sections of *Panicum* s.l. and to test their monophyly where possible. Our study is based on the chloroplast gene *ndh*F, building on the earlier study of Giussani et al. (2001). We also consider morphological characters of the various sections and their placement within Panicoideae. Molecular characters were matched with the diagnostic morphological characters, chromosome numbers, and with different photosynthetic pathways; similarly our results were contrasted with proposed classifications for *Panicum*. Validity of infrageneric taxa is discussed and new taxonomic arrangements are proposed wherever possible. Recent studies (Källersjö et al., 1999, 2000) have pointed out the relevance of mutations in the third codon position to resolve the phylogeny. In order to explore their role in the evolution of Panicoideae, we also analyzed the three positions independently and compared supported groups with bootstrap results of the whole data set.

MATERIALS AND METHODS

DNA sequencing—Most plants were field collected and dried in silica gel, although a few samples were taken from herbarium material. Voucher information is given in Appendix 1. (This information has been archived at the Botanical Society of America website [http://ajbsupp.botany.org/v90/]). DNA extractions were conducted using modified cetyltrimethylammonium bromide (CTAB) protocols published by Doyle and Doyle (1987), Murray and Thompson (1980), and Saghai-Maroof et al. (1984). The procedure to extract and amplify DNA was similar to that used by Giussani et al. (2001). A battery of 10 sequencing primers specified by Olmstead and Sweere (1994) and Clark et al. (1995) were used. Overlapping fragments were combined as follows: 5F/972R, 536F/1318R, 972F/1821R, and 1318F/2110R. For difficult taxa, including the herbarium material, smaller fragments were used: 5′F/536R or 1821F/2110′R. Additionally, two new internal primers were developed for polymerase chain reaction (PCR) amplification and sequencing of *ndh*F within the subfamily Panicoideae: 1660F, 5′CTTTTTACTTTGTTCATTGGAT3′; 1660R, 5′ATCCAATGAACAAAGTAAAAAG3′.

Forward and reverse strands were sequenced with a minimum overlap of 90% for every taxon on an ABI 377 automated sequencer (Applied Biosystems, Foster City, California, USA) using Long Ranger acrylamide gels (FMC Bioproducts, Rockland, Maine, USA). Assembly and editing of sequences used the software program Sequencher, version 3.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Sequences were translated to check for stop codons and then manually aligned, preserving the reading frame.

The aligned data matrix has been submitted to TreeBASE (http://www.treebase.org/treebase/).

Ingroup selection—*Panicum*, the largest and most problematic genus of Paniceae, was sampled to test its monophyly and infrageneric delimitation. Effort was made to encompass most of the morphological diversity and geographical distribution of the genus. Most morphological diversity appears in the Americas, but we have included selected Old World taxa as well. *Panicum* sampling includes 66 species representing all six subgenera and 22 of 24 sections of *Panicum* s.l. Sections *Discrepantia*, of subg. *Agrostoides*, and *Parviglumia*, of subg. *Phanopyrum*, were not sequenced because of lack of material. We also included two African species of sect. *Clavelligera*, an Asian species, *Panicum antidotale* of subg. *Agrostoides*, and three species from Oceania: *P. faurieri*, *P. nephelophilum* of sect. *Panicum* subg. *Panicum*, and *P. koolaunse* of sect. *Dichanthelium* subg. *Dichanthelium*, to extend the geographical sampling. Of the 66 sequences, 46 sequences were generated for this paper, and 20 were taken from Giussani et al. (2001) or GenBank (Appendix 1; http://ajbsupp.botany.org/v90/).

Outgroup selection—Since *Panicum* appears as a polyphyletic genus within Paniceae (Gómez-Martínez and Culham, 2000; Zuloaga et al., 2000; Duvall et al., 2001; Giussani et al., 2001), any study of *Panicum* needs to include as many genera as possible of Paniceae and subfamily Panicoideae. Accordingly, we used the study of Giussani et al. (2001) as a guide to taxon sampling. All genera of Paniceae already sequenced for *ndh*F were included in the analysis, and three new species, *Brachiaria eruciformis*, *Oplismenopsis najada*, and *Pennisetum montanum*, were also added. Any genus previously shown to be monophyletic (*Digitaria*, *Echinochloa*, *Homolepis*, and *Thrasya*) was represented here by one species; if the genus was shown by Giussani et al. (2001) to be para- or polyphyletic, several species were included (e.g., *Paspalum*, *Pennisetum*, *Setaria*, and *Urochloa*).

The data matrix, including ingroup and outgroup taxa, has a total of 123 sequences, with 119 belonging to subfamily Panicoideae. Of these, 111 represent the tribe Paniceae (66 representing *Panicum* s.l.,), seven represent the tribe Andropogoneae, and one (*Arundinella hirta*) represents tribe Arundinelleae. Four other taxa, from subfamily Centothecoideae, were included in the analyses as close relatives of the subfamily Panicoideae (Clark et al., 1995; GPWG, 2001): *Chasmanthium laxum* subsp. *sessiliflorum*, *Danthoniopsis dinteri*, *Thysanolaena maxima*, and *Zeugites pittieri*. *Danthoniopsis dinteri*, formerly placed in Arundinelleae, is now seen as a member of Centothecoideae (GPWG, 2001; J. G. Sanchez-Ken and L. G. Clark, Iowa State University, personal communication). *Thysanolaena*, previously placed in subfamily Arundinoideae as the tribe Thysanolaeneae, is now included in Centothecoideae (GPWG, 2001). The number of representatives for tribe Andropogoneae and subfamily Centothecoideae was reduced from the number used by Giussani et al. (2001). The tribe Andropogoneae represents a rapid radiation with few mutations on internal branches of the tree (Giussani et al., 2001) so that many equally parsimonious arrangements are possible. We were not interested in all these rearrangements in this study, so only placeholders were used.

To insure that the results are not biased by the selection of taxa, an additional analysis was performed using all available *ndhF* sequences of the tribe Paniceae, as taken from Giussani et al. (2001). The complete matrix contained 156 taxa. Appendix 1 (http://ajbsupp.botany.org/v90/) shows species used in this study and their accession numbers.

Phylogenetic analyses—Cladistic analyses based on maximum parsimony were performed using NONA version 2.0 (Goloboff, 1997a). All characters were equally weighted with respect to codon position, were unordered, and gaps were scored as missing data. Parsimony uninformative characters were excluded. Indels were mapped onto the final tree to determine whether they were synapomorphies or homoplasies. In a separate analysis, we recoded indels as binary data following the ''simple indel coding method'' proposed by Simmons and Ochoterena (2000).

Heuristic searches were carried out with the options ''amb-'' (resolve clades only if they have unambiguous support) and ''poly=' (polytomies allowed).

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anthecium in ventral view showing simple papillae all over the palea and the apiculate lemma. (H) *Hymenachne pernambucense* (Spreng.) Zuloaga, comb. nov. Upper anthecium in lateral view showing the lemma and palea not indurated and covered by prickle hairs towards the apex. (A) and (B) are taken from Zuloaga and Morrone, 1996; (C) and (D) are taken from Zuloaga et al., 1998; and (G) is taken from Zuloaga et al., 1993b.



Fig. 2. (A) *Steinchisma hians*. Spikelet in lateral view, showing an expanded and large lower palea. (B–C) *Phanopyrum gymnocarpon* (Elliott) Nash. (B) Spikelet in lateral view, showing lower and upper glume subequal. (C) Upper anthecium obovoid, shorter than the glumes and lower lemma. (D) *Hymenachne pernambucense*. Inflorescence a contracted panicle with the spikelets in unilateral racemes. (E–F) *Panicum* s.s., *P. quadriglume* (Döll) Hitchc. (E) Plant showing caespitose habit, lax and open inflorescence with spikelets in long pedicels. (F) Spikelet in lateral view. (G–H) *Dichanthelium*. (G) *Dichanthelium superatum* (Hack.) Zuloaga. Spikelets in ventral view, showing the presence of lower glume. (H) *Dichanthelium sabulorum* (Lam.) Gould & C.A. Clark. Diagram showing

Searches were performed using ''h/2,'' ''mult*3000,'' which randomizes the order of the taxa, creates a Wagner tree, and submits it to branch-swapping by tree-bisection reconnection (TBR), retaining a maximum of two trees for each initial Wagner tree; the procedure was repeated 3000 times. The shortest trees retained from the subsearches were then TBR swapped to completion with the ''max*'' command. Additionally, and only for the 156 taxon data set, we performed a parsimony ratchet analysis (Nixon, 1999) using one of the most parsimonious trees found with NONA as starting point. A total of 10 000 replicates were done as implemented in Winclada version 1.0 (Nixon, 1999–2002).

To evaluate relative support for individual clades, bootstrap analysis (Felsenstein, 1985) was performed in NONA, using Winclada as an interface (Nixon, 1999–2002). A total of 10 000 replicates was performed. Each replicate was analyzed using a Wagner tree as a starting point followed by TBR branch-swapping, saving only one tree per replicate. Supported clades are considered to be those with more than 50% bootstrap value.

Decay indices (*d*) or Bremer support values (Bremer, 1994) were also calculated using PAUP version 4.0b10 (Swofford, 2002). We used the consensus of all shortest trees as a negative constraint tree to look for trees one step longer. Constraint searches were done 70 000 times, performing TBR swapping on the tree and saving only one tree per replicate whenever it was the shortest suboptimal tree. To find clades that collapse in trees two steps longer, we used the consensus tree of the shortest plus the suboptimal trees already found as a reverse constraint tree and proceeded with a new series of 70 000 replicates. This procedure was repeated nine times.

To explore the monophyly of particular groups, constrained analyses were performed with NONA to determine the number of additional steps required to make a monophyletic group. We used a tree with a fixed monophyletic group as a starting point (using the ''force'' command) and carried out a branch-swapping search on the initial tree (''max/'' command) to look for trees with highest fit. To test for significant differences between constrained and unconstrained trees, we conducted Templeton tests (Templeton, 1983), as implemented in PAUP version 4.0b10 (Swofford, 2002).

An alternative analysis using implied weights (Goloboff, 1993) was run in Pee-Wee version 3.0 (Goloboff, 1997b) using the same search strategies as in NONA. Implied weight provides a way to resolve character conflict in favor of the characters that have less homoplasy on the trees and implies that the average weight for the characters is as high as possible (Goloboff, 1997b). The weighting is based on a concave function, with six different concavities available in the program; 6 is the mildest and 1 the strongest weighting function (Goloboff, 1998). Searches were done using all six possible concavities.

Base-pair performance—Synonymous substitutions, principally due to variation in the third codon position, occur much faster than nonsynonymous substitutions (Li, 1997; Page and Holmes, 1998). However, Källersjö et al. (1999, 2000) showed that, for *rbcL* sequences of Poaceae, the third position contains most of the phylogenetic information in the data. Hence, to test the influence of the three base-pair codon positions on phylogenetic results, we treated them independently. We examined subsets of data that represent (1) first codon positions only, (2) second codon positions only, and (3) third codon positions only. Bootstrap analyses were performed on each data set (10 000 replicates, each starting with a Wagner tree and TBR-swapped), and results were independently compared with the bootstrap analysis performed on the entire data set (2061 bp data set).

RESULTS

Parsimony analyses—*Panicum* phylogeny was estimated from a parsimony analysis based on all available sequences of the tribe Paniceae, a 156-taxon matrix, and all potentially parsimony informative characters of the complete gene. A total of 62 025 trees of 1818 steps (CI = 0.41, RI = 0.8) was found when the analysis using equal weighted characters (NONA) was stopped before completion. To find more different trees a more efficient algorithm, the parsimony ratchet, was used as implemented by Winclada. A total of 6781 trees was found of similar length (1818). All trees from both analyses (68 806) were used to calculate the consensus tree. Figure 3 shows a phylogram of one of the most parsimonious trees with results from the consensus tree overlain. These analyses, using the complete data set (156 taxa), produced results similar to that inferred from the data set of selected Paniceae (123 taxa; see below).

To allow a more thorough tree search, and to avoid a large number of trees based on ambiguous resolutions within genera not related to *Panicum*, we used the selected 123-taxa data set (see outgroup selection, and Supplementary Data, http://ajbsupp.botany.org/v90/). This matrix includes all available species of *Panicum*, genera of the subfamily Panicoideae, and its closest relatives. After excluding amplification primer regions, the data set contained 2028 nucleotides between coordinates 103 579 and 101 553 of the rice *ndhF* gene. The alignment required the addition of three indels 6 base pairs (bp) long, one indel 15-bp long, and one indel 18-bp long that lengthened the data set by a total of 33 nucleotide positions and resulted in 2061 characters. In subfamily Panicoideae, indels reported here occur in a region approximately 400 bp in length, from coordinates 102 114 to 101 729, and some represent synapomorphies of well-supported clades (see *Panicum* phylogeny). The 156-taxa data set includes two extra autapomorphic insertions, one for *Cleistachne* and the other for *Setaria sphacelata*. All these indels, previously published by Giussani et al. (2001), are listed in Table 2 and mapped on one of the most parsimonious trees (Fig. 3).

In the 123-taxa matrix, 787 out of 2061 characters are variable and 431 are informative. Base-pair composition within the Panicoideae is similar to that reported by Giussani et al. (2001); sequences are A-T rich, with thymine 37.3%, adenine 26.8%, guanine 16.7%, and cytosine 15.8%. Overall, 3.4% of the data matrix cells were scored as missing data.

Heuristic searches of the 123-taxa matrix with informative characters equally weighted (NONA) found 15 408 trees of length (L) = 1506; consistency index (CI) = 0.42; and retention index (RI) = 0.78. Bootstrap values above 50% are shown above the branches in Fig. 4. Figure 5 presents a consensus tree of the 15 408 most parsimonious trees with principal monophyletic groups or paraphyletic groups represented with triangles or thick lines, respectively. All these analyses treated gaps as missing data. Coding indels as binary characters produced identical trees with only a few additional steps (1518).

Major groups are the same as those found by Giussani et al. (2001). The subfamily Panicoideae is monophyletic (bootstrap = 97%, decay (d) = 6), and is composed of three large clades, the Andropogoneae, Paniceae with a basic chromosome number of $x = 10$, and the remaining Paniceae with a basic chromosome number of $x = 9$. Relationships among these three clades are ambiguous.

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the foliar dimorphism present in many species of the genus (a, winter form; b, spring form; c, autumn form). (A) is taken from Zuloaga et al., 1998; (B) and (C) are taken from Hitchcock and Chase, 1910; (D) is taken from Zuloaga et al., 1992; (E) and (F) are taken from Zuloaga and Morrone, 1996; (G) is taken from Zuloaga et al., 1993b; and (H) is taken from Morrone and Zuloaga, 1991.

Analyses using implied weights were performed with Pee-Wee under six different concavities ($K = 1$–6) and excluding uninformative sites. All six concavities retrieve the panicoid clade and the same three major clades (trees not shown). The consensus trees derived from $K = 4$, 5, and 6 present similar topologies ($L = 1515$, fit = 3003.5, and rescaled index = 0.46). Searches with $K = 3$ resulted in trees of length = 1519 and fit = 3003.7. Major differences appear when using $K = 1$ and 2 ($L_1 = 1543$, $\text{fit}_1 = 2996.2$; $L_2 = 1528$, $\text{fit}_2 = 3002$, respectively), though they show few differences for *Panicum* resolution. The rescaled index was similar among all concavities.

To test the influence of the three codon positions on phylogenetic results, the distributions of the 431 informative characters in the first, second, and third codon position were analyzed separately. Third codon positions account for most variation (53.1%), followed by first (29.1%), while the second position represents only 17.8% of the variable characters. Separate bootstrap analyses for the first, second, and third codon positions were compared with bootstrap results based on all codon positions together (Fig. 4). Consistent with the variation found among codon positions, the topology was better resolved by the third codon positions. The third codon position recovered 66 well-supported clades of the 82 clades found by the complete data set. The first position data set recovered 36 clades, while the second codon position recovered only 14 clades.

Few clades are exclusively supported by characters of the first codon position, e.g., the $x = 9$ Paniceae clade and the *Panicum*/*Urochloa*/*Setaria* clade (Figs. 4 and 5). On the other hand, more than 30 clades are supported by bootstrap analysis and support derived almost exclusively from the third codon position, e.g., the *Plagiantha*-*Otachyrium*-*Steinchisma* clade, *Setaria* clade, *Urochloa* clade, Forest shade clade, sect. *Cordovensia* clade, sect. *Panicum* clade, and sect. *Prionitia* clade, among others (Figs. 4 and 5). No clade is uniquely characterized by the second codon position.

Panicum phylogeny—The phylogeny of *Panicum* is practically identical in both the implied weight and equally weighted analyses; therefore, we describe the results from equally weighted characters with indels as missing data. Bootstrap values refer to the results found using all codon positions, unless explicit references are made to particular clades. Results from constrained analyses are presented in Table 3. Comments on indels, implied weight, constrained results, decay, bootstrap analyses, and also results from the 156-taxa analyses are presented when necessary.

The genus *Panicum* s.l. is clearly polyphyletic (Fig. 5); to make *Panicum* monophyletic requires the addition of 111 steps (Table 3). Species of *Panicum* s.l. are split over the $x = 9$ and $x = 10$ Paniceae clades. Among the species shown to belong in the $x = 10$ Paniceae clade, only *P. anceps* Michx. and *P. rigidulum* Bosc ex Nees of sect. *Agrostoidea* (subg. *Agrostoides*) are $x = 9$. *Panicum gouinii* E. Fourn and *P. mertensii* Roth. are polymorphic for that character ($x = 9$, 10; see http://ajbsupp.botany.org/v90/ for basic chromosome numbers of species of the genus).

Subgenus *Panicum* is clearly monophyletic and completely included in the $x = 9$ Paniceae clade (Fig. 5). Subgenus *Steinchisma* is exclusively within the $x = 10$ Paniceae clade and its monophyly requires only one more step than the shortest tree (Table 3). The monotypic subgenus *Megathyrsus* (*Panicum maximum*) is placed within the *Urochloa* clade. Subgenera *Agrostoides*, *Phanopyrum*, and *Dichanthelium* are clearly polyphyletic. Subgenus *Dichanthelium* is entirely incorporated in the $x = 9$ Paniceae clade. Making the subgenus monophyletic requires 18 more steps than the most parsimonious tree (Table 3). Subgenera *Agrostoides* and *Phanopyrum* are spread over the $x = 9$ and $x = 10$ Paniceae clades. Constraining their monophyly requires 98 and 86 extra steps, respectively (Table 3).

Though subgenera *Agrostoides* and *Phanopyrum* are spread over $x = 9$ and $x = 10$ Paniceae clades, representatives of sections *Laxa*, *Lorea*, *Megista*, *Phanopyrum*, and *Stolonifera* (subg. *Phanopyrum*), and representatives of sections *Agrostoidea*, *Obtusa*, *Prionitia*, *Tenera*, *Tuerckheimiana*, and *Valida* (subg. *Agrostoides*) are entirely in the $x = 10$ Paniceae clade (Fig. 5). On the other hand, species of sections *Monticola* and *Parvifolia* (subg. *Phanopyrum*), *P. antidotale* (not included in any section), and *P. bulbosum* from sect. *Bulbosa* (both from subg. *Agrostoides*) are included in the $x = 9$ Paniceae clade. The African species of sect. *Clavelligera* are also placed in the $x = 9$ Paniceae clade.

Paniceae $x = 10$ is a strongly supported clade (99% bootstrap, $d > 9$), divided into three major lineages (Fig. 4). One clade (82%, $d = 4$) includes five species of *Panicum* sect. *Laxa* related to *Hymenachne donacifolia*, *Plagiantha tenella*, *Otachyrium versicolor*, and three species of *Steinchisma*; *Leptocoryphium lanatum* is sister to the whole group (Fig. 5). A deletion 9-bp long characterizes the *Panicum hylaeicum* to *Steinchisma* clade (73%, $d = 2$; see Fig. 3 and Table 3). Relationships among species of *Panicum* sect. *Laxa* show that the section is polyphyletic. *Steinchisma* would have to include *Panicum laxum* to be monophyletic (95%, $d = 3$; see results of constrained analyses in Table 3).

A second major clade within Paniceae $x = 10$ (80% bootstrap, $d = 3$) includes *Panicum* sect. *Stolonifera* (subg. *Phanopyrum*), three species of the polyphyletic subg. *Agrostoides*, and representatives of *Anthaenantiopsis*, *Axonopus*, *Echinolaena*, *Ichnanthus*, *Ophiochloa*, *Paspalum*, *Streptostachys asperifolia*, and *Thrasya* (Figs. 4 and 5). Species of sect. *Stolonifera* form a monophyletic group, though with low support (62%, $d = 1$). *Echinolaena inflexa* is its sister group, linked in a better supported clade (78%, $d = 2$). However, when a weight function is applied (Pee-Wee analyses), all six concavities resolve sect. *Stolonifera* as paraphyletic, including *Echinolaena* (results not shown). In all analyses, three species of subg. *Agrostoides* join *Anthaenantiopsis*, *Paspalum*, and *Thrasya* in a well-supported clade (99%, $d > 9$). Although subg. *Agrostoides* is not monophyletic, two species, one from sect. *Tuerckheimiana* and one from *Valida* are clearly related to

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Fig. 3. One of the 68 806 most parsimonious trees (length, $L = 1818$) obtained with equally weighted characters from the 156-taxa matrix; consistency index (CI) = 0.41 and retention index (RI) = 0.80. Branch length refers to the number of nucleotide substitutions, shown above branches. Arrows show branches that collapse on the consensus tree. Length mutations (indels) characterizing particular clades or taxa are shown according to code numbers in Table 2. Black circles represent deletions, and white circles represent insertions.


Thysanolaena maxima
Danthoniopsis dinteri
Danthoniopsis petiolata
Zeugites pittieri
Chasmanthium latifolium
Chasmanthium laxum subsp. sessiliflorum
Arundinella hirta
Chionachne koenigii
Tripsacum dactyloides
Elionurus muticus
Zea mays
Ischaemum afrum
Coelorachis selloana
Apluda mutica
Chrysopogon fulvus
Phacelurus digitatus
Microstegium nudum
Miscanthus japonicus
Cleistachne sorghoides
Sorghum bicolor
Coix aquatica
Hyparrhenia hirta
Andropogon gerardii
Schizachyrium scoparium
Cymbopogon flexuosus
Heteropogon contortus
Capillipedium parviflorum
Bothriochloa bladhii
Dichanthium aristatum
Leptocoryphium lanatum
Panicum hylaeicum PHA LAX
Panicum pilosum PHA LAX
Hymenachne donacifolia
Panicum grumosum PHA LAX
Panicum pernambucense PHA LAX
Plagiantha tenella
Otachyrium versicolor
Steinchisma hians
Steinchisma spathellosa
Panicum laxum PHA LAX
Steinchisma decipiens
Panicum gymnocarpon PHA PHA
Panicum euprepes PHA LOR
Panicum subtiramulosum PHA LOR
Canastra lanceolata
Panicum petersonii AGR PRI
Panicum prionitis AGR PRI
Panicum anceps AGR AGR
Panicum rigidulum AGR AGR
Panicum tenerum AGR TEN
Homolepis glutinosa
Homolepis isocalycia
Arthropogon villosus
Altoparadisium chapadense
Panicum stenodes AGR TEN
Panicum caricoides AGR TEN
Panicum mertensii PHA MEG
Streptostachys ramosa
Oplismenopsis najada
Mesosetum chaseae
Tatianyx arnacites
Streptostachys asperifolia
Axonopus fissifolius
Axonopus anceps
Ophiochloa hydrolithica
Ichnanthus pallens
Echinolaena inflexa
Panicum stoloniferum PHA STL
Panicum piauiense PHA STL
Panicum chapadense PHA STL
Panicum validum AGR VAL
Anthaenantiopsis rojasiana
Panicum tuerckheimii AGR TUE
Panicum obtusum AGR OBT
Paspalum conjugatum
Paspalum vaginatum
Paspalum conspersum
Paspalum malacophyllum
Paspalum paniculatum
Paspalum remotum
Thrasya glaziovii
Thrasya petrosa
Paspalum haumanii
Paspalum arundinellum
Paspalum wettsteinii

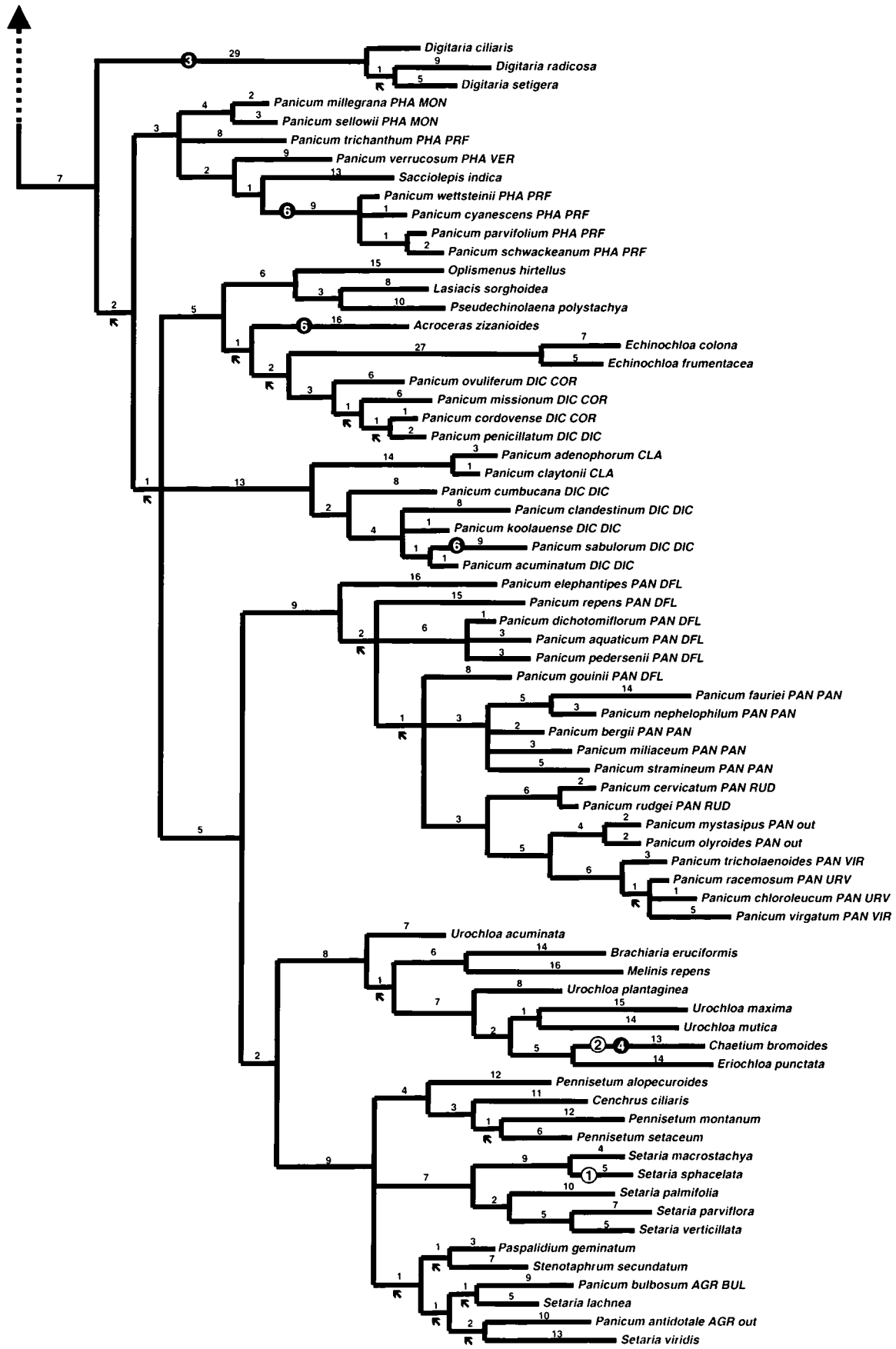


Fig. 3. Continued.

Anthaenantiopsis (89%, due to informative characters of the third codon position; $d = 3$). *Panicum obtusum*, sect. *Obtusa*, is sister to the *Paspalum-Thrasya* clade with low bootstrap support (62%, $d = 1$) or sister to the whole group that includes species of sect. *Agrostoidea*, *Anthaenantiopsis*, and the *Paspalum-Thrasya* clade, in all concavities in the Pee-Wee analyses (not shown). The resolution shown within the *Paspalum-Thrasya* clade in the 123-taxa data set is not supported by analyses of the 156 taxon (Fig. 3); results similar to the latter were shown by Giussani et al. (2001).

A third major clade within the $x = 10$ Paniceae includes several species of subgenera *Agrostoides* and *Phanopyrum*, *Oplismenopsis najada*, and species of the Ambiguous clade previously defined by Giussani et al. (2001) as a poorly supported group of morphologically dissimilar taxa: *Altoparadisium*, *Arthropogon villosus*, *Canastra*, *Homolepis*, *Mesosetum*, *Streptostachys ramosa*, *Tatianyx*, plus *Panicum euprepes* (subg. *Phanopyrum* sect. *Lorea*), and *P. prionitis* (subg. *Agrostoides* sect. *Prionitia*). The redefined Ambiguous clade (Figs. 4 and 5), still with very low bootstrap support (56%, $d = 1$), is also present in all concavities of the implied weight analyses, except for $K = 1$ where the basal branch of this clade collapses. In all analyses, two species of sect. *Tenera* (subg. *Agrostoides*) and the monotypic sect. *Megista* (subg. *Phanopyrum*) constitute a well-supported monophyletic unit (99% bootstrap, $d > 9$). The third species of sect. *Tenera* falls in a monophyletic clade with two species of sect. *Agrostoidea* (99%, $d > 9$). To make sect. *Tenera* monophyletic results in a tree 35 steps longer than the current one (Table 3). Section *Prionitia* (subgenus *Agrostoides*) is monophyletic (86%, $d = 2$) and sister to this latter clade (98% bootstrap, $d = 5$, mostly supported by third position bases; Fig. 4). Section *Lorea*, a monophyletic unit based on two sampled species (99%, $d = 8$, and a synapomorphic 15-bp deletion, Table 3), is linked with *Canastra lanceolata* to sect. *Prionitia*, sect. *Agrostoidea*, and *P. tenerum* with a bootstrap value = 72% and $d = 2$. *Panicum gymnocarpon* (from the monotypic sect. *Phanopyrum*) represents the sister taxon of that major clade. Phylogenetic relationships of the *Arthropogon villosus-Altoparadisium* clade, *Homolepis*, *Oplismenopsis najada*, *Streptostachys ramosa*, and *Tatianyx-Mesosetum* clade are still not clear within the Ambiguous clade.

Paniceae $x = 9$ is monophyletic with 98% bootstrap support and $d = 6$, due almost exclusively to informative characters of the first codon position (Fig. 4). *Digitaria* is the sister taxon of the $x = 9$ Paniceae under the equally weighted character analyses and also under all concavities of the Pee-Wee analyses. This relationship is not supported by Pee-Wee $K = 1$, and the 156-taxa analyses where it collapses (Figs. 3–5). *Digitaria* is well-differentiated by 29 changes including 14 autapomorphies in both the 123- and 156-taxa trees (Figs. 3 and 4). After *Digitaria*, four clear monophyletic groups are included in an unresolved polytomy (Figs. 3 and 5).

The Forest shade clade, including *Acroceras*, *Echinochloa*, *Lasiacis*, *Oplismenus*, *Panicum ovuliferum* (subg. *Dichanthelium* sect. *Cordovensia*), and *Pseudechinolaena* (Giussani et al., 2001), is recovered in these analyses and also includes two other species of sect. *Cordovensia*, *P. cordovense* and *P. missionum*, as well as *P. penicillatum* (sect. *Dichanthelium*; Figs. 3–5). This clade constitutes a monophyletic unit with 80% bootstrap, $d = 2$, and is principally supported by mutations in the third codon position. Section *Cordovensia* plus *P. penicillatum* are characterized exclusively by synapomorphies of the third codon position (75%, $d = 1$; Fig. 4). *Pseudechinolaena ovuliferum* is sister to the other three species, which form a trichotomy (64%). Resolution within the *Cordovensia* clade is not seen in the consensus tree of the 156-taxa analysis, where the four taxa are collapsed (Fig. 3). Results for the Forest shade clade, from Pee-Wee analyses, considering all different concavities, show *Echinochloa colona* and *Acroceras zizanioides* as sister taxa of sect. *Cordovensia* (not shown). These relationships are not supported when equally weighted characters are used (Fig. 4). In the bootstrap results of the 156-taxa data set, *Acroceras* is sister to *Oplismenus*, *Lasiacis*, and *Pseudechinolaena*, with very low support (53%); this relationship is not resolved in the 123-taxa analyses nor in the consensus tree of the 156-taxa analysis (Figs. 3 and 4). The other five species included in the analysis from sect. *Dichanthelium* (subg. *Dichanthelium*) are assembled in a clade with sect. *Clavelligera* (99%, $d > 9$). Both sect. *Clavelligera* and sect. *Dichanthelium* are monophyletic (100%, $d > 9$ and 89%, $d = 2$, respectively; Figs. 4 and 5).

Species from subgenus *Phanopyrum*, representing sects. *Monticola*, *Parvifolia*, and *Verrucosa*, form a clade with *Sacciolepis indica* (bootstrap = 82%, $d = 2$; Figs. 4 and 5). The two sampled species of the three that constitute sect. *Monticola* form a monophyletic group (95%, $d = 3$). *Panicum cyanescens*, *P. parvifolium*, *P. schwackeanum*, and *P. wettsteinii*, of sect. *Parvifolia*, also form a highly supported clade (99%, $d = 8$) with *Sacciolepis* as its sister taxon; *P. trichanthum* is not included in this group, making sect. *Parvifolia* paraphyletic. However, these four species are included in the *Parvifolia* clade, sharing a 15-bp deletion (Figs. 3 and 5), a homoplastic change also present in *Acroceras*, *P. sabulorum*, and sect. *Lorea* (Table 3).

The fourth $x = 9$ Paniceae subclade includes species of the *Panicum*/*Setaria*/*Urochloa* clade (Fig. 5; see also Giussani et al., 2001) with 87% bootstrap and $d = 4$. The monotypic subgenus *Megathyrsus* is included in the *Urochloa* clade (97%, $d = 6$), while *Panicum antidotale* (unassigned to section) and *P. bulbosum* (sect. *Bulbosa*), both from subg. *Agrostoides*, are grouped within the *Setaria* clade (99%, $d > 9$; Figs. 4 and 5). Although not supported by bootstrap analysis, *Panicum antidotale* and *P. bulbosum* are related to two species of *Setaria*, *S. viridis* and *S. lachnea*, in a clade that appears in the consensus tree with $d = 1$ (Figs. 3–5) and that is also present under all concavities of Pee-Wee analyses (not shown).

Subgenus *Panicum* is highly supported as monophyletic (97% bootstrap, $d = 6$; Fig. 4). Section *Rudgeana* (99%, $d = 5$) and sect. *Panicum* are each monophyletic, although the latter has a low bootstrap value (59%). Section *Panicum* also appears as monophyletic in the consensus tree from NONA (Fig. 5) and in the consensus trees from $K = 3$–6 of Pee-Wee analyses (not shown). Section *Dichotomiflora* is paraphyletic within the *Panicum* clade, while sects. *Virgata* and *Urvilleana* form a monophyletic unit supported by informative characters of the third codon position (91%, $d = 5$, and also present with $K = 3$–6, not shown).

DISCUSSION

To explore whether evolution acts differently on different characters within the gene, different data sets with the first, second, and third codon position were analyzed independently. In agreement with previous authors (Källersjö et al., 1999, 2000), even though changes at the third codon position occur

TABLE 2. Insertions and deletions in *ndhF* for panicoid grasses, adding *Panicum* sequences. Indels are mapped on one of the most parsimonious trees (see Fig. 4). Bp = base pairs.

Code letter	Insertion/ deletion	Size (bp)	Coordinate number	Indel identity	Taxa
1	Insertion	6	102 703	Autapomorphy	*Setaria sphacelata*
2	Insertion	6	102 114	Homoplasy	*Chaetium bromoides, Danthoniopsis dinteri, D. petiolata*
3	Deletion	18	102 114	Synapomorphy	*Digitaria ciliaris, D. radicosa, D. setigera*
4	Deletion	9	102 092	Homoplasy	*Chaetium bromoides, Danthoniopsis dinteri, D. petiolata*
5	Insertion	6	102 065	Synapomorphy	*Axonopus anceps, A. fissifolius, Ophiochloa hydrolithica*
6	Deletion	15	101 951	Homoplasy	*Acroceras zizanioides, Panicum cyanescens, P. euprepes, P. parviflorum, P. sabulorum, P. schwackeanum, P. subtiramilosum, P. wettsteinii*
7	Deletion	9	101 739	Synapomorphy	*Hymenachne donacifolia, Panicum grumosum, P. hylaeicum, P. laxum, P. pernambucense, P. pilosum, Plagiantha tenella, Otachyrium versicolor, Steinchisma decipiens, S. hians, S. spathellosa*
8	Insertion	6	101 735	Synapomorphy/Autapomorphy[a]	$x = 10$ Paniceae clade, *Thysanolaena maxima*
9	Insertion	6	101 704	Autapomorphy	*Cleistachne sorghoides*

[a] See Giussani et al. (2001) for base-pair comparison and explanation of identities.

at higher rates than the other codon positions, they should not be discarded or downweighted a priori. When we analyzed the three data sets the topology was recovered mostly by the third position followed by the first one. The second codon position was the most conservative, as expected. However, all codon positions were required to produce the well-resolved topology found with the complete gene data set. Variation in the third codon position characterizes some monophyletic clades also supported by morphological synapomorphies as in the *Plagiantha-Otachyrium-Steinchisma* clade, the sect. *Cordovensia* clade, the *Setaria* clade, the *Urochloa* clade, and the Forest shade clade, among others (Fig. 3).

Panicum s.s.—Our results show clearly that the name *Panicum* must ultimately be restricted to subg. *Panicum*; all five sections, *Panicum*, *Virgata*, *Dichotomiflora*, *Rudgeana*, and *Urvilleana* form a monophyletic group. This clade is very well supported and our results are congruent with previous studies (Gómez-Martínez and Culham, 2000; Duvall et al., 2001; Giussani et al., 2001; J. Barber, L. Giussani, F. Zuloaga, and E. Kellogg, unpublished data).

Relationships within *Panicum* s.s. are, on the other hand, not completely clear. Sections *Panicum* and *Rudgeana* are both monophyletic, while further studies are needed to understand relationships among *Dichotomiflora*, *Virgata*, and *Urvilleana*. Section *Virgata* (*P. tricholaenoides* and *P. virgatum*) and sect. *Urvilleana* (*P. chloroleucum* and *P. racemosum*) are together in an unresolved clade and related to another clade that includes *P. olyroides* and *P. mystasipus*, both ungrouped species in previous treatments (Zuloaga, 1987a; Zuloaga et al., 1993a); sect. *Rudgeana* is a sister taxon of this clade. Section *Dichotomiflora* (here represented by *P. aquaticum*, *P. dichotomiflorum*, *P. elephantipes*, *P. gouinii*, *P. pedersenii*, and *P. repens*) is paraphyletic, and affinities among its species are not resolved.

Morphologically, *Panicum* s.s. includes caespitose species, with membranous-ciliate ligules, open panicles with spikelets on long pedicels, the spikelets with upper glume and lower lemma 7–13-nerved (Fig. 2E–F), and upper anthecium indurate, with compound papillae at the apex of the upper palea (Fig. 1B), these papillae also present in some species at the apex of the upper lemma. All species are C_4, of the NAD-me subtype, with specialized chloroplasts centrifugally or centripetally located in the outer parenchymatous sheath (Fig. 1A); the basic chromosome number for subgenus *Panicum* is $x = 9$.

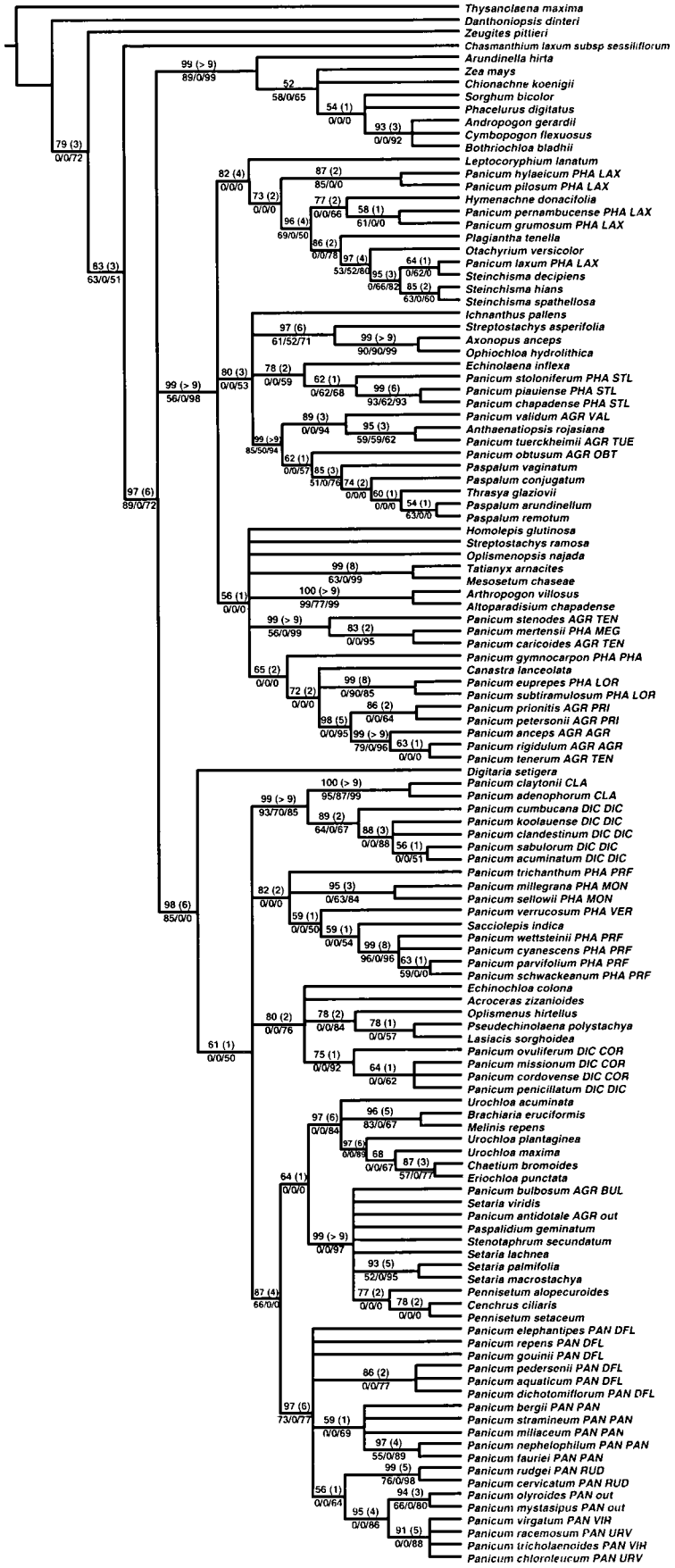
Sections *Panicum*, *Dichotomiflora*, and *Virgata* are distributed worldwide, with species in America, Africa, Europe, Asia, and Oceania. Section *Urvilleana* is restricted to America (with one possibly related species present in northern Africa), while species of sect. *Rudgeana* grow from Central to South America (Zuloaga, 1987b).

Steinchisma—*Steinchisma* clearly has to be considered independent from *Panicum* s.s., as previously stated by several authors (Brown, 1977; Renvoize, 1998; Zuloaga et al., 1998). This subgenus is characterized by the presence of an expanded and large lower palea (Fig. 2A), five-nerved upper glume and lower lemma, and upper anthecium covered with compound papillae regularly distributed over the lemma and palea (Fig. 1D). All species have a basic chromosome number of $x = 10$. Some of these characters are shared by sister taxa in the cladogram, such as *Plagiantha* and *Otachyrium*. *Steinchisma* differs from its sister taxa in being a C_3/C_4 intermediate (Fig. 1C).

Panicum laxum, the type species of sect. *Laxa*, falls within the monophyletic *Steinchisma* clade (Fig. 5). Zuloaga et al. (1992) noted that, in some specimens of *P. laxum*, the anatomy tends to the intermediate C_3/C_4 type and resembles *Steinchisma* in having specialized chloroplasts present in the outer bundle sheath cells. Some specimens of *P. laxum* share morphological features with *Steinchisma*, such as enlargement of the lower palea and upper anthecium with compound papillae (Zuloaga

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Fig. 4. Bootstrap analyses (10 000 replicates) of different subsets of characters were based on the 123-taxa matrix. Above branches: all codon positions, the complete data set (431 informative characters); below branches: containing only informative characters of (a) first codon position (123 informative characters), (b) second codon position (77 informative characters), and (c) third codon position (229 informative characters), respectively. Decay values are in parentheses above branches.


Thysanolaena maxima
Danthoniopsis dinteri
Zeugites pittieri
Chasmanthium laxum subsp sessiliflorum
Arundinella hirta
Zea mays
Chionachne koenigii
Sorghum bicolor
Phacelurus digitatus
Andropogon gerardii
Cymbopogon flexuosus
Bothriochloa bladhii
Leptocoryphium lanatum
Panicum hylaeicum PHA LAX
Panicum pilosum PHA LAX
Hymenachne donacifolia
Panicum pernambucense PHA LAX
Panicum grumosum PHA LAX
Plagiantha tenella
Otachyrium versicolor
Panicum laxum PHA LAX
Steinchisma decipiens
Steinchisma hians
Steinchisma spathellosa
Ichnanthus pallens
Streptostachys asperifolia
Axonopus anceps
Ophiochloa hydrolithica
Echinolaena inflexa
Panicum stoloniferum PHA STL
Panicum piauiense PHA STL
Panicum chapadense PHA STL
Panicum validum AGR VAL
Anthaenatiopsis rojasiana
Panicum tuerckheimii AGR TUE
Panicum obtusum AGR OBT
Paspalum vaginatum
Paspalum conjugatum
Thrasya glaziovii
Paspalum arundinellum
Paspalum remotum
Homolepis glutinosa
Streptostachys ramosa
Oplismenopsis najada
Tatianyx arnacites
Mesosetum chaseae
Arthropogon villosus
Altoparadisium chapadense
Panicum stenodes AGR TEN
Panicum mertensii PHA MEG
Panicum caricoides AGR TEN
Panicum gymnocarpon PHA PHA
Canastra lanceolata
Panicum euprepes PHA LOR
Panicum subtiramulosum PHA LOR
Panicum prionitis AGR PRI
Panicum petersonii AGR PRI
Panicum anceps AGR AGR
Panicum rigidulum AGR AGR
Panicum tenerum AGR TEN
Digitaria setigera
Panicum claytonii CLA
Panicum adenophorum CLA
Panicum cumbucana DIC DIC
Panicum koolauense DIC DIC
Panicum clandestinum DIC DIC
Panicum sabulorum DIC DIC
Panicum acuminatum DIC DIC
Panicum trichanthum PHA PRF
Panicum millegrana PHA MON
Panicum sellowii PHA MON
Panicum verrucosum PHA VER
Sacciolepis indica
Panicum wettsteinii PHA PRF
Panicum cyanescens PHA PRF
Panicum parvifolium PHA PRF
Panicum schwackeanum PHA PRF
Echinochloa colona
Acroceras zizanioides
Oplismenus hirtellus
Pseudechinolaena polystachya
Lasiacis sorghoidea
Panicum ovuliferum DIC COR
Panicum missionum DIC COR
Panicum cordovense DIC COR
Panicum penicillatum DIC DIC
Urochloa acuminata
Brachiaria eruciformis
Melinis repens
Urochloa plantaginea
Urochloa maxima
Chaetium bromoides
Eriochloa punctata
Panicum bulbosum AGR BUL
Setaria viridis
Panicum antidotale AGR out
Paspalidium geminatum
Stenotaphrum secundatum
Setaria lachnea
Setaria palmifolia
Setaria macrostachya
Pennisetum alopecuroides
Cenchrus ciliaris
Pennisetum setaceum
Panicum elephantipes PAN DFL
Panicum repens PAN DFL
Panicum gouinii PAN DFL
Panicum pedersenii PAN DFL
Panicum aquaticum PAN DFL
Panicum dichotomiflorum PAN DFL
Panicum bergii PAN PAN
Panicum stramineum PAN PAN
Panicum miliaceum PAN PAN
Panicum nephelophilum PAN PAN
Panicum fauriei PAN PAN
Panicum rudgei PAN RUD
Panicum cervicatum PAN RUD
Panicum olyroides PAN out
Panicum mystasipus PAN out
Panicum virgatum PAN VIR
Panicum racemosum PAN URV
Panicum tricholaenoides PAN VIR
Panicum chloroleucum PAN URV

et al., 1992). Later, Zuloaga et al. (1993a) showed in a phenetic analysis that *P. laxum* appeared segregated from sect. *Laxa* and related to species of *Steinchisma*; nevertheless, these authors maintained *P. laxum* within sect. *Laxa*. This study provides additional data to support exclusion of *P. laxum* from section *Laxa* and its inclusion in *Steinchisma* (see taxonomic treatment).

This study also shows that *Plagiantha*, characterized by its enlarged lower palea and upper anthecium with compound papilla all over its surface, and *Otachyrium*, a genus with a conspicuous enlarged lower palea, are sister to the *Steinchisma* clade. This relationship was previously suggested based on morphological characters by Clayton and Renvoize (1986) and Zuloaga et al. (2000).

Dichanthelium—As stated above, the systematic position of *Dichanthelium*, as an independent genus or a subgenus of *Panicum*, has been extensively discussed in the last three decades. Our analysis shows sect. *Dichanthelium* as a monophyletic group, with the African sect. *Clavelligera* as its sister taxon. The two sampled species are sisters.

Our results support recognition of *Dichanthelium* as an independent genus, excluding from it sect. *Cordovensia*, and placing *P. penicillatum* under the latter section. The taxonomic position of these taxa is discussed below. *Dichanthelium* is therefore considered as an American genus, with approximately 55 species ranging from Canada and the United States through Central America, reaching the center of Argentina and Chile in South America. The genus includes taxa usually with vegetative and floral dimorphism (Fig. 2H), ligules membranous-ciliate, spikelets with the upper glume and lower lemma 7–11(–15)-nerved, exceptionally five-nerved in two species, lower palea present (Fig. 2G), upper anthecium indurate, with simple papillae all over its surface, the lemma apiculate or crested at the apex (Fig. 1G), non-Kranz anatomy and a basic chromosome number of $x = 9$; most of the species grow in forest edges in humid places, from sea level to 3000 m a.s.l.

Section *Clavelligera* includes approximately 10 African species with distinctive and conspicuous clavellate hairs on the inflorescence branches, with overall morphology similar to species of *Dichanthelium* (except for the foliar and floral dimorphism, absent in species of *Clavelligera*). Although section *Clavelligera* should clearly be segregated from *Panicum* s.l., including it in *Dichanthelium* should wait until more species are scrutinized.

Cordovensia clade—Section *Cordovensia* was established by Parodi (1925) based on the informal group *Cordovensia* and was subsequently included in subg. *Dichanthelium* (Zuloaga et al., 1986). Section *Cordovensia* is distinguished from sect. *Dichanthelium* by the absence of foliar dimorphism, presence of a lower glume three-quarters the length of the spikelet, and absence of a palea in the lower anthecium. Our study indicates that *P. penicillatum* Nees ex Trin. and sect. *Cordovensia* were erroneously placed within *Dichanthelium* (Zuloaga et al., 1993b). All these taxa are within the Forest shade clade, together with *Acroceras*, *Echinochloa*, *Lasiacis*, *Oplismenus*, and *Pseudechinolaena*. Section *Cordovensia*, now including *P. penicillatum*, is morphologically similar to the genus *Acroceras*. Both taxa include species of forest shade, with plants decumbent and leaning in the vegetation, ligules membranous, open panicles with spikelets with the lower glume one-half to four-fifths the length of the spikelet, upper glume and lower lemma five- (occasionally seven-) nerved, lower palea present or absent, and upper anthecium crested or apiculate at the apex; all species are non-Kranz and have a basic chromosome number of $x = 9$. Despite their similarity this analysis does not support the relationship of sect. *Cordovensia-Acroceras*. Without obvious unique characters for sect. *Cordovensia*, and without broader sampling of the ''Forest shade clade,'' we feel that taxonomic changes would be premature.

Urochloa clade—Subgenus *Megathyrsus* of *Panicum* s.l., characterized by C_4 of the PEP-ck photosynthetic subtype (Fig. 1E) and the upper anthecium transversely rugose (Fig. 1F), needs to be segregated from the genus. The single species of subg. *Megathyrsus*, *Panicum maximum*, belongs in the genus *Urochloa*, as previously stated by Webster (1987) and confirmed by Giussani et al. (2001).

Subgenus Phanopyrum—*Phanopyrum*, as a subgenus of *Panicum* s.l., is polyphyletic, with sections and species both in the $x = 9$ and $x = 10$ Paniceae clades. Our results indicate that *Phanopyrum* has to be considered a monotypic genus with a single species, *Phanopyrum gymnocarpon*. The name *Phanopyrum* already exists at the generic level, so no nomenclatural changes are necessary (see Taxonomic Treatment). This genus is isolated in a basal position in a clade that also includes the recently described genus *Canastra* (Morrone et al., 2001) and unrelated species of *Panicum* s.l., previously considered within subg. *Agrostoides* and belonging to sects. *Lorea*, *Prionitia*, *Agrostoidea*, and *Tenera* (Zuloaga, 1987a). *Phanopyrum* is distinguished by its unilateral inflorescences, with glabrous spikelets having a long first glume (Fig. 2B), and a short, stipitate, obovoid, and smooth upper anthecium (Fig. 2C). This species, restricted to the southeastern United States, is non-Kranz and has a basic chromosome number of $x = 10$.

The remaining taxa considered by Zuloaga (1987a) within subg. *Phanopyrum* need to be segregated from *Panicum* s.l., either as new genera or within other existing genera of the Paniceae. However, relationships of several sections and species are still unclear or more species need to be sampled prior to a final decision on this matter. Section *Parviglumia* was not included in this study as material was not available.

Monticola clade-Parvifolia clade-Verrucosa—Sections *Monticola*, *Parvifolia*, and *Verrucosa* are together in a well-supported clade within the $x = 9$ clade of the Paniceae. All these sections share a similar inflorescence type, with open and lax panicles, spikelets usually on long pedicels, spikelets

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Fig. 5. Consensus of the 15 408 most parsimonious trees based on the 123-taxa matrix. Principal monophyletic clades are represented with triangles, paraphyletic groups with thick lines, and isolated species or genera are shown with narrow lines. Grey color identifies *Panicum* species or groups, black color labels other genera different from *Panicum* sensu lato (s.l.). Names above branches correspond to monophyletic clades discussed in the manuscript; those with asterisks were discussed by Giussani et al. (2001). Arrows show branches that collapse on the consensus tree of the 156-taxa tree. Numbers in parentheses represent the number of species sampled and the total number of species within each section as defined by Zuloaga's classification (Table 1).

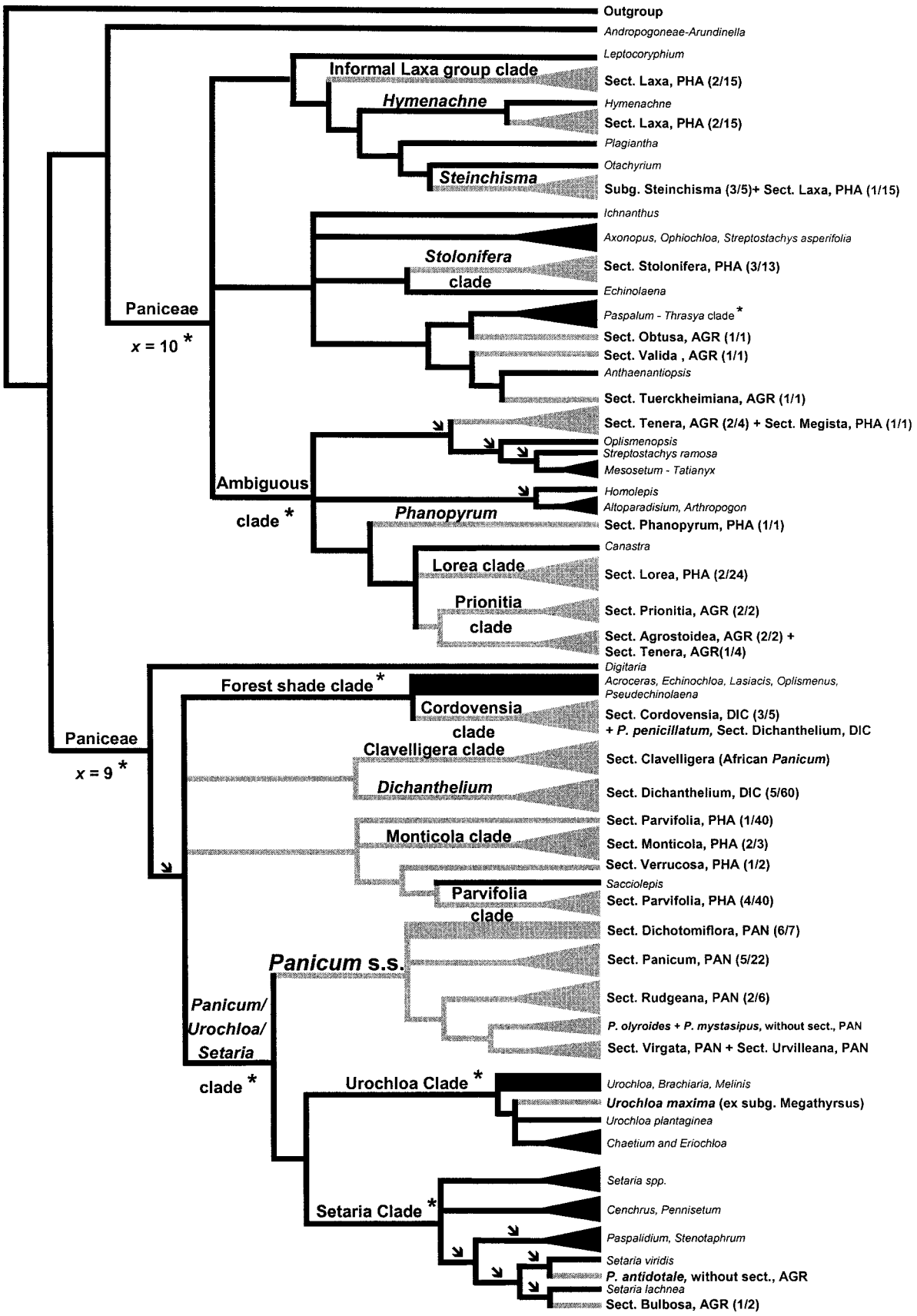

Outgroup
Andropogoneae-Arundinella
Leptocoryphium
Informal Laxa group clade
Sect. Laxa, PHA (2/15)
Hymenachne
Hymenachne
Sect. Laxa, PHA (2/15)
Plagiantha
Otachyrium
Steinchisma
Subg. Steinchisma (3/5)+ Sect. Laxa, PHA (1/15)
Ichnanthus
Axonopus, Ophiochloa, Streptostachys asperifolia
Stolonifera
clade
Sect. Stolonifera, PHA (3/13)
Echinolaena
Paniceae
x = 10 *
Paspalum - Thrasya clade *
Sect. Obtusa, AGR (1/1)
Sect. Valida , AGR (1/1)
Anthaenantiopsis
Sect. Tuerckheimiana, AGR (1/1)
Sect. Tenera, AGR (2/4) + Sect. Megista, PHA (1/1)
Oplismenopsis
Streptostachys ramosa
Mesosetum - Tatianyx
Ambiguous
clade *
Homolepis
Altoparadisium, Arthropogon
Phanopyrum
Sect. Phanopyrum, PHA (1/1)
Canastra
Lorea clade
Sect. Lorea, PHA (2/24)
Prionitia
clade
Sect. Prionitia, AGR (2/2)
Sect. Agrostoidea, AGR (2/2) +
Sect. Tenera, AGR(1/4)
Digitaria
Forest shade clade *
Acroceras, Echinochloa, Lasiacis, Oplismenus,
Pseudechinolaena
Cordovensia
clade
Sect. Cordovensia, DIC (3/5)
+ P. penicillatum, Sect. Dichanthelium, DIC
Paniceae
x = 9 *
Clavelligera clade
Sect. Clavelligera (African Panicum)
Dichanthelium
Sect. Dichanthelium, DIC (5/60)
Sect. Parvifolia, PHA (1/40)
Monticola clade
Sect. Monticola, PHA (2/3)
Sect. Verrucosa, PHA (1/2)
Sacciolepis
Parvifolia
clade
Sect. Parvifolia, PHA (4/40)
Sect. Dichotomiflora, PAN (6/7)
Panicum s.s.
Sect. Panicum, PAN (5/22)
Sect. Rudgeana, PAN (2/6)
Panicum/
Urochloa/
Setaria
P. olyroides + P. mystasipus, without sect., PAN
Sect. Virgata, PAN + Sect. Urvilleana, PAN
clade *
Urochloa Clade *
Urochloa, Brachiaria, Melinis
Urochloa maxima (ex subg. Megathyrsus)
Urochloa plantaginea
Chaetium and Eriochloa
Setaria spp.
Setaria Clade *
Cenchrus, Pennisetum
Paspalidium, Stenotaphrum
Setaria viridis
P. antidotale, without sect., AGR
Setaria lachnea
Sect. Bulbosa, AGR (1/2)

TABLE 3. Results of constrained analyses, showing the number of additional steps required to make a particular monophyletic clade: genus *Panicum*, its subgenera, and sections. Significance values between constrained and unconstrained trees (using Templeton test) are also shown: ** = $P < 0.001$, *** = $P < 0.0001$, NS = not significant. Shortest unconstrained trees require 1506 steps.

Taxon	Length for constrained trees	Additional steps	Significance values
Panicum	1617	111	***
Steinchisma (= subg. Steinchisma)	1507	1	NS
Subgenus *Agrostoides*	1604	98	***
Dichanthelium (= subg. Dichanthelium)	1524	18	***
Subgenus *Phanopyrum*	1592	86	***
Section *Tenera* (subg. *Agrostoides*)	1541	35	***
Section *Cordovensia* (subg. *Dichanthelium*)	1507	1	NS
Section *Dichanthelium* (subg. *Dichanthelium*) when including *Panicum penicillatum*	1531	25	***
Section *Laxa* (subg. *Phanopyrum*)	1521	15	**
Section *Parvifolia* (subg. *Phanopyrum*)	1509	3	NS
Section *Dichotomiflora* (subg. *Panicum*)	1507	1	NS

ellipsoid to obovoid, with the lower glume three-nerved and the upper glume and lower lemma five-nerved, having an indurate upper anthecium, and with simple papillae and bicellular microhairs over the lemma and palea. These species are sufficiently homogeneous that they could be recognized as a new genus. However, the distinctive genus *Sacciolepis* is nested within this clade and no apparent morphological relationship exists between this genus and the previously mentioned sections. *Sacciolepis* is characterized by a spiciform panicle, the spikelets with glumes prominently ribbed, and the upper glume conspicuously gibbous. We have sampled only five of 31 species in sect. *Parvifolia*, two of the three species in sect. *Monticola*, one of two species in sect. *Verrucosa*, and one of 30 species in *Sacciolepis*. Broader sampling is necessary before making taxonomic changes.

Stolonifera clade—Zuloaga (1987a) considered that sect. *Stolonifera* was related to sects. *Phanopyrum* and *Laxa*; however, molecular data do not support this conclusion. Three of the 13 species of sect. *Stolonifera* (Zuloaga and Sendulsky, 1988) were studied and these formed a monophyletic clade (in NONA analyses) or were placed in a clade with the genus *Echinolaena* (in Pee-Wee analyses). Species of sect. *Stolonifera* share a forest shade habit, membranous ligules, spikelets arranged in unilateral racemes, with a short, three-nerved lower glume, upper glume and lower lemma five-nerved, and upper anthecium, smooth, glabrous and stipitate; many species of this group have conspicuous crateriform glands on the lower lemma (Zuloaga and Sendulsky, 1988). They differ from *Echinolaena*, a pantropical genus with approximately eight species (Filgueiras, 1994), by the lack of wings or excavations at the base of the upper lemma. *Echinolaena* is morphologically similar to *Ichnanthus*, a genus that appears in an unresolved polytomy and may or may not be related to sect. *Stolonifera* plus *Echinolaena*. The systematic position of sect. *Stolonifera* remains unresolved until more species of this section are studied and its relation with *Echinolaena* is clarified.

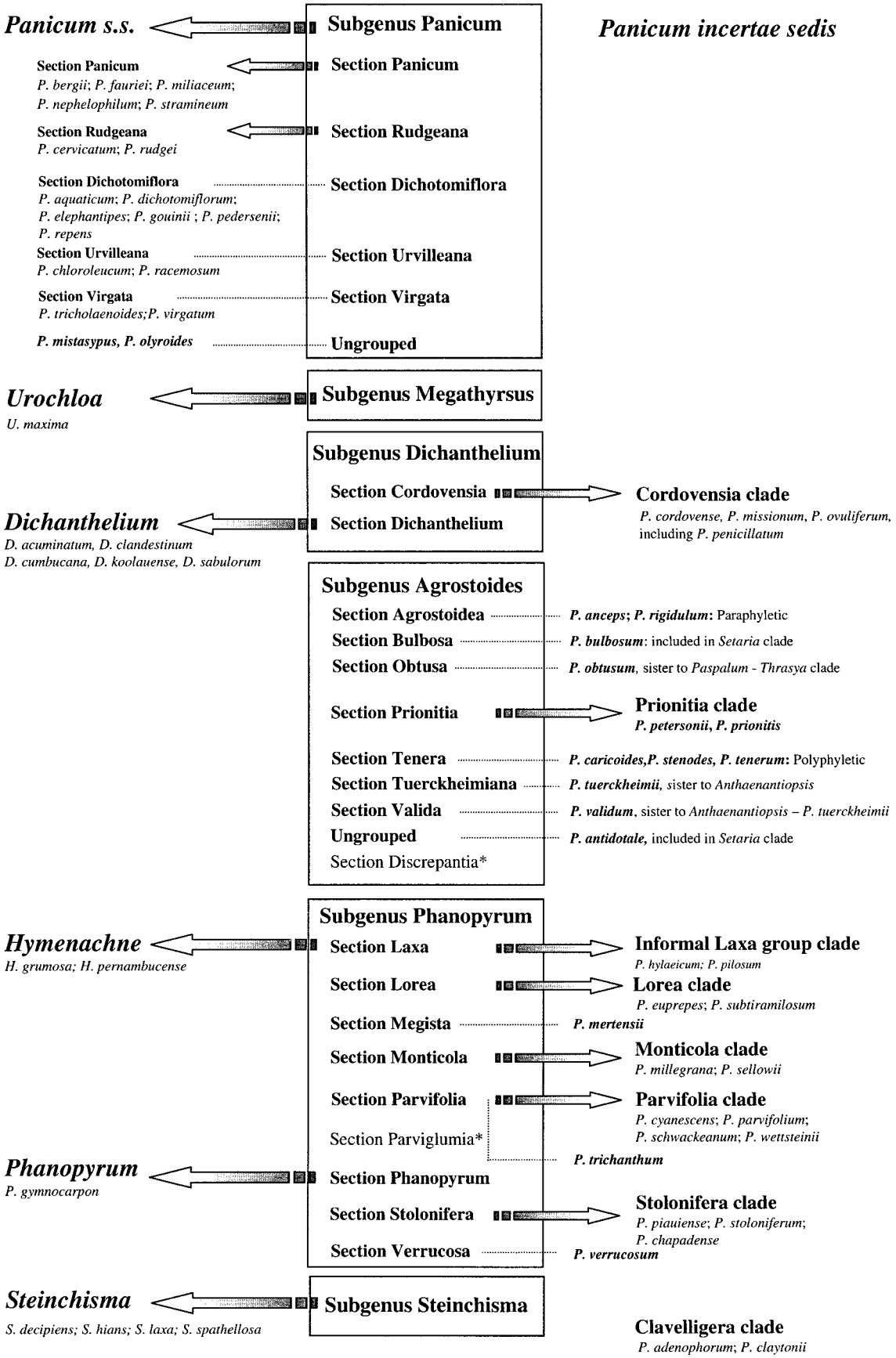
Lorea clade—''Lorea'' was described as an informal group by Renvoize (1978), who stressed it as a unique group within *Panicum* distinguished by its tussock habit, pungent leafblades and usually indistinct junction of the sheath and blade. Section *Lorea* has many species without ligules, spikelets in open and lax panicles, with the upper glume and lower lemma five-nerved, and upper anthecium smooth, indurate and glabrous. Renvoize (1978) included 17 species in this group, and later Renvoize and Zuloaga (1984, 1995) added several new species, raising the number of species to 27. These species are restricted to, and characteristic of, the Brazilian and Guiana shield, where they are dominant in open, rocky areas.

Two species of sect. *Lorea* were included in this study, together forming a strongly supported clade, joining, in an unresolved trichotomy, the monotypic genus *Canastra*, sects. *Prionitia*, *Agrostoidea*, and *Tenera* (discussed above). ''Lorea'' may form an independent genus of the Paniceae, but we are hesitant to make taxonomic changes on the basis of only two gene sequences.

Hymenachne—Section *Laxa* (established by Pilger in 1931) is clearly polyphyletic in this analysis, its species showing affinities with different taxa. *Panicum grumosum* and *P. pernambucense* form a clade with *Hymenachne donacifolia* (Raddi) Chase, an American species of the pantropical genus *Hymenachne*. These species are similar in overall morphology, being robust plants of stream banks, with membranous ligules, inflorescence an open and contracted panicle, with the spikelets arranged in unilateral racemes (Fig. 2D), the spikelets with the lower glume short, three-nerved, upper glume and lower lemma five-nerved, lower palea reduced or absent, and upper anthecium membranous, with the lemma and palea covered by simple papillae and prickle hairs towards the apex (Fig. 1H). The single distinction between these taxa is that the upper palea is not free at the apex in species of *Panicum*, with the borders of the upper lemma covering it, a character somewhat controversial in distinguishing taxa in the Paniceae when the

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Fig. 6. Summary of taxonomic results of this study. Boxes show the classification proposed by Zuloaga (1987a) plus subsequent modifications prior to the current research (see also Table 1). Genera recognized by this study are shown on the left side of the diagram. Species still named *Panicum* but unrelated to *Panicum* s.s. are shown on the right side as *Panicum* incertae sedis. Arrows indicate monophyletic clades shown in Figs. 3–5. * = Sections for which material was unavailable.


Panicum s.s.
Subgenus Panicum
Panicum incertae sedis
Section Panicum
P. bergii; P. fauriei; P. miliaceum;
P. nephelophilum; P. stramineum
Section Panicum
Section Rudgeana
P. cervicatum; P. rudgei
Section Rudgeana
Section Dichotomiflora
P. aquaticum; P. dichotomiflorum;
P. elephantipes; P. gouinii ; P. pedersenii;
P. repens
Section Dichotomiflora
Section Urvilleana
P. chloroleucum; P. racemosum
Section Urvilleana
Section Virgata
P. tricholaenoides;P. virgatum
Section Virgata
P. mistasypus, P. olyroides
Ungrouped
Urochloa
U. maxima
Subgenus Megathyrsus
Subgenus Dichanthelium
Section Cordovensia
Cordovensia clade
P. cordovense, P. missionum, P. ovuliferum,
including P. penicillatum
Dichanthelium
D. acuminatum, D. clandestinum
D. cumbucana, D. koolauense, D. sabulorum
Section Dichanthelium
Subgenus Agrostoides
Section Agrostoidea
P. anceps; P. rigidulum: Paraphyletic
Section Bulbosa
P. bulbosum: included in Setaria clade
Section Obtusa
P. obtusum, sister to Paspalum - Thrasya clade
Section Prionitia
Prionitia clade
P. petersonii, P. prionitis
Section Tenera
P. caricoides,P. stenodes, P. tenerum: Polyphyletic
Section Tuerckheimiana
P. tuerckheimii, sister to Anthaenantiopsis
Section Valida
P. validum, sister to Anthaenantiopsis – P. tuerckheimii
Ungrouped
P. antidotale, included in Setaria clade
Section Discrepantia*
Subgenus Phanopyrum
Hymenachne
H. grumosa; H. pernambucense
Section Laxa
Informal Laxa group clade
P. hylaeicum; P. pilosum
Section Lorea
Lorea clade
P. euprepes; P. subtiramilosum
Section Megista
P. mertensii
Section Monticola
Monticola clade
P. millegrana; P. sellowii
Section Parvifolia
Parvifolia clade
P. cyanescens; P. parvifolium;
P. schwackeanum; P. wettsteinii
Section Parviglumia*
P. trichanthum
Phanopyrum
P. gymnocarpon
Section Phanopyrum
Section Stolonifera
Stolonifera clade
P. piauiense; P. stoloniferum;
P. chapadense
Section Verrucosa
P. verrucosum
Steinchisma
S. decipiens; S. hians; S. laxa; S. spathellosa
Subgenus Steinchisma
Clavelligera clade
P. adenophorum; P. claytonii

upper anthecium is not indurate. Anatomically, sect. *Laxa* has been characterized by the presence of fusoid cells (Killeen and Clark, 1986), although Zuloaga et al. (1992) pointed out that there is a tendency among species of this section to reduction or replacement of the fusoid cells by lacunae, as occurs in both *P. grumosum* and *P. pernambucense*. Both species of *Panicum* and *Hymenachne* share conspicuous lacunae in transverse section, a feature stressed previously by Zuloaga et al. (1992), who placed *P. grumosum* and *P. pernambucense* in the informal Grumosum group. Pohl and Lersten (1975) considered the presence of aerenchyma a good character to separate *Hymenachne* from related genera, such as *Sacciolepis* and *Panicum*. Also, Zuloaga and Soderstrom (1985) noted the similarity of *P. grumosum* and *P. pernambucense* to *Hymenachne* and suggested that these species could all be congeneric. *Hymenachne* and the two species of *Panicum* share a membranous upper anthecium and other features.

Our study supports placement of the Grumosum group within the genus *Hymenachne*, and we are formally transferring them (see Taxonomic Treatment).

The remaining two studied species of the informal Laxa group (Zuloaga et al., 1992), *P. hylaeicum* and *P. pilosum*, were clustered together in a monophyletic clade, suggesting their segregation as another genus. However, no relationships with other genera are evident, and more species of sect. *Laxa* need to be examined before a final taxonomic decision is made for this group.

Megista-Tenera—Section *Megista* of subg. *Phanopyrum*, with a single species, *P. mertensii* Roth (Zuloaga, 1989), is in a monophyletic clade with the very different species *P. stenodes* and *P. caricoides* of sect. *Tenera*, subg. *Agrostoides*. *Panicum mertensii* departs from both species by its lanceolate blades and a single terminal inflorescence, with branches disposed in 4–8 nearly equidistant verticils, each verticil containing 10–60 branches. *Panicum stenodes* and *P. caricoides* have, on the other hand, blades linear and inrolled, and several inflorescences, terminal and axillary, consisting of few-flowered, contracted panicles. No obvious morphological characters correlate with the strong molecular support for this group.

Subgenus Agrostoides—Subgenus *Agrostoides* is clearly polyphyletic and its species show no evident relationship with other genera of the Paniceae; nevertheless, it is clear that not a single species of this subgenus should remain within *Panicum*. Zuloaga (1987a) considered seven sections within this subgenus, three of them monotypic and the remaining oligotypic; another monotypic section was later added (Zuloaga et al., 1989) to accommodate *P. validum* Mez. Species of the subgenus were grouped by having Kranz syndrome of the NADP-me subtype; basic chromosome number varies from $x = 9$ to $x = 10$; exomorphologically, the species of this subgenus are also variable and do not show clear affinities with other genera of the Paniceae. Giussani et al. (2001) postulated that the C_4 NADP-me condition arose several times during the evolution of the Paniceae; accordingly, our study shows a polyphyletic condition for species of *Agrostoides*. Zuloaga et al. (2000) mentioned that species of this subgenus can be regarded as different genera, though some of its relationships are still not completely solved.

Most species of subg. *Agrostoides* fall within the $x = 10$ clade of the Paniceae, with the exception of *P. bulbosum* and *P. antidotale*, grouped in the *Setaria* clade (within the $x = 9$ Paniceae). Section *Discrepantia* is the only section not represented for the subgenus as material was not available. It is remarkable that *P. bulbosum* Kunth, an American species growing from Mexico to Ecuador, with a corm-like base and a transversely rugose upper anthecium, is related to *P. antidotale* Retz., an Asian species with conspicuous rhizomes and a smooth upper anthecium. Additionally, both species lack the bristles present in other genera of the *Setaria* clade, such as *Cenchrus*, *Setaria*, and *Pennisetum*. The systematic position of these species is currently under study.

Prionitia clade-Panicum tenerum-section Agrostoidea—Section *Prionitia*, which includes *P. petersonii* Hitchc. and Ekman, endemic to Cuba, and *P. prionitis* Nees ex Trin., a species of eastern South America (Brazil, Paraguay, Uruguay, and Argentina), is monophyletic. This is sister to a clade consisting of sect. *Agrostoidea* plus *P. tenerum* Beyr. ex Trin. from sect. *Tenera*.

Sections *Prionitia* and *Agrostoidea*, plus *P. tenerum*, form a strongly supported monophyletic group sharing the following characters: caespitose plants with keeled leaf blades; ligules membranous, inflorescences terminal, lax; spikelets glabrous, the lower glume short and three-nerved; upper glume and lower lemma subequal, five-nerved, and upper anthecium indurate, smooth and shiny, glabrous. Anatomically all species are Kranz of the MS subtype; two vascular bundle sheaths are sometimes present around the vascular bundles in sect. *Prionitia*, the inner mestome sheath with specialized chloroplasts. The combination of morphological, anatomical, and the molecular synapomorphies given in this treatment may justify the segregation of these five species as a genus independent of *Panicum*.

Obtusa-Valida-Tuerckheimiana—The other three sections of subg. *Agrostoides*, *Tuerckheimiana*, *Valida*, and *Obtusa*, are monotypic and related to *Anthaenantiopsis* and the *Paspalum-Thrasya* clade.

Section *Obtusa* includes only *P. obtusum* Kunth, which inhabits dry areas of southern United States and Mexico. This species, ungrouped in the treatment of Hitchcock and Chase (1910) and subsequently placed in its own section (Pilger, 1931, 1940; Zuloaga, 1987a), appears as the sister taxon of *Paspalum* and *Thrasya*, the latter genera characterized by spikelets arranged in unilateral racemes, with the lower glume usually absent; this relationship was already emphasized in other phylogenetic studies (Giussani et al., 2001; Denham et al., 2002; Rua and Aliscioni, 2002). *Panicum obtusum* shares with *Paspalum* and *Thrasya* the arrangement of spikelets in the inflorescence, but differs by having its lower glume almost the same length as the upper glume and lower lemma, five-nerved, upper glume and lower lemma 7–9-nerved, lower palea and lower flower present. *Panicum obtusum* may represent an extreme of variation within the genus *Paspalum*; for example, the Decumbentes group retains the lower glume, making those species more similar to *P. obtusum*. More species of both *Thrasya* and *Paspalum* need to be scrutinized before a final conclusion in this clade is achieved.

Panicum tuerckheimii Hack., of sect. *Tuerckheimiana*, an endemic of southern Mexico and Guatemala, is related to the South American genus *Anthaenantiopsis* and to *P. validum* Mez, the single species of sect. *Valida*, but is morphologically distinct. *Anthaenantiopsis* includes species with conspicuously pilose spikelets, with the lower glume developed, lower palea

and lower flower present, and upper anthecium membranous, the lemma not covering the upper margins of the palea. *Panicum tuerckheimii*, on the other hand, is a species with glabrous spikelets, lower glume scalelike, lower palea reduced or absent, lower flower absent, and upper anthecium cartilaginous. Finally, *P. validum*, a species restricted to southern Brazil and Paraguay, originally placed in sect. *Laxa* (Smith et al., 1982), is a species with glabrous spikelets, lower glume one-third the length of the spikelet, and upper anthecium cartilaginous, with no evident similarity to either *Anthaenantiopsis* or *P. tuerckheimii*. As with the *Megista-Tenera* clade, the lack of an obvious morphological synapomorphy makes us hesitant to combine these species in their own genus.

Section Tenera—Section *Tenera*, established by Pilger (1940), includes four species with a small lower palea and smooth and shiny upper anthecium, both characters shared with sect. *Agrostoidea* (Zuloaga, 1987a). Our analysis indicates sect. *Tenera* is polyphyletic, one clade being related with sect. *Megista* (see above) and *P. tenerum* embedded in another clade with species of sect. *Agrostoidea* and sect. *Prionitia*.

Conclusions—We conclude that the genus *Panicum* s.l., as previously circumscribed, is in need of taxonomic reevaluation. Based on the present results, previous anatomical, morphological, and molecular studies, and inferred morphological synapomorphies, discussed in detail in the previous section (see Discussion), some taxonomic changes are proposed; these modifications were done only in clearly defined genera, and when our results were supported by previous taxonomic research. The genus in the strict sense should be restricted to subg. *Panicum*, while all remaining species should be realigned and removed from *Panicum*. In this treatment, several genera are recognized as such, e.g., *Dichanthelium*, *Phanopyrum*, and *Steinchisma*, while other species of *Panicum* are transferred to other genera of the Paniceae (see Taxonomic Treatment). The remaining taxa, here included within *Panicum* incertae sedis and representing isolated species or species grouped within monophyletic clades, do not show evident morphological synapomorphies linked with the evaluated molecular characters; ultimately, however, these taxa will need to be treated as independent genera or within other genera of the tribe Paniceae. Figure 6 shows the proposed changes for *Panicum* related to Zuloaga's classification (Zuloaga, 1987a; Zuloaga et al., 1989, 1992, 1993b; Zuloaga and Morrone, 1996; and F. O. Zuloaga and O. Morrone, unpublished data).

TAXONOMIC TREATMENT

In this section we present descriptions for the accepted genera and a list of accepted species within each genus; most of the species here treated in *Panicum* s.l. grow in America (for a complete list of accepted species see www.darwin.edu.ar/panicum.htm). When needed, some taxonomic changes are proposed in agreement with our results and previous studies in *Panicum* and related genera. All *Panicum* species still in need of a more detailed analysis are included as incertae sedis within the genus. Although the proposed modifications of currently accepted generic circumscriptions are extensive, most names are already available.

***Panicum* L., Sp. Pl.: 55. 1753, s.s.**—*Type species: P. miliaceum L.*—Caespitose, annual or perennial plants. Ligules membranous-ciliate or ciliate. Blades lanceolate to linear lanceolate. Inflorescences lax and open, with spikelets arranged in long pedicels. Spikelets with lower glume present, 3–9-nerved, upper glume and lower lemma subequal, 7–13-nerved, lower palea and lower flower present or absent, upper anthecium indurate, smooth, with simple or compound papillae at the apex of lemma and palea. Basic chromosome number: $x = 9$. Photosynthetic pathway: Kranz, subtype NAD-me.

Pantropical genus with approximately 100 species worldwide.

Section *Dichotomiflora*

P. aquaticum Poir.
P. aquaticum Poir. var. *cartagoense* Davidse
P. bartowense Scribn. & Merr.
P. coloratum L.
P. dichotomiflorum Michx.
P. elephantipes Nees ex Trin.
P. gouinii E. Fourn.
P. lacustre Hitchc. & Ekman
P. pedersenii Zuloaga
P. repens L.
P. sublaeve Swallen
P. vaseyanum Scribn. ex Beal

Section *Panicum*

P. alatum Zuloaga & Morrone
P. alatum var. *longiflorum* Zuloaga & Morrone
P. alatum var. *minus* (Andersson) Zuloaga & Morrone
P. aquarum Zuloaga & Morrone
P. aztecanum Zuloaga & Morrone
P. bergii Arechav.
P. bergii var. *pilosissimum* Zuloaga
P. capillare L.
P. capillarioides Vasey
P. chasei Rosengurtt, B.R. Arrillaga & Izaguirre
P. decolorans Kunth
P. diffusum Sw.
P. ephemeroides Zuloaga & Morrone
P. exiguum Mez
P. fauriei Hitchc.
P. flexile (Gattinger) Scribn.
P. furvuum Swallen
P. ghiesbreghtii E. Fourn.
P. hallii Vasey
P. hallii var. *filipes* (Scribn.) F.R. Waller
P. hillmanii Chase
P. hirsutum Sw.
P. hirticaule J. Presl
P. hirticaule var. *verrucosum* Zuloaga & Morrone
P. hispidifolium Swallen
P. lepidulum Hitchc. & Chase
P. magnispicula Zuloaga, Morrone & Valls
P. miliaceum L.
P. mohavense Reeder
P. mucronulatum Mez
P. nephilophilum Gaudich.
P. pampinosum Hitchc. & Chase
P. parcum Hitchc. & Chase
P. peladoense Henrard
P. philadelphicum Bernhardi ex Trin.

P. quadriglume (Döll) Hitchc.
P. stramineum Hitchc. & Chase
P. tamaulipense F.R. Waller & Morden

Section *Rudgeana*

P. campestre Nees ex Trin.
P. cayennense Lam.
P. cervicatum Chase
P. ligulare Nees ex Trin.
P. rudgei Roem. & Schult.

Section *Urvilleana*

P. chloroleucum Griseb.
P. racemosum P. Beauv.
P. urvilleanum Steud.

Section *Virgata*

P. altum Hitchc. & Chase
P. amarum Elliott
P. amarum var. *amarulum* (Hitchc. & Chase) Palmer
P. deciduum Swallen
P. glabripes Döll
P. havardii Vasey
P. longissimum (Mez) Henrard
P. tricholaenoides Steud.
P. tricholaenoides var. *flavomarginatum* (Mez) Zuloaga
P. virgatum L.

***Dichanthelium* (Hitchc. and Chase) Gould, Brittonia 26(1): 59. 1974. *Panicum* subg. *Dichanthelium* Hitchc. and Chase, Contr. U.S. Natl. Herb. 15: 142. 1910.** *Type species: Dichanthelium dichotomum (L.) Gould [= Panicum dichotomum L.]*—Perennials with or without a basal rosette of shorter, broader leaves than those of the culms. Ligules membranous-ciliate. Blades linear to ovate-lanceolate; foliar dimorphism present or absent. Inflorescences terminal and axillary, lax, open to occasionally contracted. Spikelets ellipsoid, cleistogamous spikelets present or absent. Lower glume 1–7-nerved, upper glume and lower lemma subequal, (5–)7–15-nerved; lower palea present, occasionally absent; lower flower staminate or absent. Upper anthecium indurate, smooth, with simple papillae all over its surface, shortly apiculate or crested. Basic chromosome number $x = 9$. Photosynthetic pathway: non-Kranz.

An American genus, with 55 species growing from Canada and the United States to center of Argentina and Chile, from sea level to approximately 3000 m a.s.l., frequent in forest edges, in wet habitats, some species in open places, on moist or dry sandy soils.

D. aciculare (Desv. ex Poir.) Gould & C.A. Clark
D. aciculare var. *ramosum* (Griseb.) Davidse
D. acuminatum (Sw.) Gould & C.A. Clark
D. acuminatum var. *densiflorum* (E.L. Rand & Redfield) Gould & C.A. Clark
D. acuminatum var. *fasciculatum* (Torr.) Freckmann
D. acuminatum var. *implicatum* (Scribn.) Gould & C.A. Clark
D. acuminatum var. *lindheimeri* (Nash) Gould & C.A. Clark
D. acuminatum var. *longiligulatum* (Nash) Gould & C.A. Clark
D. adenorhachis (Zuloaga & Morrone) Zuloaga, comb. nov. *Panicum adenorhachis* Zuloaga & Morrone, Ann. Missouri Bot. Gard. 78(1): 154, f. 2. 1991.
D. aequivaginatum (Swallen) Zuloaga, comb. nov. *Panicum aequivaginatum* Contr. U.S. Natl. Herb. 29: 271. 1949.
D. assurgens (Renvoize) Zuloaga, comb. nov. *Panicum assurgens* Renvoize, Kew Bull. 37: 325. 1982.
D. boreale (Nash) Freckmann
D. boscii (Poir.) Gould & C.A. Clark
D. cabrerae (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum cabrerae* Zuloaga and Morrone, Ann. Missouri Bot. Gard. 78: 156. 1991.
D. caparoense (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum caparoense* Zuloaga and Morrone, Ann. Missouri Bot. Gard. 80: 153. 1993.
D. clandestinum (L.) Gould
D. commutatum (Schult.) Gould
D. congestum (Renvoize) Zuloaga, comb. nov. *Panicum congestum* Renvoize, Kew Bull. 37: 329. 1984.
D. cucaense (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum cucaense* Zuloaga and Morrone, Ann. Missouri Bot. Gard. 78: 158. 1991.
D. cumbucana (Renvoize) Zuloaga, comb. nov. *Panicum cumbucana* Renvoize, Kew Bull. 37: 332. 1982.
D. davidsei (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum davidsei* Zuloaga and Morrone, Ann. Missouri Bot. Gard. 78: 158. 1991.
D. depauperatum (Muhl.) Gould
D. dichotomum (L.) Gould
D. dichotomum var. *nitidum* (Lam.) LeBlond
D. dichotomum var. *ramulosum* (Torr.) LeBlond
D. dichotomum var. *roanokense* (Ashe) LeBlond
D. dichotomum var. *tenue* (Muhl.) Gould & C.A. Clark
D. dichotomum var. *unciphyllum* (Trin.) Davidse
D. ensifolium (Baldwin ex Elliott) Gould
D. ensifolium var. *breve* (Hitchc. & Chase) B.F. Hansen & Wunderlin
D. hebotes (Trin.) Zuloaga, comb. nov. *Panicum hebotes* Trin., Mém. Acad. Imp. St.-Pétersb., Ser. 6, Sci. Math 1: 201. 1834.
D. heliophilum (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum heliophilum* Chase ex Zuloaga and Morrone, Ann. Missouri Bot. Gard. 78: 152. 1991.
D. itatiaiae (Swallen) Zuloaga, comb. nov. *Panicum itatiaiae* Swallen, Phytologia 14: 82. 1966.
D. koolauense (H. St. John & Hosaka) C.A. Clark & Gould, 1978
D. latifolium (L.) Harvill
D. laxiflorum (Lam.) Gould
D. leibergii (Vasey) Freckmann
D. linearifolium (Scribn.) Gould
D. macrospermum Gould
D. malacophyllum (Nash) Gould
D. nodatum (Hitchc. & Chase) Gould
D. nudicaule (Vasey) B.F. Hansen & Wunderlin
D. oligosanthes (Schult.) Gould
D. ovale (Elliott) Gould & C.A. Clark
D. pedicellatum (Vasey) Gould
D. peristypum (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum peristypum* Zuloaga and Morrone, Novon 1: 113. 1991.
D. perlongum (Nash) Freckmann
D. petropolitanum (Zuloaga and Morrone) Zuloaga, comb.

nov. *Panicum petropolitanum* Zuloaga and Morrone, Ann. Missouri Bot. Gard. 78: 161. 1991.
D. polyanthes (Schult.) Mohlenbr.
D. portoricense (Desv.) B.F. Hansen & Wunderlin
D. pycnoclados (Tutin) Davidse
D. ravenelii (Scribn. & Merr.) Gould
D. sabulorum (Lam.) Gould & C.A. Clark
D. sabulorum (Lam.) Gould & C.A. Clark var. *cordatum* (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum sabulorum* Lam. var. *cordatum* Zuloaga and Morrone, Novon 1: 117. 1991.
D. sabulorum (Lam.) Gould & C.A. Clark var. *polycladum* (Ekman) Zuloaga, comb. nov. *Panicum polycladum* Ekman, Ark. Bot. 11(4): 24. 1912.
D. scabriusculum (Elliott) Gould & C.A. Clark
D. sciurotis (Trin.) Davidse
D. sciurotoides (Zuloaga & Morrone) Davidse
D. scoparium (Lam.) Gould
D. sendulskyii (Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum sendulskyii* Zuloaga and Morrone, Novon 6(3): 310. 1996.
D. sphaerocarpon (Elliott) Gould
D. sphaerocarpon var. *floridanum* (Vasey) Davidse
D. stigmosum (Trin.) Zuloaga, comb. nov. *Panicum stigmosum* Trin., Gram. Panic.: 194. 1826.
D. stipiflorum (Renvoize) Zuloaga, comb. nov. *Panicum stipiflorum* Renvoize, Kew Bull. 37: 329. 1982.
D. strigosum (Muhl. ex Elliott) Freckmann
D. strigosum var. *glabrescens* (Griseb.) Freckmann
D. strigosum var. *leucoblepharis* (Trin.) Freckmann
D. superatum (Hack.) Zuloaga, comb. nov. *Panicum superatum* Hack., Oesterr. Bot. Z. 51: 427. 1901.
D. surrectum (Chase ex Zuloaga and Morrone) Zuloaga, comb. nov. *Panicum surrectum* Chase ex Zuloaga and Morrone, Novon 1: 111. 1991.
D. telmatum (Swallen) Zuloaga, comb. nov. *Panicum telmatum* Swallen, Phytologia 14: 81. 1966.
D. umbonulatum (Swallen) Davidse
D. viscidellum (Scribn.) Gould
D. wilcoxianum (Vasey) Freckmann
D. xanthophysum (A. Gray) Freckmann

***Hymenachne* P. Beauv., Ess. Agrost.: 48. 1812.** *Type species: Hymenachne amplexicaulis (Rudge) Nees [= Agrostis monostachya Poir.]*—Perennial. Ligules membranous. Leaves lanceolate to ovate-lanceolate. Inflorescence an open or contracted panicle, with the spikelets arranged in unilateral racemes. Spikelets ellipsoid to lanceolate, glabrous; lower glume less than half the length of the spikelet, three-nerved; upper glume and lower lemma five-nerved; lower palea and lower flower present or absent. Upper anthecium membranous, with simple papillae, silica bodies and prickle hairs toward the apex. Basic chromosome number $x = 10$. Photosynthetic pathway: non-Kranz. A cosmopolitan genus with approximately 10 species.

H. amplexicaulis (Rudge) Nees
H. donacifolia (Raddi) Chase
H. grumosa (Nees) Zuloaga, comb. nov. *Panicum grumosum* Nees, Fl. Bras. Enum. Pl. 2: 182. 1829.
H. pernambucense (Spreng.) Zuloaga, comb. nov. *Agrostis pernambucensis* Spreng., Syst. Veg. 1: 258. 1825.

***Phanopyrum* (Raf.) Nash, Fl. Southeast U.S.: 104. 1903. *Panicum* sect. *Phanopyrum*. Bulletin Botanique [Geneve] 1: 220. 1830.** *Type species: Phanopyrum gymnocarpon (Elliott) Nash [= Panicum gymnocarpon Elliott]*—Stout perennials with erect culms from creeping stoloniferous bases. Ligules membranous. Blades lanceolate, cordate. Inflorescences with spikelets arranged in unilateral branches. Spikelets with lower and upper glume subequal; lower palea present, lower flower absent. Upper anthecium obovoid, shorter than the glumes and lower lemma and stipitate, smooth, and glabrous. Basic chromosome number $x = 10$. Photosynthetic pathway: non-Kranz.

A monotypic genus, with a single species growing in southeastern United States, where it is common in wet woodlands or forest edges.

***Steinchisma* Raf., Bull. Bot. Geneva 1: 220. 1830. *Panicum* subg. *Steinchisma* (Raf.) Zuloaga, Grass Syst. Evol.: 300. 1987.** *Type species: Steinchisma hians* (Elliott) Nash [= *Panicum hians Elliott]*—Caespitose, short to long-rhizomatous plants. Ligules membranous, short ciliate at the apex. Blades lanceolate to filiform. Inflorescences lax to contracted. Spikelets with the lower glume three-nerved, upper glume and lower lemma subequal, 3–5(–7)-nerved; lower palea conspicuous, enlarged at maturity; lower flower present. Upper anthecium covered with compound papillae, regularly distributed over the lemma and palea. Basic chromosome number: $x = 10$. Photosynthetic pathway: intermediate Kranz/non-Kranz.

An American genus, with seven species ranging from Central America to Argentina.

S. cuprea (Hitchc. & Chase) W.V. Brown
S. decipiens (Nees ex Trin.) W.V. Brown
S. exiguiflora (Griseb.) W.V. Brown
S. hians (Elliott) Nash
S. laxa (Sw.) Zuloaga, comb. nov. *Panicum laxum* Sw, Prodr.: 23. 1788.
S. spathellosa (Döll) Renvoize
S. stenophylla (Hack.) Zuloaga & Morrone

Incertae sedis

Section *Agrostoidea*

P. anceps Michaux
P. rigidulum Bosc ex Nees var. *combsii* (Scribn. & C.R. Ball) Lelong
P. rigidulum var. *condensum* (Nash) Mohlenbr.
P. rigidulum var. *elongatum* (Scribn.) Lelong
P. rigidulum var. *pubescens* (Vasey) Lelong
P. rigidulum var. *rigidulum*

Section *Bulbosa*

P. bulbosum Kunth
P. plenum Hitchc. & Chase

Section *Clavelligera*

P. adenophorum K. Schum.
P. adenophyllum Pilg.
P. bullockii Renvoize
P. claytonii Renvoize
P. deustum Thunb.
P. ecklonii Nees

P. flacciflorum Stapf
P. habrothrix Renvoize
P. hymeniochilum Nees
P. lukwangulense Pilg.
P. nigromarginatum Robyns
P. pectinellum Stapf
P. peteri Pilg.
P. pole-evansii C.E. Hubb.
P. sadinii (Vanderyst) Renvoize

Section *Cordovensia*

P. cordovense E. Fourn.
P. missionum Ekman
P. ovuliferum Trin.
P. pantrichum Hack.
P. penicillatum Nees ex Trin.
P. rhizogonum Hack.

Section *Discrepantia*

P. discrepans Doell

Section *Laxa*

P. bresolinii L.B. Sm. & Wassh.
P. condensatum Bertol.
P. hylaeicum Mez
P. leptachne Doell
P. longum Hitchc. & Chase
P. pilosum Sw.
P. polygonatum Schrad.
P. stagnatile Hitchc. & Chase
P. stevensianum Hitchc. & Chase

Section *Lorea*

P. acicularifolium Renvoize & Zuloaga
P. animarum Renvoize
P. bahiense Renvoize
P. chnoodes Trin.
P. cipoense Renvoize & Send.
P. durifolium Renvoize & Zuloaga
P. eligulatum N.E. Br.
P. euprepes Renvoize
P. fontanale Swallen
P. glaziovii Hack.
P. jauanum Davidse
P. lagostachyum Renvoize & Zuloaga
P. loreum Trin.
P. lutzii Swallen
P. marauense Renvoize & Zuloaga
P. molinioides Trin.
P. poliophyllum Renvoize & Zuloaga
P. restingae Renvoize & Zuloaga
P. sacciolepoides Renvoize & Zuloaga
P. sipapoense Swallen
P. steyermarkii Swallen
P. subtiramulosum Renvoize & Zuloaga
P. teretifolium Hack.
P. tijucae Renvoize
P. trinii Kunth
P. vaginiviscosum Renvoize & Zuloaga

Section *Megista*

P. mertensii Roth

Section *Monticola*

P. millegrana Poir.
P. sellowii Nees
P. trichoides Sw.

Section *Obtusa*

P. obtusum Kunth

Section *Parvifolia*

P. arctum Swallen
P. auricomum Nees ex Trin.
P. bartlettii Swallen
P. brevifolium L.
P. caaguazuense Henrard
P. cyanescens Nees ex Trin.
P. fonticolum Swallen
P. granuliferum Kunth
P. hirtum Lam.
P. ichunense Swallen
P. machrisiana Swallen
P. micranthum Kunth
P. nervosum Lam.
P. noterophilum Renvoize
P. nutabundum Zuloaga & Morrone
P. orinocanum Luces
P. pandum Swallen
P. parvifolium Lam.
P. petilum Swallen
P. petrense Swallen
P. polycomum Trin.
P. pseudisachne Mez
P. pyrularium Hitchc. & Chase
P. rivale Swallen
P. rupestre Trin.
P. schwackeanum Mez
P. subulatum Spreng.
P. tepuianum Davidse & Zuloaga
P. trichanthum Nees
P. wettsteinii Hack.
P. yavitaense Swallen

Section *Parviglumia*

P. arundinariae Trin. ex E. Fourn.
P. cayoense Swallen
P. guatemalense Swallen
P. incumbens Swallen
P. parviglume Hack.
P. trichidiachne Doell

Section *Prionitia*

P. petersonii Hitchc. & Ekman
P. prionitis Nees

Section *Stolonifera*

P. andreanum Mez
P. biglandulare Scribn. & J.G. Sm.
P. brachystachyum Trin.
P. chapadense Swallen
P. crateriferum Sohns
P. irregulare Swallen
P. latissimum Mikan ex Trin.
P. piauiense Swallen
P. pulchellum Raddi
P. rude Nees
P. soderstromii Zuloaga & Send.
P. stoloniferum Poir.
P. venezuelae Hack.

Section *Tenera*

P. beyeri Hitchc. & Ekman
P. caricoides Nees ex Trin.
P. stenodes Griseb.
P. tenerum Beyr. ex Trin.

Section *Tuerckheimana*

P. tuerckheimii Hack.

Section *Valida*

P. validum Mez

Section *Verrucosa*

P. brachyanthum Steud.
P. verrucosum Muhl.

Ungrouped species

P. antidotale Retz.
P. aristellum Doell
P. grande Hitchc. & Chase
P. haenkeanum J. Presl
P. hemitomon Schult.
P. longipedicellatum Swallen
P. scabridum Doell
P. trichocladum Hack. ex K. Schum.

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