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Phylogenetics and Character Evolution in the Grass Family (Poaceae): Simultaneous Analysis of Morphological and Chloroplast DNA Restriction Site Character Sets

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I. Abstract

A phylogenetic analysis of the grass family (Poaceae) was conducted using two character sets, one representing variation in 364 mapped and cladistically informative restriction sites from all regions of the chloroplast genome, the other representing variation in 42 informative "structural characters." The structural character set includes morphological, anatomical, chromosomal, and biochemical features, plus structural features of the chloroplast genome. The taxon sample comprises 75 exemplar taxa, including 72 representatives of Poaceae and one representative of each of three related families (Flagellariaceae, Restionaceae, and Join-villeaceae); *Flagellaria* served as the outgroup for the purpose of cladogram rooting. Among the grasses, 24 tribes and all 16 subfamilies of grasses recognized by various modern authors were sampled. Transformations of structural characters are mapped onto the phylogenetic hypotheses generated by the analysis, and interpreted with respect to biogeography and the evolution of wind pollination in the grass family. A major goal of the study was to test the monophyly of several putatively natural groups, including Bambusoideae, Pooideae, Arundinoideae, and the "PACC clade" (the latter comprising subfamilies Panicoideae, Arundinoideae, Chloridoideae, and Centothecoideae), as well as to analyze the phylogenetic structure within these groups and others. Several genera of controversial placement (*Amphipogon, Anisopogon, Anomochloa, Brachyelytrum, Diarrhena, Eremitis, Ehrharta, Lithachne, Lygeum,*

Nardus, Olyra, Pharus, and *Streptochaeta*) also were included, with the goal of determining their phylogenetic affinities. The two character sets were analyzed separately, and a simultaneous analysis of the combined matrices also was conducted. The combined data set also was analyzed using homoplasy-implied weights. Among major results of the combined unweighted analysis were resolution of a sister-group relationship between *Joinvillea* and Poaceae; resolution of a clade comprising *Anomochloa* and *Streptochaeta* as the sister of all other grasses, with *Pharus* the next group to diverge from the lineage that includes all remaining grasses; and resolution of other taxa often assigned to Bambusoideae s.l. (including *Ehrharta* and Oryzeae, and excluding a few other taxa as noted) as a paraphyletic assemblage, within which is nested a clade that consists of *Brachyelytrum*, the PACC clade (including *Amphipogon*), and Pooideae (including Brachypodieae, Stipeae, *Anisopogon, Diarrhena, Lygeum,* and *Nardus*). Within the PACC clade, *Aristida* is identified as the sister of all other elements of the group; Chloridoideae, Centothecoideae, and Panicoideae are each resolved as monophyletic, the latter two being sister-groups; and the remaining Arundinoid elements constitute a paraphyletic group within which are nested these three subfamilies. Within the Pooideae, four "core tribes" (Bromeae, Hordeae [i.e., Triticeae], Agrostideae [i.e., Aveneae], and Poeae, the latter including *Sesleria*) are resolved as a monophyletic group that is nested among the remaining elements of the subfamily (Brachypodieae, Meliceae, Stipeae, *Anisopogon, Diarrhena, Lygeum,* and *Nardus*). A second principal goal of the analysis was to identify structural synapomorphies of clades. Among the synapomorphies identified for some of the major clades are the following: gain of a 6.4 kb inversion in the chloroplast genome in *Joinvillea* and the grasses; reduction to 1 ovule per pistil, gain of a lateral "grass-type" embryo, and gain of an inversion around the gene *trn*T in the chloroplast genome in the grasses; loss of arm cells in the clade that consists of *Brachyelytrum*, Pooideae, and the PACC clade; loss of the epiblast and gain of an elongate mesocotyl internode in the PACC clade; gain of proximal female-sterile florets in female-fertile spikelets, gain of overlapping embryonic leaf margins, and gain of *Panicum*-type endosperm starch grains in the clade that comprises Centothecoideae and Panicoideae; and loss of the scutellar tail of the embryo in Pooideae (in one of two alternative placements of Pooideae among other groups). These findings are consistent with an origin and early diversification of grasses as forest understory herbs, followed by one or more radiations into open habitats, concomitant with multiple origins of C_4 photosynthesis and specialization for wind pollination.

II. Introduction

In recent years agrostologists have generated several explicit phylogenetic hypotheses concerning major diversification patterns in the grass family (Poaceae). In cases where cladistic analysis was used, these analyses have been based on morphological characters (Baum, 1987; Kellogg & Campbell, 1987); on chloroplast DNA (cpDNA) restriction sites (Davis & Soreng, 1993; Yaneshita et al., 1993); on nucleotide sequences of nuclear ribosomal RNA (rRNA; Hamby & Zimmer, 1988, 1992), genes of the chloroplast genome (Doebley et al., 1990; Cummings et al., 1994; Nadot et al., 1994; Barker et al., 1995; Clark et al., 1995; Duvall & Morton, 1996; Hongping Liang & Hilu, 1996), and the nuclear gene Alcohol-dehydrogenase (Morton et al., 1996); and on various combinations of these character sets (Kellogg & Linder, 1995). Most of these analyses have yielded results consistent with the recognition of two major clades in the family, one of them corresponding to subfamily Pooideae, the second comprising subfamilies Panicoideae, Arundinoideae, Chloridoideae, and Centothecoideae, collectively referred to as the "PACC clade" (Davis & Soreng, 1993). However, there have

been substantial differences in the circumscription of Bambusoideae and, within the PACC clade, of various taxa recognized as Arundinoids.

Any discussion of conflicting hypotheses of phylogenetic structure in Poaceae must grapple with the varied hypotheses implicit in a long series of noncladistic classifications and hypotheses of relationships published since the late 1950s (Stebbins, 1956; Reeder, 1957, 1962; Tateoka, 1957; Prat, 1960; Stebbins & Crampton, 1961; Butzin, 1965; Clifford, 1965; Clifford et al., 1969; Sharma, 1979; Caro, 1982; Hilu & Wright, 1982; Watson et al., 1985; Clayton & Renvoize, 1986; Soderstrom & Ellis, 1987; Tzvelev, 1977, 1989; Watson & Dallwitz, 1992), some of which circumscribed groupings similar to the Pooideae and the PACC clade, as later detected by cladistic analyses. Although there are many areas of agreement among these treatments, classification of a subset of taxa in one or the other of these two major clades, aside from the disposition of taxa assigned to Bambusoideae, remains unsettled. Among genera and generic assemblages that have been particularly difficult to place are *Ampelodesmos* Link, *Anisopogon* R. Br., *Danthoniastrum* Holub, *Duthiea* Hack., *Lygeum* L., *Metcalfia* Conert, *Nardus* L., *Pseudodanthonia* Bor & C. E. Hubb., *Stephanachne* Keng, and Stipeae. These so-called orphan genera and tribes usually are placed either in Pooideae or Arundinoideae (compare the classification of Clayton & Renvoize, 1986, with that of Watson & Dallwitz, 1992) or their informal equivalents (Tzvelev, 1977, 1989).

Beyond the problems posed by these orphan taxa, a historical emphasis by systematists on temperate and widespread tropical taxa has resulted in inadequate representation in exemplar-based studies of a third assemblage of grasses, subfam. Bambusoideae s.l. The general neglect of Bambusoideae in higher-level studies is particularly troublesome, for it is a diverse group that has been divided into as many as 13 tribes (Clayton & Renvoize, 1986) or 8 subfamilies (Caro, 1982). Meanwhile, evidence has mounted that an understanding of the earliest diversification of grasses requires broad, unconstrained representation from the Bambusoideae (Davis & Soreng, 1993; Clark et al., 1995).

While the Pooideae and PACC clades have been recognized as monophyletic groups in most cladistic studies, cladistic results concerning Bambusoideae are limited and frequently contradictory. Bambusoideae may be monophyletic (Kellogg & Campbell, 1987; Kellogg & Watson, 1993) or may be paraphyletic or polyphyletic in a number of different ways (Davis & Soreng, 1993; Barker et al., 1995; Clark et al., 1995; Kellogg & Linder, 1995; Duvall & Morton, 1996; Hongping Liang & Hilu, 1996). However, most exemplar-based cladistic analyses conducted to date have included such limited sampling among supposed elements of Bambusoideae and other putatively early-diverging taxa that it is difficult and perhaps premature to make more than general comparisons among them.

In many of the noncladistic classifications and hypotheses cited above, Bambusoideae are recognized as a natural group. Even in some cladistic analyses, Bambusoideae have been constrained as monophyletic (Kellogg & Campbell, 1987) or treated as a natural group (Kellogg & Watson, 1993). Other noncladistic hypotheses, dating back to Warming (1895), Bessey (1917), Bews (1929), Roshevits (1937), and Tateoka (1957), have suggested that Bambusoideae represent an archaic group from which are derived groups now conventionally placed in Pooideae or in the various subfamilies of the PACC clade.

Discussions of Bambusoideae are complicated by the fact that circumscriptions of the group vary widely. For example, among the genera and tribes omitted from this subfamily by one or more modern authors are *Anomochloa*, *Brachyelytrum* P. Beauv., Centotheceae, Diarrheneae, Ehrharteae, Oryzeae, Parianeae, *Phaenosperma* Benth., Phareae, Phyllorachideae C. E. Hubb., and *Streptochaeta* Schrad. When excluded, these orphan taxa are included in other subfamilies (usually Arundinoideae, Chloridoideae, or Pooideae) or are segregated to small

subfamilies of their own (e.g., Anomochlooideae Potztal, Streptochaetoideae [C. E. Hubb.] Butzin, Pharoideae L. G. Clark & Judz., Parianoideae [C. E. Hubb.] Butzin, Oryzoideae [Ehrhartoideae Link if *Ehrharta* is included], and Centothecoideae).

Another complicating factor encountered by grass systematists is that most existing classifications of the grasses are intuitive and idiosyncratic to one degree or another. Because the grass family is so large, groups, once recognized, often are considered to be coherent without objective analyses of data to demonstrate their naturalness. Among numeric methods, phenetic analyses of grass data sets without constrained groups have provided phenograms of the family (Hilu & Wright, 1982; Watson et al., 1985; and others reviewed in Baum, 1987). However, in their dependence on similarity measures, and absence of explicit rooting, phenetic results are logically compromised for inferring phylogeny (Farris, 1980; Watrous & Wheeler, 1981; Wiley, 1981).

One way to achieve broad sampling within large and diverse groups in analyses, cladistic or otherwise, has been to use conglomerate taxa, such as genera, tribes, or subfamilies, as the terminals of analysis (e.g., Hilu & Wright, 1982; Watson et al., 1985; Baum, 1987, and others reviewed therein; Kellogg & Campbell, 1987; Kellogg & Watson, 1993). An advantage in this approach is that all putative groups of interest can be considered concurrently. However, this approach involves theoretical and methodological difficulties (e.g., assumption of monophyly of groups, creation of nonexistent character-state combinations, and adoption of various ad hoc approaches to the treatment of polymorphism within the artificial terminals that are created; Nixon & Davis, 1991; Nixon, 1996). Apart from the methodological compromises inherent in such approaches, it should also be recognized that the monophyly of a group is tested when its constituent elements are treated as separate terminals, and that, in contrast, the practice of "terminal fusion," which results in conglomerate groups that are used as individual taxa, or "composite terminals," assumes rather than tests their unity (Nixon & Davis, 1991; Nixon, 1996; Nixon & Carpenter, 1996). For these reasons we recognize exemplar sampling as a superior alternative to the use of conglomerate terminals. Exemplar sampling uses individual specimens, or individual species, as terminal taxa that serve as representatives of putative higher-level groups.

In most molecular phylogenetic studies, all data for each terminal are drawn from a single DNA isolation and therefore from a single species, if not a single organism; studies of this sort epitomize exemplar sampling. Structural character sets (e.g., morphology, anatomy, palynology) also could employ exemplar sampling, but most published studies draw upon a literature assembled over many years by numerous investigators, and observations of all characters included in a study usually are not available for any but the most economically important species (e.g., *Oryza sativa*). A major practical difficulty with exemplar-based phylogenetic analyses of large groups, apart from computation, is sampling large subgroups in a depth sufficient to demonstrate their monophyly. At the same time, it is essential that orphan taxa be sampled, as these, like fossils, are often pivotal in phylogenetic reconstruction (Farris, 1976; Rieppel, 1993; Nixon, 1996).

Here we present a study of the phylogenetic structure of the grass family, using exemplar sampling to test the monophyly of the PACC clade, Pooideae, Bambusoideae s.l., and many lesser groupings. We have conducted simultaneous and separate parsimony analyses of two data sets, one comprising a miscellaneous set of "structural characters," representing variation in morphology, anatomy, biochemistry, and structural sequences of the chloroplast genome, the second reflecting cpDNA restriction site variation. Simultaneous analysis, an approach sometimes called "total evidence" or "combined analysis" has been advocated by, among others, Eernisse and Kluge (1993), Kluge and Wolf (1993), Wheeler et al. (1993), Kim

and Jansen (1994), Smith and Littlewood (1994), Williams et al. (1994), Chase et al. (1995), and Nixon and Carpenter (1996).

The taxon sample includes representative species of 24 tribes and all 16 subfamilies of grasses recognized by various modern authors, and includes 10 of 13 tribes of Bambusoideae as delimited by Clayton and Renvoize (1986). Three nongrass outgroups also are included (Nixon & Carpenter, 1994); the outgroups represent Flagellariaceae, Restionaceae, and Joinvilleaceae, all of which were included in Poales by Dahlgren et al. (1985).[1] Also included are exemplars from orphan genera and tribes that are postulated to be either among the earliest diverging elements within the family or situated in the critical nexus between the Arundinoideae, Pooideae, and Bambusoideae (*Aristida* L., *Ampelodesmos* R. Br., *Amphipogon*, *Anisopogon*, *Anomochloa*, *Brachyelytrum*, *Chasmanthium* Link, *Diarrhena* P. Beauv., *Eremitis* Döll, *Ehrharta* Thunb., *Lygeum*, *Nardus*, *Pharus* P. Browne, Stipeae, and *Streptochaeta*).

We find that both character sets, analyzed separately or simultaneously, support the monophyly of a major clade that consists of the Pooideae, the PACC clade (as sister taxa), and a series of less inclusive taxa that are often placed within the Bambusoideae but here are placed within one or the other of these two major groups; the larger clade that includes Pooideae and the PACC clade is itself nested among tribes that are often assigned to Bambusoideae. Although the phylogenetic relationships supported by the present study are largely consistent with the classification of Clayton and Renvoize (1986), significant differences exist, and we note these and suggest appropriate alterations to the classification. Among the taxa placed within the Pooideae are *Anisopogon* and *Diarrhena*. The PACC clade includes all sampled elements of Panicoideae, Arundinoideae (except *Anisopogon*), Chloridoideae, and Centhothecoideae, but subfam. Arundinoideae is not resolved as monophyletic, and Aristideae is resolved as sister of the rest of the PACC clade. Thus, the various elements conventionally placed in Arundinoideae need to be reclassified, and we suggest that the subfamily be abandoned altogether. Results of the present analysis suggest that Bambusoideae, by any but the most restrictive circumscription, are a non-monophyletic assemblage. Monophyly of the Bambusoideae requires, at the minimum, the exclusion of seven tribes. Anomochloeae and Streptochaeteae should be placed in Anomochlooideae; Phareae in Pharoideae; Oryzeae with Ehrharteae in Ehrhartoideae (i.e., Oryzoideae); Diarrheneae in Pooideae; and Brachyelytreae either in Pooideae or in a small subfamily closely related to Pooideae and the PACC clade. The precise placement of Brachyelytreae remains tentative, for there is conflicting support for its placement as sister of Pooideae or sister of PACC plus Pooideae.

The discussion of suprageneric taxonomy in the present paper is affected by several nomenclatural innovations and name changes, due to priority of date (verified by J. Reveal, pers. comm.), which have been established or uncovered since the publication of *Genera Graminum* (Clayton & Renvoize, 1986). Subfamily Pharoideae was newly published (Clark & Judziewicz, 1996). Ehrhartoideae Link has priority over Oryzoideae Burmeist. or Bambusoideae Asch. & Graeb. when *Ehrharta* is included in the same subfamily as *Oryza* or *Bambusa*, respectively. Bambusoideae also is predated by Oryzoideae, but in the present work we apply the former name to a narrowly circumscribed group that includes neither *Oryza* nor *Ehrharta*; we use the term "Bambusoideae s.l." to refer to a variety of inclusive (and demonstrably paraphyletic) circumscriptions of this subfamily. Agrostideae Bertch. & J. Presl has priority over Aveneae Dumort. when *Agrostis* is included in the latter tribe; Chlorideae Bertch. & J. Presl has priority over Cynodonteae Dumort. when *Chloris* Sw. is included in that tribe; Hordeeae Bertch. & J. Presl has priority over Triticeae Dumort. when *Hordeum* L. is included in that tribe; and Sacchareae Bertch. & J. Presl has priority over Andropogoneae Dumort. when *Saccharum* L. is included in that tribe. Table I and most figures use the Clayton and Renvoize

classification, unchanged, to facilitate reference to other contemporary literature, but the above changes in tribal names are noted in Table I. In the text, names with nomenclatural priority are used (except Bambusoideae, as noted above), or are cross-referenced if the text specifically refers to a group name employed by other authors.

III. Methods

A. TAXON SAMPLE

The exemplar species sampled for the present analysis are listed in Table I, in which the grasses are arranged according to the classification by Clayton and Renvoize (1986). Voucher specimens are housed at BH unless otherwise noted in the table. To assist the reader in evaluating the selection of exemplar taxa in the study, the number of species, genera, and tribes (if any), are reported for subfamilies and tribes (Table I). We sampled 72 grass species representing 24 tribes and including all 16 subfamilies proposed in various modern treatments of the family. Because reticulate origins might distort the phylogenetic history between structural characters susceptible to recombination and the linearly inherited chloroplast genome, we excluded genera from the present analysis if there was reasonable evidence from our larger analyses of their origin through intertribal hybridization (Soreng et al., 1990; Davis & Soreng, 1993, and unpubl. data).

Three genera, from three different families closely related to the grasses (Dahlgren et al., 1985; Linder & Ferguson, 1985; Campbell & Kellogg, 1987; Linder, 1987; Doyle et al., 1992; Duvall et al., 1993; Linder & Rudall, 1993; Chase et al., 1995; Davis, 1995; Kellogg & Linder, 1995; Linder & Kellogg, 1995; Stevenson & Loconte, 1995), were used as outgroups: *Flagellaria* L. (Flagellariaceae), *Baloskion* Raf. (Restionaceae), and *Joinvillea* Brongn. and Gris (Joinvilleaceae). The sampled representative of Restionaceae, an Australian species widely known as *Restio tetraphyllus* Labill., is recognized as belonging to a separate genus, *Baloskion* (B. Briggs, pers. comm.), but as the formal combination has not been made in that genus we refer to it either as *Baloskion* or as *Restio tetraphyllus*.

B. CHLOROPLAST DNA RESTRICTION SITE CHARACTERS

Methods for DNA extraction and restriction site analysis are the same as in earlier studies (Soreng et al., 1990; Davis & Soreng, 1993; Choo et al., 1994). Briefly, total DNA was extracted, then digested with 10 restriction enzymes: *Bam* HI, *Bcl* II, *Bgl* II, *Cla* I, *Hind* III, *Kpn* I, *Pst* I, *Pvu* II, *Sal* I, and *Sma* I, using methods described by the supplier (Gibco/Bethesda Research Lab [G/BRL]). After electrophoresis in agarose gels (0.6–1%), the DNA was transferred to nylon membranes (Zetaprobe-GT+; G/BRL). The membranes first were probed with a set of large probes (10–21 kb) cloned from the grasses *Pennisetum americanum* (L.) Leeke (Thomas et al., 1984) and *Triticum aestivum* L. (Bowman et al., 1981). One additional large clone also was used, from *Phaseolus vulgaris* L., (Palmer & Thompson, 1981) to cover the small single copy (SSC) region. Up to 34 smaller probes (1–4 kb) from *Nicotiana tabacum* L. (Sugiura et al., 1986) were used as needed to assess the homology and map the restriction sites that fell within and between the larger probe regions. This overall combination of probes covers more than 99% of the chloroplast genome. Mapping was facilitated by reference to the 271 restriction sites for the above enzymes in the *Oryza sativa* cpDNA sequence (Hiratsuka et al., 1989; Sugiura, 1989). The distribution of these sites by region within the chloroplast genome of *Oryza sativa* is as follows: 172 in the large single copy (LSC) region, 62 in the inverted re-

Table I. Taxa used for cpDNA restriction site and morphological analysis, and accessions sampled for DNA analysis. Taxa are arranged by family, subfamily, tribe, and subtribe as classified by Clayton and Renvoize (1986).

Abbreviations[a]	Taxa[b]	Sources of material used in DNA analyses[c]
	Flagellariaceae Dumort. (1 gen., 4 spp.)	
	Flagellaria indica L.	BHC-77394
	Restionaceae R. Br. (40 gen., 400 spp.)	
	Restio tetraphyllus Labill. (recognized by B. Briggs [pers. comm.] as a species of *Baloskion* Raf., but a combination in that genus has not been published)	KEW-6565-1977
	Joinvilleaceae D.F. Cutler & Airy Shaw (1 gen., 2 spp.)	
	Joinvillea ascendens Gaudich. ex Brongn. & Gris	NTBG-800379 *H. Moore 10,438*
B	Poaceae Barnhart (651 gen., 10,000 spp.)	
BAM	Bambusoideae Asch. (13 tribes, 91 gen., 1110 spp.)	
	Bambuseae Bertch. & J. Presl (49 gen., 840 spp.)	
	subtr. Bambusinae J. Presl	
	Bambusa multiplex (Lour.) Raeusch. ex Schult. & Schult. f.	HC-71470
	Guadua angustifolia Kunth	*PMP 9527*, US
	subtr. Arundinariinae Nees	
	Chusquea aff. *subulata* L. G. Clark	*PMP 9499*, US
	Pseudosasa japonica (Siebold & Zucc. ex Steud.) Makino ex Nakai	BHC-71467
ANO	*Otatea fimbriata* Soderstr.	MBG-896580
	Anomochloeae C. E. Hubb. (1 gen., 1 sp.)	
STR	*Anomochloa marantoidea* Brongn.	*Clark 1299*, ISC
	Streptochaeteae C. E. Hubb. (1 gen., 3 spp.)	
PHA	*Streptochaeta sodiroana* Hack.	*PMP 9525*, US
	Phareae Stapf. (4 gen., 13 spp.)	
PAR	*Pharus latifolius* L.	BHC from USNZ
	Parianeae C. E. Hubb. (2 gen., 40 spp.)	
	Eremitis sp.	USNHG-153, *Soderstrom 2182*, US; or USNHG-286, US[d]
OLY	Olyreae Bertch. & J. Presl (16–17 gen., 100 spp.)	
	Olyra latifolia L.	*PMP 7311*, US
	Lithachne humilis Soderstr.	BHC from USNZ (*RJS 4291*)
EHR	Ehrharteae Nevski (1[–4] gen., 44 spp.)	
	Ehrharta calycina Sm.	PI-208983
ORY	Oryzeae Bertch. & J. Presl (12 gen., 70 spp.)	
	Leersia virginica Willd.	*RJS 3399*
	Oryza sativa L.	Sugiura, 1989 (GenBank X15901)
BRA	Brachyelytreae Ohwi (1 gen., 1 sp.)	
	Brachyelytrum erectum (Schreb.) P. Beauv.	*RJS 3427*
DIA	Diarrheneae (Ohwi) Tateoka ex C. S. Campb. (1[–2] gen., 5 spp.)	
	Diarrhena obovata (Gleason) Brandenb.	*Tiedye 5186*, DAO
PO	Pooideae Benth. (10 tribes, 132 gen., 3300 spp.)	
NAR	Nardeae W. D. J. Koch (1 gen., 1 sp.)	
	Nardus strictus L.	BBG: *Royl & Schiers s.n.* (1988), B
LYG	Lygeeae J. Presl (1 gen., 1 sp.)	
	Lygeum sparteum L.	*RJS 3698*
STI	Stipeae Dumort. (9 gen., 400 spp.)	
	Nassella viridula (Trin.) Barkworth	PI-387938
	Piptatherum miliaceum (L.) Coss. [sent as *Oryzopsis miliacea* (L.) Asch. & Schweinf.]	PI-284145
	Stipa barbata Desf.	PI-229468

Table I (continued)

Abbreviations[a]	Taxa[b]	Sources of material used in DNA analyses[c]
AVE	Aveneae Dumort. (= Agrostideae Bertch. & J. Presl) (57 gen., 1050 spp.)	
	subtr. Aveninae J. Presl	
	Amphibromus scabrivalvis (Trin.) Swallen	*K. Clay s.n.*, IND
	Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	*JID & RJS s.n.*
	Avena barbata Pott ex Link subsp. *barbata*	*RJS 3625b*
	subtr. Trisetinae Holub	
	Koeleria macrantha (Ledeb.) Schult. [sent as *K. cristata* sensu Pers.]	PI-477978
	Trisetum canescens Buckley	*RJS 3383a*
	Deschampsia caespitosa (L.) P. Beauv.	PI-311043
	subtr. Phalaridinae Fr.	
	Anthoxanthum odoratum L.	*RJS 4292*
	Phalaris arundinacea L.	*RJS 3427*
	subtr. Alopecurinae Dumort.	
	Agrostis gigantea Roth	*RJS 3429*
	Ammophila arenaria (L.) Link	*RJS 3389*
	Calamagrostis canadensis (Michx.) P. Beauv.	PI-371717
MEL	Meliceae (Link) Endl. (8 gen., 130 spp.)	
	Glyceria striata (Lam.) Hitchc.	*JID & RJS s.n.*
	Glyceria declinata Bréb.	*RJS 3659*
	Melica altissima L.	PI-325418
	Melica cupanii Guss.	PI-383702
	Schizachne purpurascens (Torr.) Swallen	*RJS 3348*
POE	Poeae R. Br.: 49 genera, 1200 species	
	Lolium arundinacea (Schreb.) Darbysh.	PI-304844
	Ampelodesmos mauritanica (Poir.) T. Durand & Schinz	BBG: *Royl & Schiers s.n.* (1988), B
	Catabrosa aquatica (L.) P. Beauv.	*JID s.n.*
	Festuca longifolia Thuill. (*F. "ovina"* of local trade)	*RJS 3928*
	Lolium perenne L.	PI-418710, PI-253719
	Poa eminens J. Presl	SJD 85-73, DAO
	Puccinellia distans (Jacq.) Parl. cv. Fults	NPI-pudi5591
	Sesleria insularis Sommier subsp. *sillageri* (Deyl) Deyl [sent as *Sesleria elongata* Host]	PI-253719
	Vulpia alopecuros (Schousb.) Dumort.	PI-238315
BRO	Bromeae Bertch. & J. Presl (3 gen., 150 spp.)	
	Boissiera squarrosa (Banks & Soland.) Nevski	*E. Collenette 4398*, E
	Bromus inermis Leyss.	*RJS 3428*, PI-314071[e]
TRI	Triticeae Dumort. (= Hordeae Bertch. & J. Presl) (18 gen., 360 spp.)	
	Brachypodium distachyon (L.) P. Beauv.	PI-422452
	Brachypodium pinnatum (L.) P. Beauv.	PI-440170
	Brachypodium sylvaticum (Huds.) P. Beauv.	PI-251102
	Elymus trachycaulus (Link) Gould ex Shinners	*RJS 4291*
	Peridictyon sancta (Janka) Seberg & Fred.	H 6410[f]
	Triticum aestivum L. cv. Susquehanna	*RJS s.n.*
CENTO	Centothecoideae Soderstr. (1 tribe)	
	Centotheceae Ridley (10 gen., 30 spp.)	
	Chasmanthium latifolium (Michx.) H. Yates	CU
	Chasmanthium nitidum (Baldwin) H. Yates	*Wipff & Jones 2075*, TAES
A, ARU	Arundinoideae Burmeist. (4 tribes, 45 gen., 600 spp.)	
	Arundineae Dumort. (40 gen., 300 spp.)	
	Amphipogon strictus R. Br.	*Linder 5634*, BOL

Table I (continued)

Abbreviations[a]	Taxa[b]	Sources of material used in DNA analyses[c]
	Anisopogon avenaceus R. Br.	Linder 5590, BOL
	Arundo donax L.	FTG-83-130
	Danthonia californica Bolander	PI-232247
	Molinia coerulea (L.) Moench	RJS 3305
	Phragmites australis (Cav.) Trin. ex Steud.	RJS 3884
ARI	Aristideae C. E. Hubb. (3 gen., 300 spp.)	
	Aristida purpurea Nutt.	Allred s.n.
C	Chloridoideae Burmeist. (5 tribes, 146 gen., 1400 spp.)	
ERA	Eragrostideae Stapf (77 gen., 1000 spp.)	
	subtr. Eleusininae Dumort.	
	Eragrostis curvula (Schrad.) Nees [sent as Stipagrostis uniplumis (A. Licht.) De Winter]	PI-365034
	subtr. Uniolinae Clayton	
	Uniola paniculata L.	JID s.n.
	subtr. Monanthochloinae Potztal	
	Distichlis spicata (L.) E. Green subsp. stricta (Torr.) R. F. Thorne	K. Allred s.n.
	subtr. Sporobolinae Benth.	
CYN	Sporobolus giganteus Nash	PMP 10008, US
	Cynodonteae Dumort. (= Chlorideae Bertch. & J. Presl) (59 gen., 300 spp.)	
	subtr. Chloridinae J. Presl	
	Spartina pectinata Link	J. LaDuke s.n.
	subtr. Zoysiinae Benth.	
	Zoysia sp.	JID s.n.
PA	Panicoideae Link (7 tribes, 210 gen., 3300 spp.)	
AND	Andropogoneae Dumort. (= Sacchareae Bertch. & J. Presl) (85 gen., 960 spp.)	
	Miscanthus sinensis Andersson var. gracillimus Hitchc.	CU, RJS s.n.
PAN	Paniceae R. Br. (101 gen., 2000 spp.)	
	Panicum virgatum L.	USDA 421520
	Pennisetum alopecuroides (L.) Spreng.	CU, RJS s.n.

[a]Abbreviations for names of subfamilies and tribes, as used in Figures 1–4, precede full names in table.

[b]The approximate number of tribes, genera, and species is indicated for each subfamily of Poaceae, and the number of genera and species is indicated for each of the other three families and for each tribe of Poaceae. Several author citations have been corrected from Clayton and Renvoize, and older synonyms are provided (in parentheses) for some suprageneric taxa (see text).

[c]Abbreviations for collectors and other sources of plant material are as follow: BBG = Berlin Botanic Garden; BHC = L. H. Bailey Hortorium Conservatory; CU = Cornell University gardens; FTG = Fairchild Tropical Gardens; JID = J. I. Davis; KEW = Royal Botanic Gardens, Kew; MBG = Missouri Botanical Garden; NPI = Native Plants Inc., Utah; NTBG = U.S. National Tropical Botanical Garden; PI = U.S.D.A. Plant Introduction Station (Pullman, Washington); PMP = P. M. Peterson; RBGE = Royal Botanic Gardens, Edinburgh; RJS = R. J. Soreng; SJD = S. J. Darbyshire; USNHG = U.S. National Herbarium greenhouse; USNZ = U.S. National Zoological Gardens. Vouchers are held at BH unless indicated otherwise with herbarium acronyms following Holmgren et al., 1990.

[d]Because of a clerical error, it is not certain which of these two collections was sampled.

[e]PI-314071 was used for Kpn I, Pvu II, Sal I, and Sma I; RJS 3428 was used for BamH I, Bgl I, Bcl II, Cla I, Hind III, and Pst I.

[f]See Seberg et al., 1991.

peat (IR) region, and 37 in the small single copy (SSC) region. Restriction site maps were encoded as a data matrix in which each of 616 differentiable sites was scored as a binary character, with each site specified by restriction enzyme and map location, the latter keyed to the enumeration of nucleotides in the cpDNA sequence of Oryza sativa; cladistically informative characters of the matrix are published here (Appendix 1).

C. STRUCTURAL CHARACTERS

Forty-two characters representing anatomy and gross morphology, physiology, and chloroplast genome structural mutations also were scored. These characters constituted the "structural" character set. The principal reference for most structural characters is Watson and Dallwitz's (1992) Grass Genera of the World. With the goal of minimizing the number of polymorphisms, questionable homologies, and missing data, we consulted the primary literature and specimens of the exemplar species. Primary literature sources included surveys of particular structural attributes of grasses (e.g., lodicules, embryos) and taxonomic monographs; secondary sources include floras and prior reviews of structural variation and taxonomy of the grasses. Personal observations were made of living material, DNA vouchers, and other specimens. The structural characters are described in Appendix 2, which includes comments on their scoring when the scores used in the analysis are absent in Watson and Dallwitz (1992) or differ from those provided there. The structural data are presented in Appendix 3.

The following rules were adopted for the reconciliation of polymorphisms, ambiguity, and contradictory statements in the literature:

1. If a species consistently has a structure in fully developed organs, but not in vestigial ones, it is scored as having that structure.
2. If a monotypic genus is reported to have one character state by Watson and Dallwitz (1992), and another state in a primary source, the taxon is scored as polymorphic unless ancillary evidence suggests that one or the other source is in error.
3. If all reports for a polytypic genus specify the same state, but there is no report for the exemplar species in the analysis, the exemplar species is scored as having the state reported for the genus.
4. If a polytypic genus is reported to have one state by Watson and Dallwitz, and this is contradicted by a primary source, the primary source is followed if it includes an observation of the exemplar species; if the primary source does not mention the exemplar species, the taxon is scored as polymorphic.
5. If a polytypic genus is reported to be polymorphic by Watson and Dallwitz, and if a primary or secondary source reports an observation of the exemplar species as having a single state, or (for multistate characters) a subset of the states reported for the genus by Watson and Dallwitz, the species is scored as in the primary or secondary source. Thus, some polymorphisms in the data set represent generic polymorphisms where the state has not been observed for the exemplar species, and others represent observed infraspecific variation.
6. If the exemplar species has a character state that is intermediate between two recognized states, it is scored as ambiguous.
7. An additional situation pertains in multistate characters where one or more states of a multistate character are determined to be absent, but the observed attribute is not assigned to one of the remaining states. In this situation, termed "subset ambiguity," the taxon is scored as polymorphic for all states that have not been determined to be absent.

8. A situation that combines aspects of subset polymorphism and subset ambiguity also is recognized. If some individuals of an exemplar species have one state, and other individuals have a state that is intermediate between that and a second state, the taxon is scored as "polymorphic" for the two states. Similarly, polymorphism coding might be used if the state of an exemplar species is unknown, and one or more representatives of a genus have one state, while one or more others are intermediate between that state and another.

The 42 structural characters fall into several groups: morphology of culm and leaf (6 characters), morphology of spikelet (7), morphology of flower (9), morphology of fruit and embryo (9), morphology of seedling (1), anatomy of vegetative structures (5), biochemistry (2), and structure of the chloroplast genome (3). The character selection reflects consideration of ease of scoring, minimal ambiguity in the determination of states, and historical use in grass classification. All multistate structural characters were treated as nonadditive.

D. DATA ANALYSIS

Cladistically uninformative characters were removed from the data matrices prior to analysis, with the *mop* command of *Dada* ver. 1.1.4 (Nixon, 1997). However, when there are multistate characters in a matrix (as in the structural character set of the present analysis) removal of uninformative characters may leave autapomorphies. An informative multistate character can include one or more uninformative states, as it would, for example, if states 0 and 1 each occurred in several terminals and state 2 occurred in one terminal. In this case, state 2 would be an uninformative state (an autapomorphy) of an informative character if the character were treated as nonadditive (note, however, that if the character were additive, state 2 would be informative, though present in only one taxon). In the structural character set of the present analysis, with all characters treated as nonadditive, any state that occurs in only one terminal is autapomorphic, and as such it contributes one step to any possible tree and does not influence tree structure. Recoding of such a state as missing removes the autapomorphic step from all trees without altering the results of cladistic analysis. Note, however, that results obtained from analytical methods such as neighbor joining and maximum likelihood estimation are influenced by cladistically uninformative data, including uninformative states of informative characters.

The present structural matrix includes two informative characters with uninformative states (char. 23, state 2 unique to *Baloskion*; char. 38, state 2 unique to *Aristida*; Appendix 3). These data are included in the matrix published here, but all analyses (except character optimization on trees for the purpose of determining synapomorphies of clades and autapomorphies of terminals) were conducted with these two states recoded as missing. Thus, tree lengths obtained with the structural character matrix (Appendix 3) are two steps longer than those reported below, as are those obtained by simultaneous analysis of both matrices. Consistency indices (CI; Kluge & Farris, 1969), reported below, also were calculated using matrices with uninformative characters and uninformative states of informative multistate characters removed.

Cladistic analysis, with characters equally weighted, was conducted on the two character sets (restriction sites and structural characters) separately, and a simultaneous analysis was conducted of the combined matrix of all characters. The separate analysis of the structural character set was conducted with monophyly of Poaceae (see results), and a second analysis of this character set was conducted with monophyly of Poaceae constrained, to explore implications of this data set under that condition. All four cladistic analyses were conducted with *Nona* ver. 1.16 (Goloboff, 1993b), using the default settings *amb-* (clades resolved only if they have un-

ambiguous support) and *poly=* (polytomies allowed). In each analysis 3500 subsearches were conducted, each consisting of tree-construction using a random taxon entry sequence, followed by tree bisection-reconnection (tbr) swapping with up to 20 most-parsimonious trees retained (*hold/20 mult*3500*); shortest trees retained from the subsearches then were tbr-swapped to completion (*max**), except for the two analyses of the structural character set. Neither of the analyses based on just the structural character set (unconstrained and with monophyly of grasse. constrained) identified a small number of most-parsimonious trees, and in each case swapping was aborted after 10,000 trees had been accumulated and tbr-swapping had been conducted on all of those trees.

One additional cladistic analysis was conducted, based on the combined matrix of both character sets and using implied weighting (Goloboff, 1993a), as implemented in *Piwe* ver. 2.15 (Goloboff, 1993c), using the default weighting function (concavity = 3), and the same ambiguity and polytomy settings, plus the same search procedures as used in the unweighted analyses conducted with *Nona* (Goloboff, 1993b).

Bootstrap support (Felsenstein, 1985) was assessed with a "strict-consensus" bootstrap analysis. In this form of the bootstrap a clade is recognized as having been resolved by a particular bootstrap replicate only if it occurs in all most-parsimonious trees (i.e., if it occurs in the strict-consensus tree) obtained in that replicate. Thus, every potential clade receives a score of either 0 or 1 for each bootstrap replicate. In contrast, in the "frequency-within-replicates" bootstrap, as implemented in most software packages that conduct bootstrap analysis, each clade is assigned a score in each replicate in proportion to its frequency of occurrence among most-parsimonious trees. If a group occurs in all most-parsimonious trees in a particular replicate, it receives a score of 1.0 under both forms of the bootstrap; but if it occurs in some but not all trees, it receives a score of 0 in the strict-consensus bootstrap and a score >0 in the frequency-within-replicates bootstrap. Thus, if equally effective tree searches are conducted, observed strict-consensus bootstrap scores must be less than or equal to frequency-within-replicates bootstrap scores, and in empirical studies with various data sets the strict-consensus bootstrap frequency for a clade that occurs in the strict-consensus tree for a given data set is usually 0–10% lower than the frequency-within-replicates bootstrap frequency for the same clade (pers. obs.). In the present analysis two strict-consensus bootstrap analyses were conducted, one on the restriction site data set, the other on the combined data set, using *Clados* ver. 1.4.98 (Nixon, 1993) running *Nona* (Goloboff, 1993b) as a daughter process for tree searches. In each analysis 1000 bootstrap replicates were conducted with the same ambiguity and polytomy settings as in the basic analyses, and with each replicate comprising 20 random taxon entry sequences with tbr-swapping to up to four trees, followed by tbr-swapping of all shortest trees obtained from the 20 subanalyses, with a total of up to 80 shortest trees saved (*hold/4 hold80 mult*20 max**).

Minimum character removal (MCR) scores were determined by successive character removal analysis (Davis, 1993; Davis et al., 1993) conducted on the combined matrix. With 406 informative characters in the combined matrix it was not feasible to conduct more than one round of analysis (i.e., 406 analyses, each with a different one of the 406 characters removed from the matrix). The analyses were conducted with *Nona* (Goloboff, 1993b), using the same ambiguity and polytomy settings as in the basic analyses, and with analysis comprising 100 random taxon entry sequences with tbr-swapping to up to five trees, followed by tbr-swapping of all shortest trees obtained from the 100 subanalyses, with a total of up to 500 shortest trees saved (*hold/5 hold500 mult*100 max**).

Unambiguous structural character apomorphies of terminals and clades were determined by optimizing the structural data matrix on most-parsimonious trees obtained by analysis of

the combined data sets using the *apo-* command of *Nona* (Goloboff, 1993b). Character changes of ambiguous placement and other patterns of character variation were examined with *Clados* (Nixon, 1993).

The Mickevich/Farris incongruence index (I_{MF}; Mickevich & Farris, 1981; Kluge, 1989) and lengths of various data subsets as optimized on trees obtained from the combined data or from the other data set (related to the Miyamoto incongruence index; Kluge, 1989) were calculated from tree lengths of the various character sets on trees obtained in the various analyses and from minimum possible tree lengths for data sets obtained using the *fit* command of *Nona* (Goloboff, 1993b). All analyses yielded more than one most-parsimonious tree, and for all calculations based on the number of extra steps required to map the various data sets on the various sets of trees, the minimum required length was used (Swofford, 1991).

IV. Results

A. COLINEARITY OF THE CHLOROPLAST GENOMES

Restriction site mapping indicates that all of the grass cpDNAs sampled here are colinear with respect to the 27 kb and 6.4 kb inversions (relative to the chloroplast genome of *Nicotiana* L.) previously documented among grasses (Quigley & Weil, 1985; Howe et al., 1988; Hiratsuka et al., 1989; Downie & Palmer, 1992; Doyle et al., 1992) and in *Joinvillea* (Doyle et al., 1992). Specifically, these mapping results are consistent with previously reported results obtained by polymerase chain reaction (PCR) assays using diagnostic primer combinations (Doyle et al., 1992; see char. 40 of the present analysis, Appendix 2). New PCR data demonstrate that *Baloskion* lacks the 6.4 kb inversion, like the two genera of Restionaceae previously tested (Doyle et al., 1992), whereas the restriction site data suggest that *Baloskion*, again like the other two genera, has the 27 kb inversion. Because *Flagellaria* is the only taxon in the present analysis that lacks the 27 kb inversion, that character is cladistically uninformative in this set of taxa and is not included in the structural character set. New PCR data for six of the exemplar grasses in this study (*Anisopogon*, *Anomochloa*, *Brachyelytrum*, *Lygeum*, *Molinia* Schrank, and *Poa* L.; see Table I for species names and voucher information) have the small *trn*T inversion that has been detected in all grasses sampled to date, and that is absent in all nongrasses (Doyle et al., 1992).

B. CHARACTERISTICS OF THE DATA MATRIX

The restriction site and structural character data in the present analysis represent 89.7% and 10.3% of the total data set, respectively. Of a total of 616 restriction sites mapped and scored as cladistic characters, 364 are cladistically informative (Appendix 1). In the restriction site data matrix, 11% of the cells (9% in Poaceae) are scored missing (i.e., unobserved or of ambiguous homology). In the structural character matrix of 42 characters scored for 75 taxa, 14% of all cells (12% in Poaceae) are scored missing (i.e., unobserved, of ambiguous homology, or inapplicable) and another 4% are scored as polymorphisms or subset ambiguities (Appendix 3).

A principal cause of missing data in the restriction site character set is attributable to difficulty in the differentiation of pairs of restriction sites that occur in close proximity to one another (primarily where sites are mapped within <300 bp of each other). This difficulty arose in part because of the availability of precise locations for restriction sites that were detected by searching for the appropriate nucleotide sequences in the published cpDNA sequence of

Oryza. When two sites for the same restriction enzyme occurred in close proximity to each other (e.g., at a distance of 300 bp or less from each other), and a site detected by restriction digest in another taxon was mapped near those two locations, it could not be determined in some cases (e.g., when the site was flanked by large restriction fragments) whether that taxon had one or the other or both of the sites observed in *Oryza*.

A second difficulty occurred in the alignment of restriction sites when slight size variation was apparent between adjacent fragments among exemplars. This difficulty was encountered most frequently in the alignment of maps of the three nongrass accessions with those of grasses, often in the LSC region, and particularly in areas of known inversion endpoints and in areas where length variation was detected among the grasses. Even within the grasses, ease of alignment between taxa tended to be correlated with proximity of phylogenetic relationship, and this resulted in a greater amount of missing data in phylogenetically isolated species and sparsely sampled large groups than occurred in Pooideae, where depth of sampling was greatest.

C. CLADISTIC ANALYSES

The provisional tribe and subfamily designations adopted for this study, and used in Table I and in figures, are those of Clayton and Renvoize (1986). However, the following changes, reflecting the results of the analyses presented here, are adopted in the text from this point onward: First, we recognize a monophyletic Pooideae that includes *Diarrhena* and *Anisopogon*, which are placed by Clayton and Renvoize (1986) in Bambusoideae and Arundinoideae, respectively. Second, Clayton and Renvoize place *Ampelodesmos* and *Brachypodium* within tribes Poeae and Triticeae (= Hordeeae), respectively, of subfam. Pooideae; although the results presented here favor the placement of these two genera within Pooideae, their phylogenetic positions are not within the tribes in which they are placed by Clayton and Renvoize (1986), and we recognize these genera as constituting separate tribes, Ampelodesmeae and Brachypodieae, respectively. Third, *Brachyelytrum* is removed from Bambusoideae, but because its placement is ambiguous it is left unassigned to subfamily. Fourth, five additional tribes are removed from subfam. Bambusoideae and placed in small subfamilies that represent early-diverging clades within the Poaceae: Ehrharteae and Oryzeae are recognized as tribes within Ehrhartoideae; Anomochloeae and Streptochaeteae as tribes within Anomochlooideae; and Phareae as a tribe within Pharoideae (Clark & Judziewicz, 1996). Further discussion of "early-diverging" lineages refers to Anomochlooideae, Pharoideae, Bambusoideae (including Bambuseae, Parianeae, and Olyreae), and Ehrhartoideae, four putative lineages that are often placed within a broadly defined Bambusoideae and that diverge earliest from the diverse lineage that includes *Brachyelytrum*, Pooideae, and the PACC clade. Finally, subfam. Arundinoideae is abandoned, and we refer to this group as the "Arundinoid" assemblage.

In the text that follows, and in Table II, where two or more genera of a tribe, or two or more of the tribe or subfamily that they represent in a consensus tree, we usually refer to them by the name of the tribe or subfamily that they represent (e.g., Olyreae for *Lithachne* + *Olyra*; Ehrhartoideae for Oryzeae + Ehrharteae) rather than repeatedly citing sets of genera. For monogeneric tribes we simply cite the genus (e.g., *Anomochloa*).

1. Chloroplast DNA Restriction Site Data

Cladistic analysis of the restriction site data recovered 10 most-parsimonious trees of length (L) 1277, consistency index (CI) 0.28, and retention index (RI; Farris, 1989) 0.70; 62 clades are resolved in the strict consensus of these trees (Fig. 1). All polytomies in the consen-

Table II. Structural autapomorphies of terminals, and synapomorphies of clades resolved by simultaneous analysis of restriction site and structural data.[a]

Terminal or clade	Character and state transformation[b]	Terminal or clade	Character and state transformation[b]
Flagellaria	2: 1 → 0	Oryza	13: 0 → 1
	3: 0 → 1	Leersia	19: 6 → 12
	20: 1 → 0		22: 2 → 3
Baloskion	19: 6 → 3	13	6: 1 → 0 (a1, -a2)
	21: 3 → 2		10: 0 → 1 (a1, -a2)
	23: 3 → 2		20: 1 → 0 (a1, -a2)
	32: 0 → 1		32: 0 → 1 (a1, -a2)
1	40: 0 → 1		36: 1 → 0
Joinvillea	none		37: 1 → 0 (a1, -a2)
2	23: 3 → 1	Brachyelytrum	2: 1 → 0
	25: 0 → 1		31: 1 → 4
	41: 0 → 1		34: 1 → 0 (a2, -a1)
3	4: 0 → 1	14	26: 1 → 0
Anomochloa	2: 1 → 0		28: 0 → 1
	19: 6 → 4	Aristida	2: 1 → 0
	21: 3 → 1		13: 0 → 1
	29: 1 → 0		38: 0 → 2
Streptochaeta	26: 1 → 0	15	17: 1 → 0
4	none		24: 0 → 1
Pharus	2: 1 → 0	16	4: 0 → 1
	32: 0 → 1		35: 0 → 1
	34: 1 → 0	Amphipogon	13: 0 → 1
5	19: 6 → 3 (a2, -a1)		18: 1 → 0
	21: 3 → 2 (a1, -a2)		20: 0 → 1
	42: 0 → 1 (a2, -a1)	17	10: 1 → 0
	19: 3 → 2 (a2, -a1)		38: 0 → 3
Eremitis	21: 23 → 1	18	none
6	1: 0 → 1	Eragrostis	none
	5: 0 → 1	Uniola	8: 0 → 1
7	21: 2 → 3 (a1, -a2)		20: 0 → 1
	19: 3 → 6	19	none
Bambusa		Distichlis	4: 1 → 0
Pseudasasa	none		31: 1 → 034
6	none		14: 1 → 0
Chusquea	2: 1 → 0	20	39: 0 → 1
	8: 0 → 1		10: 0 → 1
	10: 0 → 1		12: 1 → 0
	19: 3 → 6	Zoysia	none
	21: 2 → 3 (a1, -a2)	21	2: 0 → 1
9			20: 0 → 1
Guadua	none	Spartina	none
10	13: 0 → 1	Sporobolus	none
Platea		22	
Lithachne	12: 1 → 0 (a1, -a2)	23	none
Olyra	none	Arundo	1: 0 → 1
11	6: 1 → 0 (a1, -a2)	24	4: 0 → 1
	15: 3 → 2 (a1, -a2)		24: 1 → 0
	19: 3 → 6 (a1, -a2)	Molinia	none
	20: 1 → 0 (a1, -a2)	Phragmites	8: 0 → 1
	37: 1 → 0 (a1, -a2)		20: 0 → 1
	26: 1 → 0		36: 0 → 1
Ehrharta	32: 0 → 1 (a1, -a2)		11: 0 → 1
	27: 1 → 0	Danthonia	
12	33: 1 → 0	25	8: 0 → 1
	42: 1 → 0 (a2, -a1)		

Table II (continued)

Terminal or clade	Character and state transformation[b]	Terminal or clade	Character and state transformation[b]
26	29: 0 → 1	Diarrhena	10: 1 → 0
	31: 1 → 3	45	none
	19: 3 → 1	46	31: 1 → 0
	20: 0 → 1	47	3: 0 → 1
	26: 0 → 1	Bromus	26: 1 → 0
Chasmanthium l	none	Boissiera	none
Chasmanthium n	n ne	48	7: 1 → 0
27	12: 1 → 0	Triticum	none
	38: 0 → 1	49	none
Miscanthus	2: 1 → 0	Elymus	none
	11: 0 → 1	Peridictyoa	none
	31: 3 → 2	50	24: 0 → 1
28	13: 0 → 1	51	3: 0 → 1
Panicum	38: 1 → 3	Sesleria	20: 0 → 1
Pennisetum	none	Poa	10: 1 → 0
29	27: 1 → 0 (a2, -a1)		30: 0 → 1
30	14: 1 → 0	52	none
	21: 2 → 1	53	10: 1 → 0
Lygeum	2: 1 → 0	Puccinellia	none
	9: 1 → 0	Catabrosa	none
	10: 1 → 0	54	3: 1 → 0
Nardus	35: 0 → 1		24: 1 → 0
31	22: 2 → 1	55	none
Anisopogon	34: 1 → 0 (a2, -a1)	Festuca	none
32	11: 0 → 1	Vulpia	30: 0 → 1
33	none	56	none
Ampelodesmos	none	Lolium a	none
34	2: 1 → 0	Lolium p	7: 1 → 0
Stipa	none	57	11: 0 → 2
35	none		30: 0 → 1
Nassella	31: 1 → 03	Amphibromus	none
Piptatherum	none	58	8: 0 → 1
36	none	Anthoxanthum	14: 1 → 0
37	none		19: 3 → 2
38	31: 1 → 0	Phalaris	10: 1 → 0
Brachypodium d	none		12: 1 → 0
39	none	59	none
Brachypodium p	none	Ammophila	none
Brachypodium s	26: 1 → 0	60	none
40	3: 0 → 1	Calamagrostis	none
	17: 1 → 0	61	24: 0 → 1
	22: 2 → 3	Agrostis	12: 1 → 0
41	none	Deschampsia	9: 1 → 0
Glyceria s	19: 3 → 2	62	none
Glyceria d	none	Arrhenatherum	8: 0 → 1
42	none		9: 1 → 0
Schizachne	none	63	9: 1 → 0
43	12: 1 → 0	Avena	none
Melica n	none	64	24: 0 → 1
Melica c	none	Koeleria	none
44	none	Trisetum	none

Table II (continued)

Terminal or clade	Character and state transformation[b]	Terminal or clade	Character and state transformation[b]

Four clades present in all most-parsimonious trees with Alternative Topology 1, absent from all trees with Alternative Topology 2:

8 = 6 + 10 + 13 + *Eremitis*	none		
9 = 6 + 10 + 13	none	13 = 10 + 13	none
		24 = 29 + *Brachyelytrum*	none

Four clades present in all most-parsimonious trees with Alternative Topology 2, absent from all trees with Alternative Topology 1:

i + *Eremitis*	none		
0 + 11 + 13	none		20: 1 → 0
1 + 13	6: 1 → 0		37: 1 → 0
	10: 0 → 1	14 + 29	29: 1 → 0
	15: 3 → 2		33: 1 → 0

[a]Top section of table lists apomorphies that occur in all most-parsimonious trees and are unambiguous (bold type), plus those that occur in some but not all most-parsimonious trees, but are unambiguous in trees in which they occur (normal type). Among the latter group, those synapomorphies that occur in all six trees with alternative topology 1 (early divergence of Ehrhartoideae, see text and Figs. 1, 4) or all six trees with alternative topology 2 (late divergence of Ehrhartoideae, Figs. 4–7) are marked "a1" or "a2," respectively, and those that occur in none of the six trees with alternative topology 1 or 2 are marked "-a1" or "-a2," respectively (e.g., transformation of character 19 from state 6 to state 3 is a synapomorphy of all six trees of alternative topology 2, and of none of the trees of alternative topology 1). In the lower two sections of the table, unambiguous synapomorphies are specified for clades that occur in all most-parsimonious trees of each alternative topology, and are absent from all trees of the other set. The four groups present in all most-parsimonious trees with Alternative Topology 1 and absent from all trees with Alternative Topology 1 also were resolved by analysis of just the restriction site data (Fig. 1); each is specified by a number in bold type that corresponds to a clade number in Fig. 1, and by a list of individual terminals and clade numbers in normal type that correspond to those in Fig. 3. Similarly, contents of the four groups present in all most-parsimonious trees with Alternative Topology 2 and absent from all trees with Alternative Topology 1 are specified in terms of their constituent individual terminals and clades as numbered in Fig. 3.
[b]Characters and states correspond to those in Appendices 2 and 3.
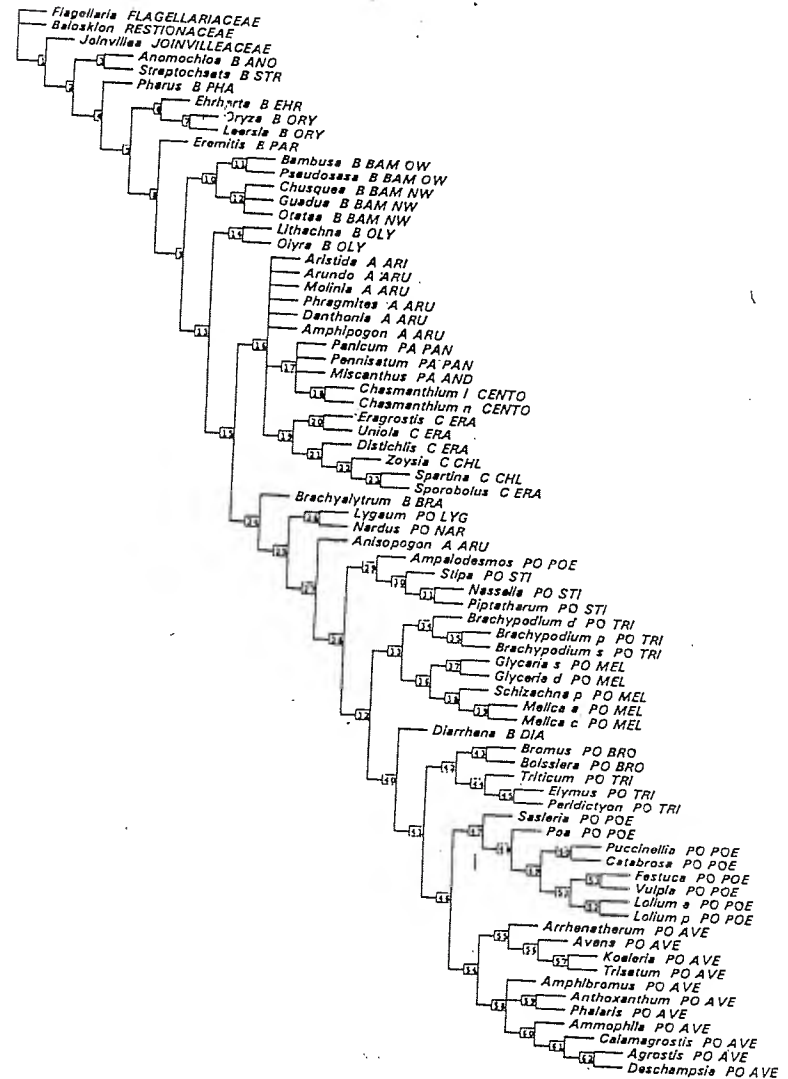
Fig. 1. Strict consensus of 10 most-parsimonious cladograms (1277 steps, CI = 0.28, RI = 0.70) for 72 representative accessions of grasses and three outgroup taxa, obtained by equal-weighted analysis of 364 informative restriction site characters (cf. Table I, Appendix 1).

sus tree represent lack of resolution below the tribal level, except for two multichotomies within the PACC clade. *Joinvillea* is placed as sister of Poaceae, and a lineage that consists of *Anomochloa* and *Streptochaeta* is placed as sister of all other grasses. Within the latter group (i.e., all grasses except *Anomochloa* and *Streptochaeta*) there is a pectinate arrangement among a series of lineages that have often been assigned to Bambusoideae, with *Pharus*, Ehrhartoideae, *Eremitis*, Bambuseae, and Olyreae diverging sequentially from the lineage that includes the PACC clade as sister to a clade in which *Brachyelytrum* is sister to Pooideae. One notable aspect of this structure, which is not universal among the relationships supported by the various analyses conducted in this study, is the sister-group relationship between Ehrhartoideae and all other grasses except *Anomochloa*, *Streptochaeta*, and *Pharus*; we refer to this relationship as the hypothesis of an "early-diverging" Ehrhartoideae. Another notable aspect of this structure, also inconstant among the various analyses, is the placement of *Brachyelytrum* as sister of Pooideae.

The PACC clade does not include *Anisopogon*, which is placed within the Pooideae. Within the PACC clade there is, in the consensus tree, a basal polytomy of all other individual Arundinoid exemplars (*Aristida*, *Arundo* L., *Amphipogon*, *Danthonia* DC., *Molinia*, and *Phragmites* Adans.) plus two subclades that together include all elements of Panicoideae, Centothecoideae, and Chloridoideae. The first of the subclades includes the three elements of Panicoideae, relationships among which are unresolved, and a monophyletic group consisting of the two elements of Centothecoideae; the second subclade consists of all elements of Chloridoideae. Five alternative sets of relationships underlie the overall lack of higher-level resolution in the PACC clade. The alternative relationships, which occur in various combinations among the 10 most-parsimonious trees are 1) *Aristida* sister of all other members of the PACC clade vs. the clade consisting of Panicoideae and Centothecoideae sister to all other members of the PACC clade; 2) Panicoideae and Centothecoideae both monophyletic and sister to each other vs. Panicoideae paraphyletic with Centhothecoideae nested among its three elements; 3) Chloridoideae sister to a monophyletic set of all Arundinoids except *Aristida* vs. Chloridoideae nested within a paraphyletic set of all Arundinoids vs. Chloridoideae nested within a paraphyletic set of all Arundinoids except *Aristida* vs. Chloridoideae sister of *Amphipogon*, a structure that coincides with the placement of *Aristida* as sister of all other members of the PACC clade and with all remaining Arundinoids sister of the clade that consists of Centothecoideae plus Panicoideae.

Diarrhena and *Anisopogon* are situated within Pooideae, where each is provisionally recognized as the sole genus of a tribe. All tribes of Pooideae represented by more than one exemplar were resolved as monophyletic, except that *Ampelodesmos* does not fall within Poeae and *Brachypodium* does not fall within Hordeeae. Five separate pairwise combinations of tribes also are supported as monophyletic: *Lygeum* + *Nardus*; *Ampelodesmos* + *Stipeae*; Brachypodieae + Meliceae; Bromeae + Hordeeae; and Poeae + Agrostideae. The results support a pectinate structure within the Pooideae, with the following series of lineages diverging in sequence: *Lygeum* + *Nardus*; *Anisopogon*; *Ampelodesmos* + *Stipeae*; Brachypodieae + Meliceae; *Diarrhena*; and a clade in which Bromeae + Hordeeae is sister of Agrostideae + Poeae.

2. Structural Character Data

Unconstrained analysis of the structural character set was aborted after 10,000 most-parsimonious trees of length 158, CI = 0.32, and RI = 0.77 had been discovered, and each had been subjected to tbr-swapping. The consensus of these 10,000 trees (not illustrated), with 34

resolved clades, does not include a monophyletic Poaceae, for *Baloskion* is placed within a group that consists of all members of Pooideae and the PACC group, plus *Brachyelytrum*. In this tree *Streptochaeta* is the sister of all other grasses plus *Baloskion*, and within this group the next deepest branch is a multichotomy from which emerge three individual terminals (*Anomochloa*, *Pharus*, and *Eremitis*) and a clade that includes all other grasses plus *Baloskion*. There is a dichotomy in the latter group, with one of the two sister groups consisting of a monophyletic association of *Lithachne*, *Olyra*, and all sampled elements of Bambuseae, and the other consisting of Oryzeae as sister of a clade in which *Ehrharta* is sister of a group that includes *Baloskion* and all remaining grasses (i.e., *Brachyelytrum*, the PACC group, and Pooideae. Phylogenetic structure is highly unresolved within the group that is sister of *Ehrharta*; 25 individual terminals (including *Baloskion*, *Brachyelytrum*, and various elements of Chloridoideae, Arundinoideae, and Pooideae) and seven multitaxon clades emerge from a single multichotomy. The largest of the multitaxon groups consist of 1) a monophyletic Centothecoideae as sister of a monophyletic Panicoideae, 2) all elements of Chloridoideae except *Uniola*, 3) all elements of Meliceae, and 4) *Vulpia* as sister of all elements of Agrostideae.

Analysis of the structural data, with the grasses constrained to be monophyletic, also was aborted after 10,000 trees had been identified and each had experienced tbr-swapping. These trees are one step longer than those yielded by the unconstrained analysis (length 159 steps, CI = 0.32, RI = 0.76), and 45 clades are resolved in the strict-consensus tree (Fig. 2). In the consensus tree *Streptochaeta* is the sister of all other grasses, and within the latter group there is a multichotomy in which relationships are unresolved among three individual terminals (*Anomochloa*, *Pharus*, and *Eremitis*) and a clade that includes all remaining grasses. Within the latter group there is a sister-group relationship between two clades, the first including a monophyletic grouping of *Lithachne* and *Olyra* as sister to a monophyletic grouping of all elements of Bambuseae, the second including a monophyletic grouping of *Oryza* and *Leersia* as sister to a monophyletic grouping of all remaining grasses. In the latter there is a pectinate structure in which *Ehrharta* and *Brachyelytrum* diverge successively from a clade that includes all remaining grasses (Pooideae plus the PACC group), and within which there is a sister-group relationship between a clade that includes all elements of the PACC group and one that includes all elements of Pooideae. Within the PACC clade, *Aristida* is sister to a clade that includes all other elements of the group, and the remaining Arundinoid elements constitute a paraphyletic assemblage, within which is nested a monophyletic grouping that consists of a monophyletic Centothecoideae as sister of a monophyletic Panicoideae; the sister clade of this group includes *Phragmites*, *Amphipogon*, and all elements of Chloridoideae. Within Pooideae there is a basal multichotomy from which emerge 17 individual terminals and four multitaxon clades. These four clades are a grouping of *Lygeum* and *Nardus*; a group of four genera of Poeae (*Sesleria* Scop. as sister of a clade that includes *Poa*, *Puccinellia* Parl., and *Catabrosa* P. Beauv.); a group that includes all elements of Meliceae (with *Schizachne* sister of a clade that includes the two representatives of *Glyceria* and the two representatives of *Melica*); and a group in which *Vulpia* is sister of a clade that includes all elements of Agrostideae.

3. Simultaneous Analysis of Restriction Site and Structural Characters

Unweighted simultaneous analysis of the combined matrix of 364 restriction site characters and 42 structural characters resolved 12 most-parsimonious trees of length 1468, CI = 0.28, and RI = 0.70. The total number of steps in restriction site characters among these trees ranges from 1277 (the same number of steps as in all 10 trees resolved by the restriction sites alone) to 1284 (CI = 0.28 in all trees, RI = 0.69–0.70), and the number of steps in structural

Fig. 2. Strict consensus of the first 10,000 most-parsimonious cladograms (159 steps, CI = 0.32, RI = 0.76) resolved for 72 representative accessions of grasses and three outgroup taxa, obtained by equal-weighted analysis of 42 informative structural characters, with monophyly of Poaceae constrained (cf. Table I, Appendices 2–3).

characters ranges from 184 to 191 (CI = 0.27–0.28, RI = 0.69–0.71). Of the 12 most-parsimonious trees for the combined matrix, two (i.e., the only two with 1277 steps in the restriction site data) are among the 10 resolved by restriction sites alone, while all 12 most-parsimonious trees for the combined matrix differ from those that are most-parsimonious for the structural characters alone.

The strict-consensus tree obtained by simultaneous analysis of restriction site and structural data resolves 64 clades (i.e., 2 more than the number resolved by restriction site characters alone, 30 more than resolved by unconstrained analysis of the structural characters, and 19 more than resolved by the constrained analysis). This consensus tree is similar to elements of trees resolved by the two data sets separately, but it includes clades that are resolved by neither of the other two. In this tree *Joinvillea* is sister of the grasses, and as in trees obtained by analysis of the restriction sites alone, the next divergence event is between *Anomochloa* + *Streptochaeta* and all other grasses, and within the latter group the next divergence event is between *Pharus* and all other grasses. Within the latter group is a multichotomy from which five lineages diverge. One of the five groups is a clade that includes *Brachyelytrum*, Pooideae, and the PACC clade. This clade also occurs in most-parsimonious trees for the restriction site data alone, and in most-parsimonious trees for the structural characters alone when monophyly of grasses was constrained; the unconstrained analysis of the structural characters resolved a group that included these elements plus *Baloskion*. The four other elements within the unresolved clade that is sister to *Pharus* are *Eremitis*, Ehrhartoideae, Olyreae, and Bambuseae. Regardless of the various potential relationships among these four groups, the placement of *Brachyelytrum* with Pooideae and the PACC clade is sufficient to render Bambusoideae (as circumscribed to include *Brachyelytrum*) nonmonophyletic. Even the removal of *Brachyelytrum* from Bambusoideae leaves the remaining elements of an inclusive Bambusoideae nonmonophyletic, for the divergence of at least two lineages (*Pharus* and the clade that includes *Anomochloa* and *Streptochaeta*) from the larger lineage that includes the PACC clade, Pooideae, and other elements often assigned to Bambusoideae also is inconsistent with a monophyletic Bambusoideae.

There are five polytomies in the consensus tree (Fig. 3), each representing conflict between two alternative sets of relationships:

1. *Phragmites* and *Danthonia* sister taxa, with *Molinia* sister of that clade, vs. *Phragmites* and *Molinia* sister taxa, with *Danthonia* sister of that clade;
2. *Sesleria* and *Poa* sister taxa, with that clade sister of all other Poeae, vs. *Sesleria* sister of all other Poeae, and within that group *Poa* sister of all remaining Poeae;
3. Aveninae sister of Alopecurinae, Phalaridinae sister of that clade, and *Amphibromus* sister of that clade, vs. Phalaridinae sister of Alopecurinae, *Amphibromus* sister of that clade, and Aveninae sister of that clade;
4. *Brachyelytrum* sister of Pooideae, and PACC clade sister of that clade, vs. PACC clade sister of Pooideae, and *Brachyelytrum* sister of that clade;
5. Olyreae sister of the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade, with Bambuseae sister of that clade, *Eremitis* sister of that clade, and Ehrhartoideae sister of that clade, vs. Ehrhartoideae sister of the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade, Olyreae sister of that clade, and a monophyletic grouping of *Eremitis* and Bambuseae sister of that clade.

Only the last two of these five polytomies involve alternative relationships above the level of the tribe. The alternative relationships underlying polytomies 4 and 5 are correlated in occurrence among the 12 most-parsimonious trees such that the first of the two alternatives de-
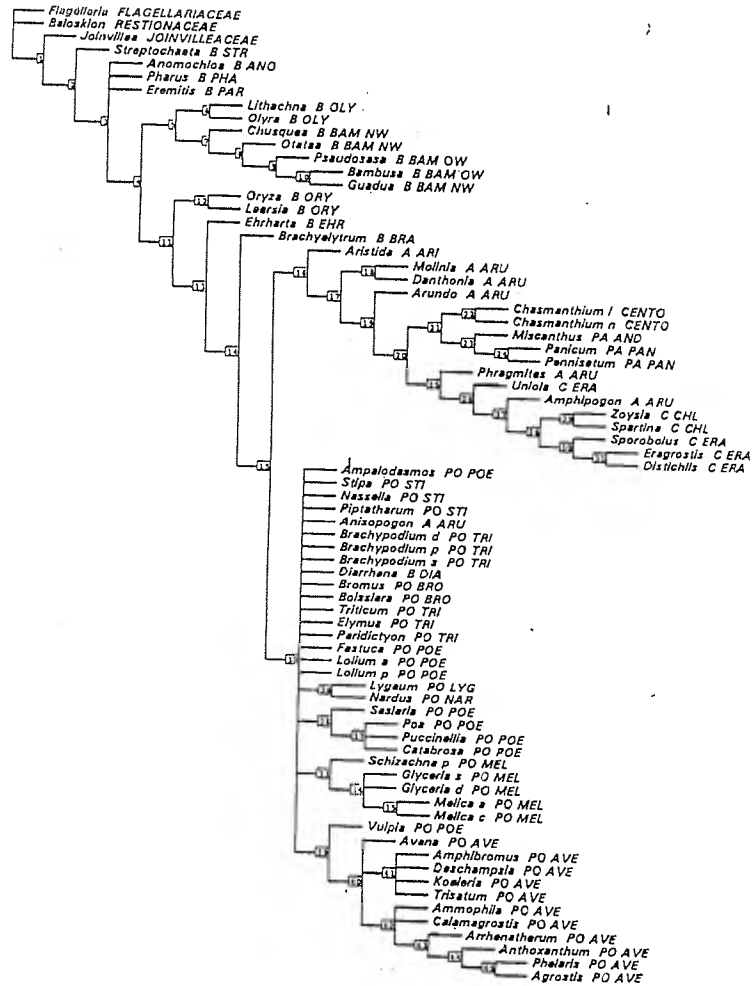
Fig. 3. Strict consensus of 12 most-parsimonious cladograms (1468 steps, CI = 0.28, RI = 0.70) for 72 representative accessions of grasses and three outgroup taxa, obtained by equal-weighted simultaneous analysis of 364 informative restriction site characters and 42 informative structural characters (cf. Table , Appendices 1–3).

scribed above for polytomy 4 occurs only with the first alternative listed for polytomy 5 (this combination occurs in six of the 12 trees), and the second alternative for polytomy 4 occurs only with the second alternative for polytomy 5 (this combination occurs in the other six trees). Thus the monophyletic grouping of Brachyelytrum plus Pooideae is associated in all cases with a pectinate structure in which the divergence of Ehrhartoideae immediately follows the divergence of Pharus, and is itself followed by divergence of the following taxa in sequence: Eremitis, Bambuseae, Olyreae, and the PACC clade from a monophyletic grouping of Brachyelytrum plus Pooideae (Figs. 1, 4a). This set of relationships, which we will refer to as "Alternative Topology 1," conforms to those obtained by analysis of the restriction site data (Fig. 1); it was described as the hypothesis of an early-diverging Ehrhartoideae, and it also can be described as the hypothesis of a sister-group relationship between Brachyelytrum and Pooideae. The second of the two alternative structures, in which the PACC clade and Pooideae are sister groups, occurs in association with the placement of Eremitis as sister of Bambuseae, and with the placement of this clade as sister to a clade in which the following taxa diverge in sequence: Olyreae, Ehrhartoideae, and Brachyelytrum, from the monophyletic grouping of Pooideae and the PACC clade (Figs. 4b, 5–7). This set of relationships, which we will refer to as "Alternative Topology 2," can be called the hypothesis of a "late-diverging" Ehrhartoideae, or that of a sister-group relationship between Pooideae and the PACC clade.

Unambiguous character transformations associated with clades resolved by the combined data set are described in Table II. Clade numbers in Fig. 3 and character placements on most-parsimonious trees (e.g., Figs. 5–7, representing one of six most-parsimonious trees exhibiting Alternative Topology 2), are used as reference points in Table II.

4. Topological Similarities among Unweighted Analyses

The separate unweighted analyses of restriction sites and structural characters (Poaceae constrained), and the analysis of the combined data set (Figs. 1–3, Table III) resolve several major groupings in common. The PACC clade is resolved by all three of these analyses; in all cases it includes all exemplars recognized by Clayton and Renvoize (1986) as elements of Arundinoideae, Centothecoideae, Chloridoideae, and Panicoideae, except Anisopogon. Within the PACC clade, Arundinoideae as circumscribed by Clayton and Renvoize (again excluding Anisopogon) are paraphyletic and include the earliest diverging lineages in the PACC clade. Centothecoideae (i.e., the two included species of Chasmanthium) always are resolved as monophyletic, Panicoideae are resolved as monophyletic (except by restriction site characters alone, where Panicoideae are paraphyletic), and Panicoideae plus Centothecoideae always constitute a monophyletic group. Chloridoideae are resolved as monophyletic by the restriction site data and by the combined character set, but not by the structural characters alone, which place Amphipogon (and no other taxa except representatives of Chloridoideae) in the smallest clade that includes all elements of Chloridoideae.

All three of these unweighted analyses resolve Pooideae as circumscribed by Clayton and Renvoize (1986), but expanded to include Anisopogon and Diarrhena, as monophyletic. Within Pooideae, three groupings at the level of tribe or above are resolved as monophyletic by all three analyses: Meliceae, Agrostideae, and the pairwise combination of Lygeum and Nardus.

As just noted, all three analyses resolve both the PACC clade and Pooideae as monophyletic, each with identical contents. All three analyses also resolve a larger monophyletic grouping that consists of these two clades plus Brachyelytrum, but two different relationships are detected among these three lineages. The restriction site data place Brachyelytrum as sis-
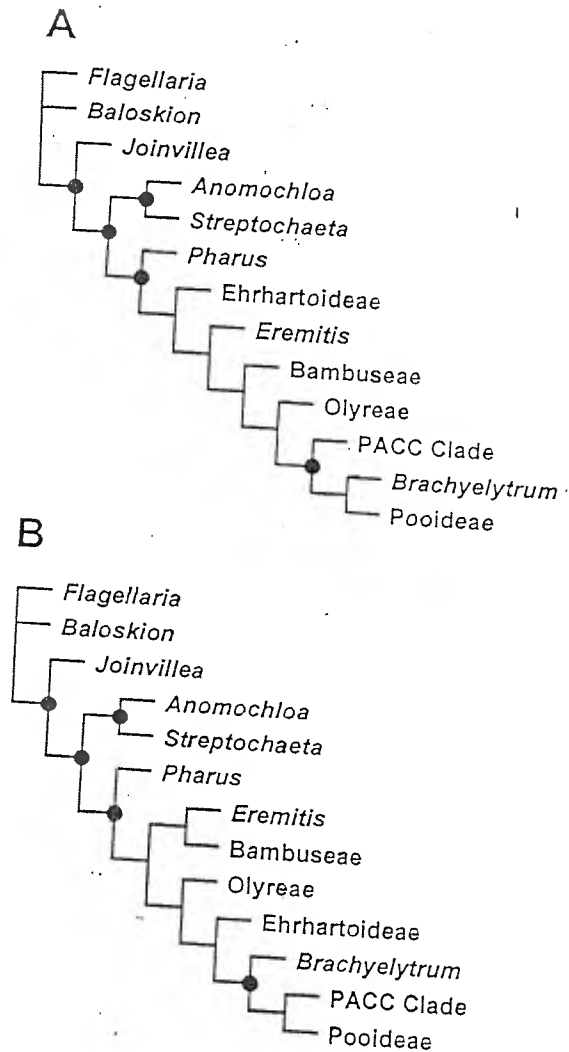
Fig. 4. Two alternative sets of higher-level relationships within Poaceae resolved by equal-weighted simultaneous analysis of 364 informative restriction site characters and 42 informative structural characters (cf. Table I, Appendices 1–3, Fig. 3). Each topology was resolved in six of the 12 most-parsimonious trees; solid circles mark clades common to both sets of relationships (cf. Fig. 3). A. Alternative Topology 1 (early-diverging Ehrhartoideae, *Brachyelytrum* sister of Pooideae). B. Alternative Topology 2 (late-diverging Ehrhartoideae, PACC clade sister of Pooideae).
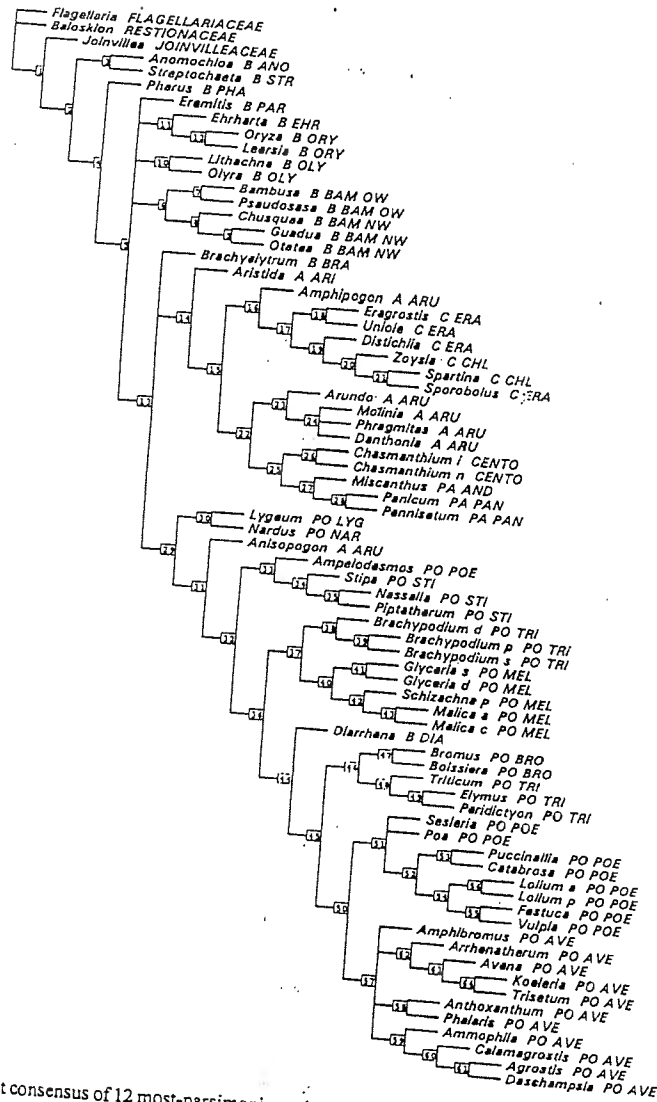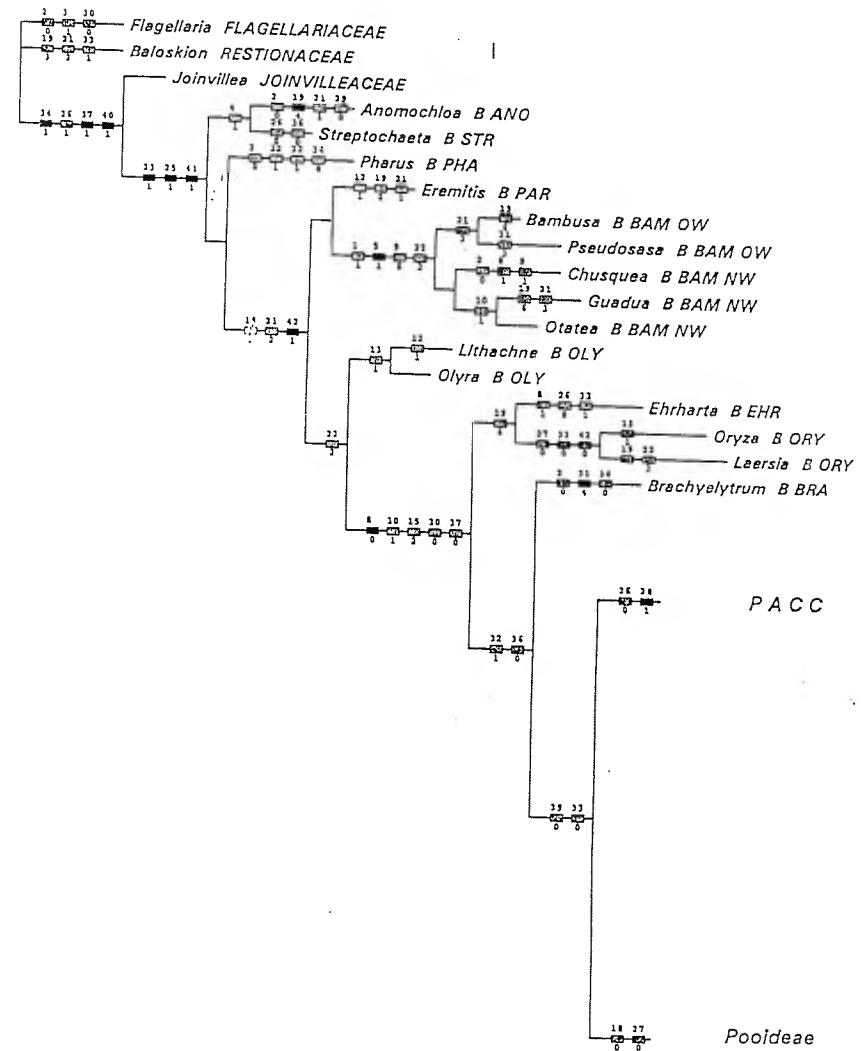
Fig. 5. Basal portion of one of 12 most-parsimonious cladograms (1468 steps, CI = 0.28, RI = 0.70) for 72 representative accessions of grasses and three outgroup taxa, obtained by equal-weighted simultaneous analysis of 364 informative restriction site characters and 42 informative structural characters (cf. Table I, Appendices 1–3, Figs. 3, 6–7); this is one of six trees with Alternative Topology 2 (Fig. 4). Transformations of structural characters are marked as bars on internodes, with the number above each bar signifying the character number, and the one below the bar signifying the apomorphic state of the transformation (Appendix 2); solid bars signify unique origins of states (whether or not a later transformation occurs) and hatched bars signify parallel origins and secondary transformations.

Fig. 6. Part of one of 12 most-parsimonious cladograms for 72 representative accessions of grasses and three outgroup taxa, obtained by equal-weighted simultaneous analysis of 364 informative restriction site characters and 42 informative structural characters (cf. Table I, Appendices 1–3, Figs. 3–5, 7); portion depicted here is the PACC clade. See caption of Fig. 5 for further information.

ter of Pooideae, with the PACC clade as sister of that pairwise grouping, while the structural data place the PACC clade as sister of Pooideae, with *Brachyelytrum* sister of that pairwise grouping. With the combined data set these two alternative relationships are equally parsimonious, and each occurs in half of the most-parsimonious trees. The constant resolution of this group of three lineages leaves a similarly constant paraphyletic assemblage of all remaining elements (i.e., a broadly defined Bambusoideae) as early-diverging lineages in the grass family. In all three consensus trees (Figs. 1–3), *Anomochloa, Streptochaeta,* and *Pharus* are among the earliest lineages to diverge from the line that includes most other grasses. Analysis of the structural characters resolves *Streptochaeta* as sister of all other grasses, with *Anomochloa, Pharus,* and *Eremitis* diverging separately from the next node, while the other two analyses resolve a monophyletic grouping of *Streptochaeta* and *Anomochloa* as sister of all other grasses, and within that group, *Pharus* as sister of all remaining grasses. Bambuseae, Olyreae, and Oryzeae also are resolved by all three analyses, while Ehrhartoideae (i.e., Oryzeae plus *Ehrharta*) are resolved by restriction sites and by the combined data set, but not by the structural data set.

Although Alternative Topology 1·(of the combined analysis) corresponds to the overall structure supported by restriction sites alone (compare Figs. 1 and 4a), Alternative Topology 2 of the combined analysis is consistent with some but not all aspects of the relationships resolved by structural characters alone (compare Figs. 2 and 4b). Alternative Topology 2 resembles the relationships supported by structural characters in the placement of *Brachyelytrum* as sister of a clade that includes Pooideae and the PACC clade, but differs in the relationships resolved among the remaining taxa.

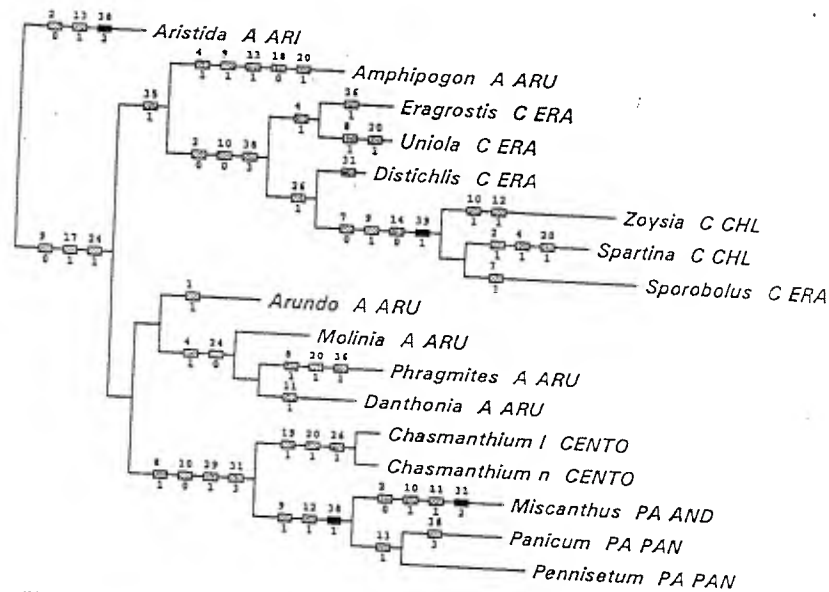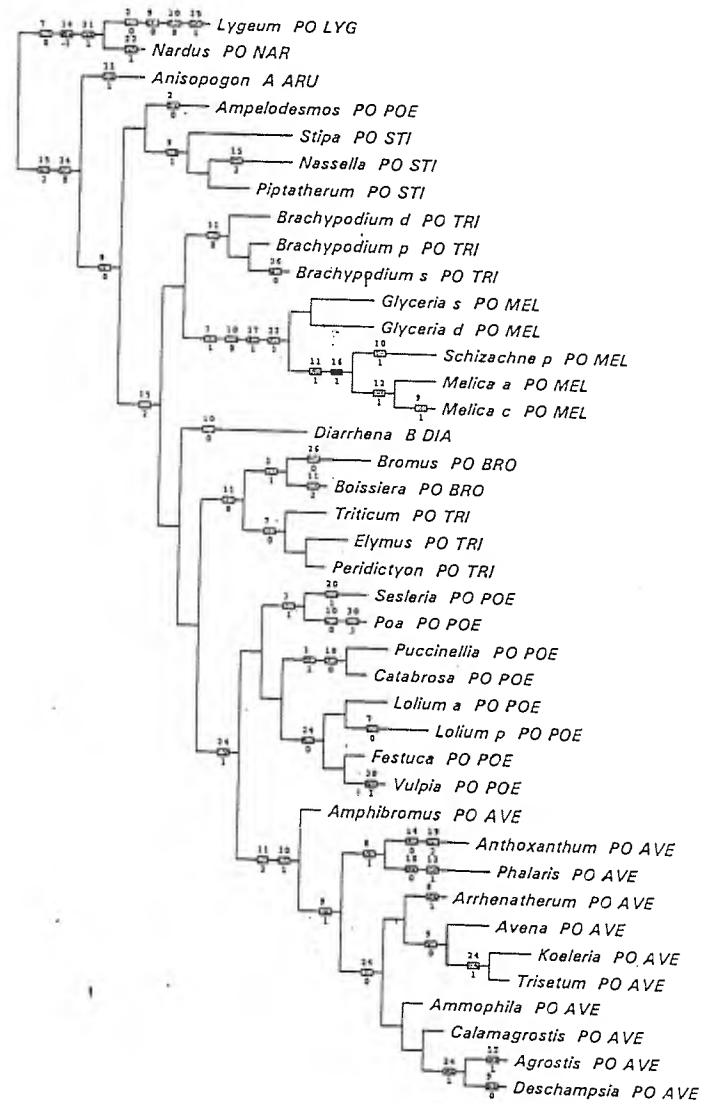Fig. 7. Part of one of 12 most-parsimonious cladograms for 72 representative accessions of grasses and three outgroup taxa, obtained by equal-weighted simultaneous analysis of 364 informative restriction site characters and 42 informative structural characters (cf. Table I, Appendices 1–3, Figs. 3–6); portion depicted here is subfamily Pooideae. See caption of Fig. 5 for further information.

Table III. Minimum character removal (MCR) scores and strict consensus bootstrap frequencies (as percentage) for 64 clades resolved by simultaneous analysis of structural and restriction site data.

Clade number[a]			MCR[b] score	Strict consensus bootstrap frequency (as percentage)[c]	
Combined data	Restriction site data	Structural data		Combined data	Restriction site data
1	1	1	++	94.9	98.1
2	2	2	++	95.8	95.5
3	3	—	++	89.7	82.4
4	4	—	++	83.6	76.7
5	5	—	++	70.8	41.1
6	10	7	++	80.6	42.3
7	11	—	++	98.3	98.8
8	12	—	++	63.7	77.9
9	—	—	++	57.4	54.5
10	14	6	++	67.4	61.5
11	6	—	++	74.6	63.2
12	7	12	++	92.6	82.0
13	15	14	+	37.5	9.6
14	16	16	++	97.6	94.9
15	—	17	+	41.4	26.2
16	—	26	+	22.1	11.7
17	19	—	++	98.0	97.5
18	20	—	++	72.8	72.8
19	21	—	++	91.5	94.7
20	22	—	++	85.6	79.2
21	23	—	++	92.3	99.0
22	—	—	+	9.2	4.9
23	—	—	+	23.3	16.6
24	—	—	+	38.7	20.3
25	17	21	++	77.6	61.5
26	18	22	++	100.0	97.6
27	—	23	++	60.8	37.3
28	—	24	++	52.1	26.6
29	25	32	++	84.7	67.8
30	26	38	++	99.6	98.8
31	27	—	++	88.3	81.6
32	28	—	+	22.2	20.1
33	29	—	++	91.9	94.2
34	30	—	+	44.6	44.0
35	31	—	+	55.7	54.0
36	32	—	++	42.5	34.1
37	33	—	+	38.4	39.5
38	34	—	++	100.0	100.0
39	35	—	++	99.8	100.0
40	36	33	++	100.0	100.0
41	37	—	++	97.8	97.3
42	38	—	+	53.3	58.5
43	39	35	++	91.1	85.0
44	40	—	+	21.5	31.0
45	41	—	++	66.5	80.1
46	42	—	++	99.9	99.9
47	43	—	++	94.8	93.9

Table III (continued)

Clade number[a]			MCR[b] score	Strict consensus bootstrap frequency (as percentage)[c]	
Combined data	Restriction site data	Structural data		Combined data	Restriction site data
48	44	—	++	97.5	93.1
49	45	—	+	45.0	50.6
50	46	—	++	98.2	98.5
51	47	—	++	93.3	93.4
52	49	—	+	31.4	51.1
53	50	—	++	99.6	99.7
54	51	—	++	78.7	70.8
55	53	—	++	93.9	92.6
56	52	—	++	99.8	100.0
57	54	40	++	99.4	99.2
58	59	—	++	97.8	95.6
59	60	—	++	98.6	99.6
60	61	—	+	72.2	85.8
61	62	—	++	97.8	97.5
62	55	—	++	78.4	87.3
63	56	—	++	58.1	59.9
64	57	—	++	92.1	87.3

[a]Numbers correspond to those in Figures 3 (combined analysis of restriction site and structural data), 1 (analysis of restriction site data), and 2 (analysis of structural data with monophyly of grasses constrained), respectively; a dash signifies absence of a given clade in strict consensus obtained from an analysis.

[b]Scores are based on analysis of the combined data set; "+" signifies MCR score of 0 (clade is not resolved in all consensus trees obtained from analyses with single characters removed); "++" signifies MCR score ≥ 1 (group is resolved in all most-parsimonious trees obtained when any single character is removed from data set).

[c]Two bootstrap numbers are provided for each clade; the first was obtained by analysis of the combined data, the second by analysis of just the restriction site data.

5. Incongruence among Unweighted Analyses

The amount of incongruence within the restriction site data set is 913 steps (1277 steps in most-parsimonious trees minus 364 steps "total variation," or minimum possible number of steps if all characters were congruent), and the amount of incongruence within the structural data set (monophyly of grasses not constrained) is 106 steps (158 - 52); thus, the total amount of within-data-set incongruence, I_W, is 1019 steps. The total amount of incongruence in the combined data set, I_T, is 1052 steps ($1468 - [364 + 52]$), and the amount of incongruence between the two data sets, I_B, is $I_T - I_W = 1052 - 1019 = 33$ steps. The Mickevich/Farris incongruence index, I_{MF}, is $I_B/I_T = 33/1052 = 0.031$. This amount of incongruence falls at the low end of the range of other published figures, such as 0.153 (Rodman et al., 1996), 0.114 (Kluge, 1989), 0.052 (Uhl et al., 1995), and a range of 0.0083–0.0497 (Davis et al., in press).

The structural character set, when optimized on the 10 shortest trees obtained by analysis of the restriction site data, has a range in lengths of 191–197, a range in CI of 0.26–0.27, and range in RI of 0.68–0.69. The restriction site character set, when optimized on the 10,000

trees retained after unconstrained analysis of the structural character set, has a range in lengths of 1552–1748 steps, a range in CI of 0.20–0.23, and a range in RI of 0.54–0.61. Because this set of trees is not a complete set of most-parsimonious trees for the structural data set, the actual ranges in length, CI, and RI of the restriction site data on most-parsimonious trees for the structural data may be greater than the observed ranges; the ranges reported here, therefore, are minimum ranges.

The restriction site data require a minimum of 0 extra steps to be optimized on trees obtained by simultaneous analysis of the two data sets, relative to the number of steps on their own most-parsimonious trees (1277 in both cases); the restriction site data require a minimum of 22% more steps (1552 vs. 1277) to be optimized on trees obtained by analysis of the structural character set. The structural data require a minimum of 16% more steps (184 vs. 158) to be optimized on trees obtained by simultaneous analysis of the two data sets, and a minimum of 21% more steps (191 vs. 158) to be optimized on trees obtained by analysis of the restriction site character set.

6. Implied Weighting

Simultaneous analysis of the combined matrix of 364 restriction site characters and 42 structural characters, using implied weighting, resolved one most-parsimonious tree of fit 2589.4 (rescaled fit 0.41). The length of this tree, when the data are optimized as unweighted characters, is 1486 steps, or 18 steps (1.2%) more than the 1468 steps of trees obtained by unweighted analysis. Of these 1486 steps, 1302 are in the restriction site data (vs. minimum length of 1277 on shortest trees obtained by unweighted analysis of all data, an increase of 25 steps, or 1.9%, and versus 1277 steps on shortest trees obtained by unweighted analysis of just the restriction site data, for the same increase of 25 steps, or 1.9%). The remaining 184 steps are in the structural data; this represents no increase relative to the 184 steps on shortest trees obtained by unweighted analysis of all of the data, and an increase of 25 steps (15.8%) relative to the minimum length of 158 steps on shortest trees obtained by unconstrained and unweighted analysis of just the structural data.

The tree resolved by implied weighting (Fig. 8) is congruent in many respects with those obtained by unweighted simultaneous analysis of both character sets, but it also exhibits some unique elements. It resembles the unweighted analysis in resolving both Pooideae (including *Anisopogon* and *Diarrhena*) and the PACC clade as monophyletic and in resolving a monophyletic grouping of *Brachyelytrum*, Pooideae, and the PACC clade. It resembles Alternative Topology 2 in resolving *Brachyelytrum* as sister of the monophyletic grouping of Pooideae and the PACC clade within this group, and in placing Ehrhartoideae and Olyreae as successively less closely related lineages. Bambuseae are the next most closely related group, and the tree obtained by implied-weighting differs from other trees in uniting *Pharus* and *Eremitis* as sister taxa that together constitute a clade that is the next most closely related group. The two remaining grasses, *Anomochloa* and *Streptochaeta*, are again identified as sister taxa, and as in the results of all other analyses except that of the structural data, this clade is the sister of all other grasses, while *Joinvillea* is sister of the grasses.

Within the PACC clade, the tree obtained by implied weighting is congruent with that obtained by unweighted analysis in supporting a sister-group relationship between *Aristida* and a clade that includes all other elements in that group, and in resolving a monophyletic group in which a monophyletic Centhothecoideae is sister of a monophyletic Panicoideae. However, this tree differs in nesting Chloridoideae within a paraphyletic assemblage of all other Arundinoid elements (except *Anisopogon*, which is placed in Pooideae, in agreement with the

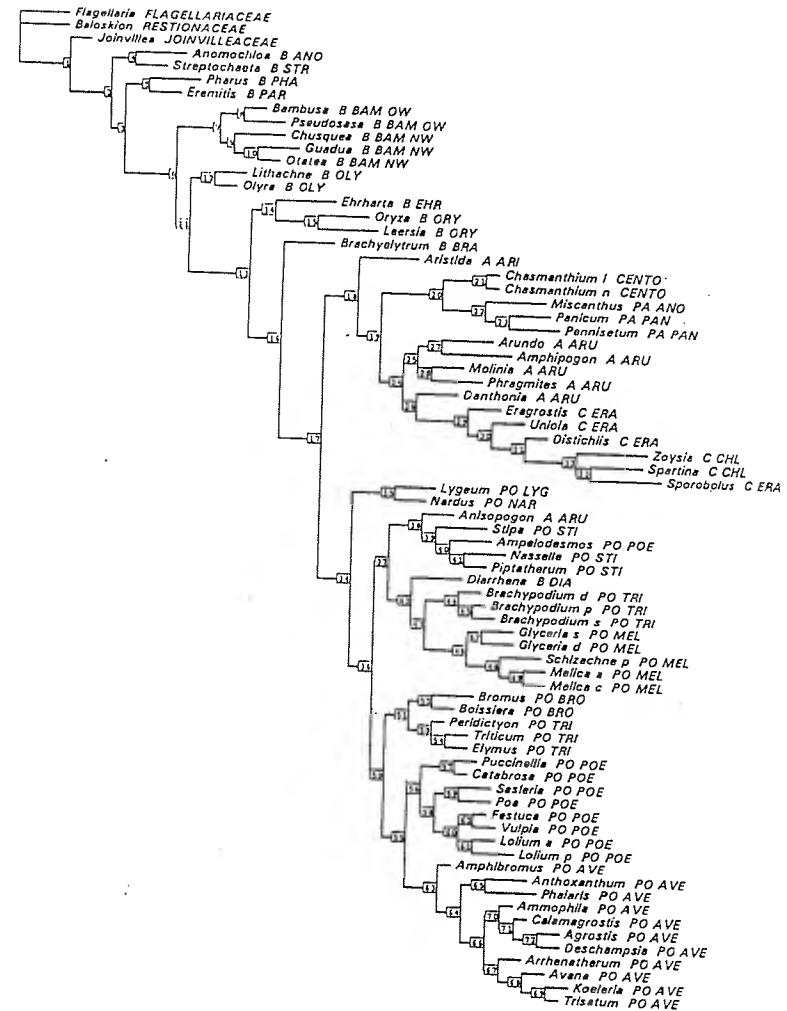Fig. 8. Single most-fit cladogram (fit 2589.4, rescaled fit 0.41) for 72 representative accessions of grasses and three outgroup taxa, obtained by implied-weighting parsimony analysis of matrix of 364 informative restriction site characters and 42 informative structural characters (cf. Table I, Appendices 1–3).

unweighted analysis). This assemblage of Chloridoideae and Arundinoid elements is sister of the clade that comprises Centothecoideae and Panicoideae.

Within Pooideae, the tree obtained by implied weighting is congruent with the results obtained by equal weighting in resolving a clade consisting of *Lygeum* and *Nardus* as sister of a clade that includes all other members of Pooideae. However, the results of implied weighting differ substantially with regard to the rest of the Pooideae. The equal-weighted analysis resolved a monophyletic grouping of Bromeae, Hordeeae, Poeae, and Agrostideae, and a pectinate series of four diverging lineages between that group and the clade that consists of *Lygeum* and *Nardus*. The implied-weighting analysis resolves the same grouping of Bromeae, Hordeeae, Poeae, and Agrostideae, but the sister of this clade is a clade that includes all other taxa of Pooideae except the grouping of *Lygeum* and *Nardus*. Within this unique group there is a sister-group relationship between a clade that includes *Anisapagan* as sister of *Ampeladesmos* and Stipeae (*Ampelodesmos* is placed among elements of a paraphyletic Stipeae), and a second clade in which *Diarrhena* is sister of a clade that consists of Brachypodieae as sister of Meliceae.

V. Discussion

A. SCORING OF STRUCTURAL CHARACTERS AND USE OF EXEMPLAR TAXA

As noted above, Watson and Dallwitz (1992) was the principal source of the structural character data employed here. This book, derived from an exhaustive database of the grass literature, represents a monumental achievement and serves as a basic source for future studies. The same database was used previously for the development of character sets for cladistic analyses of the grass family (Kellogg & Campbell, 1987), and of subfamilies Pooideae, Bambusoideae, and tribe Andropogoneae (i.e., Saccharineae) (Kellogg & Watson, 1993). However, as Kellogg and Watson (1993) note, there are limitations to the use of these data directly for the purpose of phylogenetic analyses. Any such compendium of a vast literature must be used with caution. Indeed, we found a few contradictions, errors, and omissions, relative to the primary literature (Appendix 2). A different sort of problem is that the character definitions in the book were intended chiefly for the purpose of identification, rather than as homology assessments, as is appropriate for phylogenetic analysis. Thus, we evaluated character and state definitions with the latter purpose in mind.

Another problem encountered in the use of Watson and Dallwitz (1992) is that of nonmonophyletic genera. Few genera have been studied from a phylogenetic perspective and it is clear that many conventionally recognized genera of Poaceae and other families will be found to be nonmonophyletic as such studies are conducted. There is evidence that two genera in the present study are not monophyletic as circumscribed by Watson and Dallwitz. *Bambusa* Schreb. s.l., as recognized by Watson and Dallwitz (1992) and Clayton and Renvoize (1986), is divided here into *Bambusa* (Old World) and *Guadua* Kunth (New World), which were placed in separate subtribes by Soderstrom and Ellis (1987). That determination is further substantiated by the study of Clark et al. (1995), and by the present analysis, for neither of these analyses resolves *Bambusa* and *Guadua* as sister taxa (Fig. 3). Secondly, the circumscription of *Festuca* L. has recently been refined. *Festuca* subg. *Schedonorus* (P. Beauv.) Peterm., including the *F. arundinacea* complex, belongs in *Lolium* according to Darbyshire and Warwick (1992), and that relationship also is supported by the present analysis (Fig. 3). In addition to the previous two cases, *Pariana* Aubl., as recognized by Watson and Dallwitz (1992), may not be monophyletic. It is divided into *Pariana* and *Eremitis* by Clayton and Renvoize (1986) and by Hollowell (1987), and is represented here by *Eremitis*.

The use of multispecies taxa with multiple polymorphic characters as individual "composite terminals" in cladistic analyses influences the results in unpredictable ways (Nixon & Davis, 1991). Among the more pernicious effects is the possibility for most-parsimonious resolutions to imply character state combinations that have never been observed and that may never have existed; the determination that such character combinations exist or ever existed, and the secondary effects on tree structure implied by such combinations, are, of course, artifactual. For example, if a genus has a [01] polymorphism for one character and a [01] polymorphism for a second character, four potential combinations of individual states are implied, but it is possible that only two combinations exist today, or ever existed. If an unobserved combination is most-parsimonious in the context of the complete data set, which may include any number of additional polymorphisms in other characters and taxa, the effect of polymorphism scoring on the resulting tree structure may be dramatic. These effects can be manifested even if all scored polymorphisms reflect actual polymorphisms of the monophyletic terminals that are sampled (e.g., if an actually monophyletic *Festuca* were to be polymorphic for awn presence/absence). The potential problem is magnified if some of the composite terminals actually represent separate lineages that properly belong in different positions in a phylogenetic tree, as would have been the case with "*Bambusa*" and "*Festuca*" in the present analysis, had they been treated as individual terminals. Thus, the use of polymorphism coding for multispecies taxa that are used as terminals must be regarded as an expedient. In the present analysis we eliminated many generic polymorphisms, as reported by Watson and Dallwitz (1992), by checking specimens and searching the literature for data on the exemplar species in the study. A further advantage to scoring all characters as they occur in exemplar taxa is that the procedure improves the comparability of indexes of support and character homoplasy between structural and molecular data sets.

B. ANALYSES OF MOLECULAR DATA SETS

Cladistic analyses of a variety of molecular data have been used in previous studies to analyze the major internal phylogenetic structure of the Poaceae. Chloroplast DNA restriction sites have been used previously in studies of the phylogeny of grasses by Soreng et al. (1990), Davis and Soreng (1993), Yaneshita et al. (1993), and Duvall et al. (1994). Nucleotide sequences of a variety of genes of the chloroplast genome have been used as follows: *rbc*L by Doebley et al. (1990), Barker et al. (1995), and Duvall and Morton (1996); *rpo*C2 by Cummings et al. (1994); *rps*4 by Nadot et al. (1994); *ndh*F by Clark et al. (1995); and *mat*K by Hongping Liang and Hilu (1996). Nucleotide sequences of genes of the nuclear genome have been used as follows: rRNA by Hamby and Zimmer (1988, 1992) and by Kellogg and Linder (1995: 531, a reanalysis of Hamby and Zimmer's data, with the addition of unpublished data for *Brachyelytrum* provided by Issel and Zimmer); and *Adh* by Morton et al. (1996; also see Gaut et al., 1996). The analyses based on cpDNA gene sequences and restriction sites all estimate the history of the same nonrecombining, nonreticulating organelle lineage, while *Adh* is a low-copy-number nuclear-encoded gene that may experience recombination, and rRNA is a family of multiple-copy nuclear genes that are subject to concerted evolution, and for which evolutionary patterns may be complex (e.g., Wendel et al., 1995; Cronn et al., 1996).

Some general conclusions may be drawn from these molecular studies (note that here and in the following pages we mention genera and tribes that are not part of the present study but that provide a broader context for the discussion of phylogeny and character state distributions in the grasses). First, there is broad support for the monophyly of certain ma-

jor groups, including Pooideae and the PACC clade, and within the latter, Panicoideae and Chloridoideae. In contrast, Bambusoideae, as recognized in classifications such as those of Clayton and Renvoize (1986), Watson and Dallwitz (1992), Soderstrom and Ellis (1987), and Tzvelev (1989), are paraphyletic, because the PACC clade and Pooideae arise from among elements assigned to Bambusoideae in those classifications (although different arrangements have been resolved by the various data sets). Some elements of a broadly defined Bambusoideae are resolved within or adjacent to the Pooideae or PACC clades, and these two groups can be expanded in membership to accommodate those elements. In particular, Diarrheneae and Phaenospermateae Renvoize & Clayton, two tribes included in Bambusoideae by Clayton and Renvoize (1986) or Watson and Dallwitz (1992), appear to belong in Pooideae, and one (Centotheceae) appears to belong in the PACC clade, while Brachyelytreae are resolved as closely related to the Pooideae. Among the remaining elements of a broadly defined Bambusoideae, the Bambuseae and Oryzeae (the most frequently sampled tribes of this group), plus the Anomochloeae, Streptochaeteae, Phareae, Olyreae, Parianeae, Ehrharteae, and *Streptogyno* P. Beauv. (the sole genus of Streptogyneae C. E. Calderón & Soderstr.), do not appear to belong within the PACC clade or in Pooideae, though relationships resolved among these elements vary among treatments, and some of these groups are in some cases resolved as closely related to Pooideae or the PACC clade.

C. PHYLOGENETIC STRUCTURE OF THE GRASSES

1. Support for Groups Resolved by the Present Analysis

One of the 12 most-parsimonious trees obtained by simultaneous analysis of the restriction site and structural character sets is illustrated with transformations in structural characters optimized on the internodes (Figs. 5–7; also see consensus tree, Fig. 3). This tree is one of the six with Alternative Topology 2 (late-diverging Ehrhartoideae), in which subfam. Ehrhartoideae is sister of the clade that comprises *Brochyelytrum* as sister of a subclade in which Pooideae and the PACC clade are sister groups.

The consensus tree derived by analysis of just the structural character set, constrained to resolve Poaceae as monophyletic, is poorly resolved within the Pooideae, and also includes a polytomy near the base of the family (Fig. 2). The consensus tree derived by analysis of just the restriction site character set is almost completely resolved except within the PACC clade (there is also a polytomy within the Bambuseae and another within the Agrostideae). As detailed above, the consensus obtained by simultaneous analysis of both character sets has five polytomies (Fig. 3); relationships within the PACC clade are more fully resolved by the combined character sets than by either of them separately (64 clades resolved by combined data sets, 62 by restriction sites, 44 by constrained analysis of structural characters), but polytomies 4 and 5 (see section III.C.3) represent a lesser degree of resolution than obtained with the restriction site data. Thus, the effect of combining the data is to add resolution in some areas and to decrease it elsewhere.

2. Comparison of Results of Simultaneous Analysis with Previous Classifications and Hypotheses of Phylogeny of the Grasses

The present results are congruent in many respects with modern classifications of the grasses. Of the two most comprehensive recent treatments of the family—namely, Clayton &

Renvoize, 1986, and Watson & Dallwitz, 1992—the present results are in greater agreement with the former. All of the taxa placed in Chloridoideae, Panicoideae, and Pooideae in those classifications, and sampled in the present study, were also placed in those groups by the present analysis. The Bambusoideae are circumscribed similarly in both of those classifications, except that Clayton and Renvoize (1986) exclude Centotheceae. The present results do not support a monophyletic Bambusoideae in the sense of either of these treatments, but among the various elements sometimes assigned to that group, the placement of Centothecoideae within the PACC clade, as sister of Panicoideae, is inconsistent with any circumscription of a monophyletic Bambusoideae that includes Centothecoideae and does not also include most or all elements Panicoideae, Arundinoideae, and Chloridoideae.

Other tribes of Bambusoideae recognized by Watson and Dallwitz (1992) and Clayton and Renvoize (1986), and represented by more than one exemplar in the present analysis, are resolved as monophyletic, but even after removal of Diarrheneae to Pooideae and of Centotheceae to the PACC clade, the remaining elements of Bambusoideae do not constitute a monophyletic group.

Additional incompatibilities among the present results and classifications by Clayton and Renvoize (1986) and Watson and Dallwitz (1992) reflect the broad concept of Arundinoideae and the narrow concept of Pooideae adopted by Watson and Dallwitz (1992). Watson and Dallwitz do acknowledge that the Arundinoideae they circumscribe is likely to be polyphyletic, and the present results are consistent with that determination. Clayton and Renvoize (1986) attempted to circumscribe a natural Arundinoideae, in part by placing within Pooideae several tribes and genera (e.g., *Ampelodesmos*, Lygeeae, Nardeae, Stipeae, and Aveneae [i.e., Agrostideae] subtr. Duthieinae Potztal) that have characteristics thought to have been present among early-diverging elements of Pooideae. The present results, based on sampling of the first four of these taxa, support the placement of all of them (including Duthieinae by implication), plus *Anisopogon*, within Pooideae. Even with all of these taxa removed from Arundinoideae, however, the present results also indicate that the more strictly circumscribed Arundinoideae that remain are still paraphyletic.

In comparing the present results to those obtained by other authors, it is necessary to consider the depth of sampling among studies. If the Pooideae and the PACC group represent two major monophyletic groups within the grass family, and if these two groups are closely related to each other and derived from among the various lineages of a broadly defined Bambusoideae, the deepest branches in the grass family are most likely to be resolved if the major sublineages of the Pooideae and the PACC clade are sampled, along with all major lineages assigned by various authors to Bambusoideae.

In the following discussion we consider the cladistic analyses of five molecular studies (Table IV) that have included members of at least six of the six to seven major subfamilies widely recognized in classifications: Barker et al. (1995; *rbcL* sequences); Duvall and Morton (1996; *rbcL* sequences); Clark et al. (1995; *ndhF* sequences); Hongping Liang and Hilu (1996; *matK* sequences); and the present cpDNA restriction site analysis (which supersedes Davis & Soreng, 1993). One cladistic analysis based on structural characters of grasses also is considered. Kellogg and Campbell (1987) presented a taxonomically comprehensive cladistic analysis wherein individual genera of Arundinoideae were used as terminals, and Bambusoideae, Chloridoideae, Panicoideae, and Pooideae were constrained, in large part, as putatively monophyletic composite taxa.

Despite a great deal of consensus among the results of DNA analyses, one area in which differences remain is that of the composition and relationships among three major groups or assemblages (i.e., Bambusoideae, Pooideae, and the PACC clade) that have been proposed in

Table IV. Sampling breadth in molecular analyses of the grasses in which representatives were included from of at least six of seven widely recognized subfamilies [the six recognized by Clayton and Renvoize (1986) plus Ehrhartoideae as circumscribed to include Ehrharteae and Oryzeae].

Authors	Subfamilies[a]							
	Arundinoideae (4)	Centothecoideae (1)	Chloridoideae (5)	Panicoideae (7)	Pooideae (10)	Ehrhartoideae (2)	Bambusoideae (11)	Totals (40)
Soreng & Davis, present analysis	7 (2)	2 (1)	6 (2)	3 (2)	38 (8)	3 (2)	13 (8)	72 (25)
Clark et al., 1995	6 (4)	2 (1)	4 (2)	5 (3)	4 (4)	3 (2)	21 (9)	45 (25)
Barker et al., 1995	14 (3)	1 (1)	2 (2)	7 (3)	6 (4)	2 (1)	1 (1)	33 (15)
Duvall & Morton, 1996	2 (1)	0	3 (1)	6 (2)	5 (3)	3 (1)	5 (3)	24 (11)
Hongping Liang & Hilu, 1996	2 (2)	0	6 (3)	4 (2)	3 (3)	1 (1)	1 (1)	17 (12)

[a] Total number of tribes recognized by Clayton and Renvoize in each subfamily is listed in parentheses after the subfamily name in the header, except that the two tribes of Ehrhartoideae are subtracted from the 13 recognized by Clayton and Renvoize (1986) in Bambusoideae. Number of species sampled in each study is followed by number of tribes represented (in parentheses).

classifications and resolved, to varying degrees, in phylogenetic analyses. The present study and the analysis of *ndhF* sequences (Clark et al., 1995) sampled broadly in Bambusoideae s.l. (16 and 24 taxa, respectively, including Ehrhartoideae, *Brachyelytrum*, *Diarrhena*, and *Phaenosperma*). In the present analyses based on the restriction site characters and on both sets of characters, and in the analysis of *ndhF* sequences, *Anomochloa* and *Streptochoeta* are resolved as the solitary elements of a clade that is the sister group of all other grasses, and within the latter group *Pharus* is the sister of all remaining grasses (Figs. 1, 3, 4). The consensus tree of the present structural character analysis (Fig. 2) resolves similar but not identical relationships at this juncture: *Streptochaeta* diverges first, followed by a polytomy of *Anomochloa*, *Pharus*, *Eremitis*, and a clade that includes all other grasses. Of these four genera or the tribes they represent, Duvall and Morton (1996) included *Anomochloa*, and it was resolved as the sister of all other grasses in their study. None of these genera is represented as an individual terminal in the other molecular studies. Various authorities had previously identified *Anomochloa*, *Streptochaeta*, and *Pharus* as among the "most primitive" extant grasses (e.g., Čelakovský, 1889; Arber, 1929; Roshevits, 1937; Stebbins, 1956; Tateoka, 1957; Soderstrom, 1981). Indeed, Nakai (1943) placed *Anomochloa* and *Streptochaeta* in their own families, and Clifford (1961) excluded *Anomochloa* from Poaceae. Two structural variants of the chloroplast lend additional support to the early divergence of these grasses: 1) a 15 bp insertion in the *ndhF* gene, present in other grasses sampled but absent in *Anomochloa*, *Streptochaeta*, *Pharus*, *Leersia*, *Oryza*, and nongrasses (Clark et al., 1995); and 2) a 740 bp intron in *rpoC1*, present in *Anomochloa*, *Streptochaeta*, and nongrasses, and absent in other grasses sampled (Clark et al., 1995; R. Wallace et al., unpubl. data).

If *Anomochloa*, *Streptochaeta*, and *Pharus* are recognized as representatives of the earliest lineages to diverge from the one that includes all other grasses, they must be excluded from the Bambusoideae if that subfamily is to be monophyletic. The first two of these genera can be accommodated in Anomochlooideae, and the latter in Pharoideae (Clark & Judziewicz, 1996). The present results also favor the exclusion from Bambusoideae of *Diorrhena* and *Brachyelytrum*, both of which were included in Bambusoideae by Clayton and Renvoize (1986) and Watson and Dallwitz (1992), who suggested affinities of these taxa with Oryzeae and *Ehrharta*. The present analysis, like that of Clark et al. (1995), places *Diarrhena* within Pooideae. The present analysis also resolves *Brachyelytrum* either as the sister group of Pooideae (a relationship previously detected by Clark et al. [1995] and Kellogg and Linder [1995]) or as the sister group of a clade that includes Pooideae plus the PACC clade. The first of these alternative positions for *Brachyelytrum* is supported by the restriction site data (Figs. 1, 4), and the second by the structural character data (Figs. 2, 4). In the first of these positions *Brachyelytrum* could be accommodated taxonomically either as a member of Pooideae or as the sole genus of a separate subfamily. In the second of these positions it would be appropriate to recognize a separate subfamily for *Brachyelytrum*. Clark et al. (1995) also found a third genus sometimes assigned to Bambusoideae, *Phaenosperma* (not sampled in the present analysis), to be nested within Pooideae. Henceforth in this discussion we include *Diarrhena* and *Phaenosperma* in Pooideae and consider *Brachyelytrum* as an element of a clade that also includes Pooideae and the PACC clade (Fig. 3, node 13).

Some of the most-parsimonious trees resolved by the present analysis resemble previous results based on *rbcL* (Barker et al., 1995; Duvall & Morton, 1996) and *matK* (Hongping Liang & Hilu, 1996) in resolving Pooideae plus the PACC clade as a monophyletic grouping. The analysis of *ndhF* (Clark et al., 1995) resolves Pooideae and the PACC clade as lineages arising separately from among elements of a broadly defined Bambusoideae. After the initial divergences of *Anomochloa* plus *Streptochaeta*, and then *Pharus*, the PACC clade arises as

the sister group of a clade that the authors designated the "BOP Clade," which comprises additional elements often assigned to Bambusoideae, Oryzoideae (i.e., Ehrhartoideae; and including *Streptogyna*, which was resolved as the sister of Oryzeae), and Pooideae (with *Brachyelytrum* sister of a clade that included all other elements of the subfamily), with relationships unresolved among these three groups. Clark et al. (1995) indicated that the trichotomy within the BOP clade in the consensus tree reflects two alternative equally parsimonious structures; in one tree Pooideae and Bambuseae were resolved as sister taxa, with Ehrhartoideae as the sister group of that clade, and in the other Bambuseae and Ehrhartoideae were resolved as sister taxa, with Pooideae as the sister group of that clade. The analysis by Duvall and Morton (1996) resolved one most-parsimonious tree, in which *Anomochloa* is the sister of all other grasses, and within the latter group, a clade that consists of Olyreae and Bambuseae is the sister of all remaining grasses. Within the latter group Ehrhartoideae were resolved as the sister group of a clade that consists of Pooideae plus the PACC clade. Other studies with more limited sampling among Bambusoideae s.l. favor Pooideae as sister group of a clade that includes Bambuseae, Oryzeae, and the PACC clade, or Oryzeae alone as sister group of the PACC clade (cpDNA restriction sites: Yaneshita et al., 1993; rRNA: Hamby & Zimmer, 1992; *rps4*: Nadot et al., 1994; *rbcL*: Doebley et al., 1990), or Pooideae (Morton et al., 1996). A consistent result of these molecular analyses is that both Pooideae and the PACC group are resolved as monophyletic. The five most comprehensive studies (Table IV) identify the Bambusoideae s.l. as paraphyletic, while the PACC clade and Pooideae (whether or not they are resolved as sisters of each other) are nested among the earliest diverging grass lineages.

Two narrower circumscriptions of Bambusoideae, Tzvelev's (1989) and Soderstrom and Ellis's (1987), also appear to define paraphyletic groups, as judged by the results of the *ndhF* analysis (Clark et al., 1995) and the present analysis. Tzvelev (1989) restricted the Bambusoideae by excluding not only Diarrheneae, Brachyelytreae, and Centotheceae but also *Ehrharta*, Oryzeae, Phyllorhachideae, and Phaenospermateae. Soderstrom and Ellis (1987) excluded all of these tribes except Oryzeae, and possibly Phyllorachideae, from their Bambusoideae. These treatments still circumscribe groups that would be recognized as paraphyletic, for Tzvelev included Anomochloeae, Streptochaeteae, and Phareae within the Bambusoideae, and Soderstrom and Ellis included these three tribes plus Oryzeae.

The placement of tribe Centotheceae is another area in which there is conflict between the results of phylogenetic studies and existing classifications (if it is intended that recognized taxa be monophyletic). Watson and Dallwitz (1992) place Centotheceae in Bambusoideae supertribe Oryzodae, while Clayton and Renvoize (1986) place the tribe its own subfamily, Centothecoideae, as a close relative of Chloridoideae, within a more inclusive group that is largely equivalent in composition to the PACC clade. The present results do place Centotheceae in the PACC clade, but rather than with Chloridoideae the tribe is resolved as sister group of Panicoideae (or possibly nested within Panicoideae), as previously resolved by Barker et al. (1995) and Clark et al. (1995). The present results also substantiate the conclusions of Yates (1966) that *Chasmanthium* and *Uniola* are not closest relatives.

Like the Bambusoideae s.l., many independent lines of evidence suggest that the Arundinoideae are not monophyletic. Four of the five major molecular analyses (Table IV) resolve a monophyletic PACC group that includes a nonmonophyletic Arundinoideae (minus a few disparate elements). The analysis of structural characters by Kellogg and Campbell (1987) also resolved a nonmonophyletic Arundinoideae, but all other grasses except Pooideae (i.e., the other elements of the PACC clade plus Bambusoideae s.l.) were nested among the Arundinoids. A complication in any discussion of these relationships is the broad circumscription of Arundinoideae by Watson and Dallwitz (1992). Even after several elements included among

the Arundinoids by those authors are removed from consideration (i.e., *Ampelodesmos*, *Anisopogon*, *Lygeum*, *Nardus*, Stipeae, and probably a few other taxa; see below), the remaining taxa within the PACC clade still appear to be paraphyletic. The Arundinoideae, as more narrowly circumscribed by Clayton and Renvoize (1986), and with *Anisopogon* again removed, are similarly paraphyletic, in that Chloridoideae, Centothecoideae, and Panicoideae arise from among elements of that subfamily. In the trees obtained in the present study by simultaneous analysis, as in the results of the *ndhF* analysis, *Aristida* is the sister of all other members of the PACC clade, and the latter group includes two lineages, one of them including Chloridoideae, the other including Centothecoideae and Panicoideae, with a set of Arundinoids as early-diverging elements within each of the two lineages.

If attention is restricted to Arundinoid taxa that fall within the PACC clade, relationships still are complex, partly because different analyses have sampled different Arundinoid taxa, and partly because there is conflict among the results obtained by the various analyses. In the present study, *Amphipogon* is resolved as sister of a monophyletic Chloridoideae by simultaneous analysis of all characters, and as described above, some of the alternative relationships resolved by analysis of the restriction site data place various additional Arundinoid elements as close relatives of Chloridoideae; analysis of the structural data places *Amphipogon* among genera of Chloridoideae. Clark et al. (1995) included *Micraria* F. Muell. (and not *Amphipogon*) in their study, and resolved that genus as the sister group of a monophyletic Chloridoideae. The analysis of *rbcL* variation by Barker et al. (1995) includes a broader sampling of Arundinoid elements (14 taxa), and sheds additional light on this set of grass taxa. The sampling in that analysis was guided by the separate analysis of *rpoC2* sequences of nearly all of the circa 40 genera of the Arundinoideae (Barker, 1995). With the *rbcL* data Barker et al. (1995) resolve Aristideae as the sister group of a subclade that consists of Danthonieae Zotov (a tribe subsumed in tribe Arundineae by Clayton and Renvoize, 1986), *Centrapodia* Rchb., and Chloridoideae. With the *rpoC2* data, however, Aristideae are resolved as one of three subclades within the PACC clade, with the second of the three subclades consisting of Danthonieae plus Chloridoideae, and the third including Arundineae (in a very restrictive sense), Panicoideae, and Centothecoideae (Barker, 1995); relationships among these three subclades of the PACC clade are unresolved.

In the present analysis four genera of Arundinoideae (*Arunda*, *Phragmites*, *Molinia*, and *Danthonia*; Fig. 3, node 23) are resolved as a monophyletic group that is sister of the clade that includes Centothecoideae and Panicoideae. A similar group was resolved by Clark et al. (1995; *Danthonia* not sampled), while Barker et al. (1995), who sampled Arundinoideae more deeply, resolved a somewhat different arrangement of Arundinoid taxa. They resolved a clade that includes *Arundo*, *Monachather* Steud., *Phragmites*, and *Moliniopsis* Hayata (included in *Molinia* by Clayton & Renvoize, 1986), as sister group to a clade that includes *Gynerium* Willd. ex P. Beauv. (tribe Arundineae sensu Clayton & Renvoize, 1986), *Thysanolaena* Nees (tribe Thysanolaeneae C. E. Hubb., Arundinoideae sensu Clayton & Renvoize, 1986, and Watson & Dallwitz, 1992), plus Centothecoideae and Panicoideae.

As noted earlier, the present analysis resolves a sister-group relationship between Centothecoideae and Panicoideae (or possibly a nesting of Centothecoideae among elements of Panicoideae). In analyses of nucleotide sequence variation of *ndhF* (Clark et al., 1995) and *rbcL* (Barker et al., 1995), and in a separate cpDNA restriction site analysis (Soreng & Davis, unpubl. data), Centothecoideae and Panicoideae are resolved in a clade that also includes *Thysanolaena*, and in the *ndhF* study the Panicoideae are polyphyletic. Clark et al. (1995) also resolved *Zeugites* P. Browne of Centotheceae in this clade, and demonstrated that *Chasmanthium* and *Zeugites* are closely related even if the tribe is questionably monophy-

letic. Thus, it appears from the small sampling to date that Centotheceae and Panicoideae either constitute the entirety of a monophyletic group or that the smallest monophyletic group that includes both of them also includes some Arundinoid elements.

There is a growing consensus that Pooideae are monophyletic if circumscribed to include a small number of "orphan" taxa in addition to the conventionally recognized elements. Analyses of cpDNA restriction site variation among 25 exemplar taxa of Pooideae (Soreng et al., 1990), 38 exemplars (the current study), and 72 exemplars (Soreng & Davis, unpubl. data), the latter representing 32% of the genera in the subfamily sensu Clayton & Renvoize (1986), have consistently resolved the subfamily as monophyletic under the broad circumscription proposed here. All four "core" tribes of Pooideae are resolved by the present analysis as individually monophyletic (if the additional tribe Seslerieae W. D. J. Koch is included in Poeae; see below), and the four tribes are united within a single clade in which Agrostideae and Poeae are sister taxa and together constitute the sister of a clade that includes Bromeae and Hordeeae as sister taxa (Fig. 3). This core group is included in Pooideae in all modern classifications, although its elements are grouped in different ways [e.g., compare the taxonomies of Clayton and Renvoize (1986) and Watson and Dallwitz (1992) with the present results]. As an apparently monophyletic assemblage, it would be reasonable to circumscribe the grouping of these four tribes as Pooideae, but several additional lineages are more closely related to this group than to the PACC clade or to any other major lineage, and they would have to be accommodated in some manner within a phylogenetic system, presumably as a set of additional subfamilies. Results of the present analyses suggest that Pooideae sensu Watson & Dallwitz (which includes the four "core" tribes plus Meliceae, Brachypodieae, and Seslerieae, the latter of which is nested within Poeae in the present results) remains monophyletic and nonoverlapping with the PACC clade if it is expanded to include *Lygeum*, *Nardus*, *Anisopogon*, *Ampelodesmos*, Stipeae, and *Diarrhena* (Fig. 3). If additional studies confirm a sistergroup relationship between *Brachyelytrum* and the clade that includes the four core tribes of Pooideae and these additional elements, it will be reasonable to include *Brachyelytrum* in Pooideae as well. *Phaenosperma* (not sampled in the present study) also should continue to be considered as a potential element of Pooideae (Clark et al., 1995). An inclusive circumscription of Pooideae also is supported by the studies of Davis and Soreng (1993, see their Fig. 1 and commentary, 15 taxa in Pooideae), Nadot et al. (1994, 16 taxa), Cummings et al. (1994, 4 taxa), Clark et al. (1995, 6 taxa including *Diarrhena* and *Phaenosperma*), Barker et al. (1995, 6 taxa), and Kellogg and Linder (1995, 6 taxa). This broad circumscription of Pooideae is not contradicted by the analysis of structural characters in the present study (monophyly of grasses constrained), nor by the analysis of Kellogg and Campbell (1987).

All of the taxa in the broadly circumscribed Pooideae just described, except the four core tribes and the additional tribe Brachypodieae Harz [included in Triticeae (i.e., Hordeeae) by Clayton & Renvoize, 1986], have been included in the Arundinoideae or Bambusoideae (or in equivalent groups) by one or more contemporary authors (e.g., Tateoka, 1957; Clayton & Renvoize, 1986; Watson & Dallwitz, 1992). In other words, the only tribes within clade 29 in Figure 3 that have consistently been included in Pooideae are Agrostideae, Brachypodieae, Bromeae, Poeae, and Hordeeae. The other taxa have been excluded from Pooideae in various classifications because they exhibit "anomalous" features, such as "small" chromosomes of base numbers $x = 8, 9, 10, 11,$ or 12, or in which the base number is indeterminate but it or chromosome size appears to depart from the "typical" states in core Pooideae of $x = 7$ and "large" chromosomes. The Diarrheneae include one or two genera and two to five species (if *Neomolinia* Honda & Sakis is included), and this tribe is placed in Bambusoideae by Clayton and Renvoize (1986) and Watson and Dallwitz (1992), but members of the group have some

features typical of Pooideae, or are polymorphic for features characteristic of Pooideae and other taxa sometimes assigned to Bambusoideae (Appendix 2). *Anisopogon* is similar to Stipeae in characters in addition to those used here, such as features of the guard cells (Kellogg & Campbell, 1987), and amino-acid composition of caryopses (Hock-Hin & Watson, 1987). *Phaenosperma* (Phaenospermateae, Bambusoideae, sensu Clayton & Renvoize and Watson & Dallwitz) also is placed within Pooideae by Kellogg and Campbell's (1987) analysis of structural characters, and by Clark et al.'s (1995) analysis of *ndhF*. None of the genera resolved in the Pooideae in the present analysis has been placed outside the group by phylogenetic studies other than that of Baum (1987), which placed Stipeae among members of the PACC clade.

D. STRUCTURAL CHARACTER EVOLUTION IN THE GRASSES

The associated occurrence of several morphological specializations of grasses leave little doubt that the family is monophyletic and highly derived (e.g., Dahlgren et al., 1985; Campbell & Kellogg, 1987). Simultaneous analysis of the restriction site and structural character sets provides a hypothesis of the history of diversification of the grasses that is demonstrably different from that obtained by analyzing these data individually, and that represents a best-supported overall hypothesis of relationships (Kluge & Wolf, 1993; Nixon & Carpenter, 1996). Each set of characters helps to resolve topological differences that are weakly supported or unresolved by individual analyses (Eernisse & Kluge, 1993; and Kluge & Wolf, 1993). At the same time, the resolution of two distinct and alternative sets of relationships among the deeper branches within the family highlights areas of conflict. We discuss the following character state distributions because of their support for major clades of grasses or because of their apparent adaptive significance.

Many of the structural character state changes mapped in Figs. 5–7 can be optimized on several nodes on the most-parsimonious trees, especially in the nexus where the two major clades, Pooideae and the PACC clade, diverge from among the earlier-diverging lineages. This could indicate that taxon density still is too low for confidence in exact character placement, or that for certain branching events there is a weak phylogenetic signal in the assembled data or among the extant organisms. It is possible that additional studies will not yield much improved resolution, as representation in the present study is already fairly comprehensive at the tribal and generic level (many tribes and genera being monotypic) around this nexus. On the other hand, some of the multiple optimizations around nodes are the results of polymorphisms and missing data. Whatever the reasons are for locally unstable character placements, and topological differences among studies, it is of interest to examine structural character transitions obtained from the simultaneous analysis in a broader context, as these may shed light on some controversial aspects of grass evolution. Distributions of states in taxa not included in this study, but which are of interest for extrapolation from the results, were verified in Watson & Dallwitz, 1992, unless otherwise stated.

1. Spikelets

In grasses it is a matter of convenience and tradition to identify as a spikelet the combination of one or more florets (each comprising a lemma, palea, lodicules, stamens, and pistil, or in certain grasses one or more of these parts absent) with two proximally situated bracts, the glumes (sometimes one or both absent). In the present analysis, grass spikelets with one fertile floret (char. 9) are present among all early-diverging herbaceous lineages just beyond the

point of divergence of *Anomochloa* and *Streptochaeta* (Fig. 3, nodes 4–13), and in *Chusquea* Kunth of the Bambuseae. Although the aggregations of flowers and bracts in *Anomochloa* and *Streptochaeta* cannot be identified readily as typical grasslike spikelets (see below), their flowers are solitary, or at least isolated by multiple bracts of questionable homology to "glumes," "lemmas," and "paleas." The first identifiable grass spikelets present after the divergence of these two genera have one fertile floret with a lemma, a palea, no rachilla extension (a rachilla is a primary axis that joins the florets and two glumes within a spikelet, and here it does not extend beyond the point of attachment of the fertile floret). The homology of "glumes" across the family is uncertain. There is no compelling reason to doubt the homology of glumes among Phareae, Parianeae, and Olyreae, within Pooideae, and within Arundinoids and Chloridoideae, and perhaps among these three major groups, and consequently there is no compelling reason not to call the terminal inflorescence units "true" grass spikelets in all of these groups. However, between this larger assemblage and Bambuseae, Ehrhartoideae, Centotheceae, and Panicoideae, the homology of glumes, and thus spikelets, is questionable (Clifford, 1987). In Oryzeae, glumes are rarely present. Although there is one fertile floret, there sometimes are one or two sterile florets below the fertile one that can be mistaken for glumes.

Spikelets with single fertile florets occur in early-diverging lines (Phareae) and in nearly all later-diverging herbaceous lines (Olyreae, Parianeae, Ehrharta, Oryzeae) before the point of divergence of *Brachyelytrum*, Pooideae, and the PACC clade, and this condition appears to be plesiomorphic in the Bambuseae. Spikelets of this sort appear to represent the plesiomorphic condition in genera and tribes around the nexus from which the earliest-diverging elements of the Pooideae and the PACC clades arise: *Anisopogon, Nardus, Phaenosperma* (the latter not in the present study, but placed here by the analysis of Clark et al., 1995), and Stipeae, among Pooideae; Aristideae, *Amphipogon*, and a few other genera not in the present study, among Arundinoids (see Kellogg & Campbell, 1987: figs. 28.2 & 28.3, for a similar result concerning the occurrence of a single floret and absence of rachilla extension around the nexus between Pooideae and Arundinoideae). *Brachyelytrum*, which also diverges somewhere in this nexus, also has a single floret, but is unusual among these taxa in possessing a rachilla extension. In the present analysis, spikelets with multiple fertile florets arise independently within tribe Bambuseae, Pooideae, and the PACC clade, and revert to the single fertile floret condition several times.

As difficult as it is to apply the term "spikelet" in a consistent way, it is even more difficult to define the "pseudospikelet." This term has been used to describe certain modified forms of the true grass spikelet, as well as various stages in the evolution of the proto-grass inflorescence, and has been applied to structures found in three groups of grasses. The first of these is the clade that consists of *Anomochloa* and *Streptochaeta* (Fig. 3, node 3). The other two occurrences of "pseudospikelets" are in the Bambuseae, where they are accounted for by independent origins in *Bambusa* and *Guadua* (Fig. 3), or in larger clades that include these genera. Given the relationships resolved in this study and by Clark et al. (1995)—specifically, the resolution of *Anomochloa* and *Streptochaeta* as elements of the earliest lineage of grasses to diverge from the line that includes all others—the pseudospikelets present in these taxa can be regarded either as a synapomorphy of this lineage (i.e., Anomochlooideae) or as a plesiomorphy of the grasses that is retained only in these two genera, though in modified form in *Streptochaeta* (Judziewicz & Soderstrom, 1989).

The origin of the grass spikelet has long been debated. Radically different modern proposals were presented by Soderstrom (1981) and Clayton (1990). One general interpretation of the spikelet is that it is homologous in most grasses, the exceptions being *Streptochaeta, Anomochloa*, and some Bambuseae (Clayton, 1990; for alternative interpretations, see Schuster,

1910; Núñez, 1968; Clifford, 1987). We suggest that models of the origin of the spikelet should take into account that *Streptochaeta* and *Anomochloa*, which do not have typical grass-type spikelets, are the sole living representatives of the earliest-diverging line from the one that includes all other grasses, and that *Joinvillea*, the apparent sister group of grasses, has a typical monocot panicle. The implications of this situation are 1) that the pseudospikelets of *Streptochaeta* and *Anomochloa* are not homologous with those of the Bambuseae, and 2) that the typical grass spikelet may have arisen in the lineage that includes all grasses except *Streptochaeta* and *Anomochloa*. In both Soderstrom's (1981) and Clayton's (1990) interpretations, pseudospikelets were derived from typical grass or proto-grass inflorescences, respectively, by contraction of lateral branches into condensed compound floral axes. Pseudospikelets have been interpreted as plesiomorphic for the grasses (Soderstrom, 1981), or possibly synapomorphic only within Bambuseae, and between *Anomochloa* and *Streptochaeta* (Clayton & Renvoize, 1986; Clifford, 1987). Clayton (1990) interpreted the spikelet of Bambuseae with two or more fertile florets and two glumes as plesiomorphic among all extant grasses, except possibly *Anomochloa* and *Streptochaeta*, and spikelets with single florets, as well as the pseudospikelets of Bambuseae, as independently derived from this basic arrangement. Soderstrom (1981: 43) viewed pseudospikelets of Bambuseae as proto-spikelet structures for the family, and true grass spikelets as having arisen from these. He further postulated the apomorphic nature of spikelets of the monoecious, herbaceous, early-diverging lineages that have only one floret per spikelet (Buergersiochloeae S. T. Blake, Olyreae, Parianeae, and Phareae). The present results are in conflict with Soderstrom's hypothesis, but do not fully conform to Clayton's interpretation.

The grass floret, or anthoecium, is an identifiable structure that appears to be homologous in most grasses. The presence of a palea that subtends the flower and lodicules, these together subtended by a sheathlike bract called a lemma, is the rule in the grasses. Paleas are first clearly identifiable, among the present sampling of grasses, in the clade that comprises all grasses except *Anomochloa* and *Streptochaeta* (Fig. 3, node 4). In the inflorescences of *Anomochloa* and *Streptochaeta*, the bracts that directly subtend the flowers do not appear to be paleas, and the homology of these or other bracts of pseudospikelets with prophylls in these genera is ambiguous (Soderstrom, 1981; Judziewicz & Soderstrom, 1989). Paleas (or prophylls, if these are considered homologous with paleas; Stebbins [1974] doubts this interpretation, but Gould [1975], Linder [1987], and Clayton [1990] favor it) that directly subtend flowers are absent in the flowers of the three nongrass taxa in the present study and in closely related families of Poales sensu Dahlgren et al. (1985). Although Clayton and Renvoize (1986) disagree, we also note, as did Clark et al. (1995), that the uppermost bract enveloping a flower in the inflorescence of *Anomochloa* is nearly identical in anatomical structure to the lemma of the pistillate spikelet in *Pharus*. If this bract does represent a lemma, then *Anomochloa* does not have a palea above the lemma, and thus does not have a true grass floret. Because prophylls characteristically develop only in leaf axils, a palea that was homologous with a prophyll would be absent in a truly terminal flower, and we suggest that the "lemma and flower" structures of *Anomochloa* represent terminal bracteate flowers rather than subterminal ones.

Although the most parsimonious interpretation of the character variation pattern detected in this study is that a single-flowered spikelet is plesiomorphic for the family, the later *de novo* development of a rachilla extension and subsequent additional fertile florets also is problematic. If a palea is present directly below a flower (ignoring lodicules), and if paleas are homologous with prophylls and prophylls only develop on axillary branches, then the floret is not truly terminal. It is reasonable, then, to suggest that the first true grass spikelet may have

been indeterminate, that it had several florets (Clayton, 1990), and that it was subsequently reduced to one floret as late as in the immediate ancestor of *Pharus* plus all other grasses except Anomochlooideae (Fig. 3, node 4). Later reversions to the multiple-flowered condition then might have occurred within Bambuseae, Pooideae, and the PACC clade. If *Anomochloa* retains a plesiomorphic presence of flowers that are truly terminal (see above), the indeterminate multiple-flowered grass spikelet may have evolved between nodes 2 and 4 on Fig. 3.

Thus, the trees and character state distributions in the present results lend some support to Clayton's (1990) interpretation of the evolution of the grass spikelet, with the caveat that all multiple-flowered spikelets present in living grasses, in Bambuseae, Pooideae, and the PACC clade, may represent reversions, while the plesiomorphic multiple-flowered spikelet no longer survives.

Topologies reported in two other cladistic studies (Kellogg & Campbell, 1987; Clark et al., 1995) are consistent with the interpretation that a spikelet with one fertile floret (rarely with one or more sterile "lemmas" below the fertile one as in Ehrhartoideae), and lacking a developed rachilla extension above the fertile floret, was present in most early grass lineages and that this is the plesiomorphic form of the spikelet in Pooideae and the PACC clade.

2. Lodicules

Two questions that arise when lodicules are considered are 1) the homology of lodicules and 2) the distribution and pattern of diversification of lodicule types. There are structures in *Anomochloa* and *Streptochaeta* that are sometimes called lodicules, but it is far from certain that they are homologous with the lodicules of most other grasses, and the relationship of lodicules (in *Anomochloa* and *Streptochaeta*, or in other grasses) to structures in nongrasses also is obscure. Because of this ambiguity regarding the homology of lodicules, which is reflected in the scoring of this character in the matrix of structural characters, the point of origin of lodicules (char. 14) can be fixed at any of a series of nodes in the phylogenetic structure presented here, but no later than in the last common ancestor of *Pharus* and all other grasses except Anomochlooideae (Fig. 3, node 4).

In Clifford's (1987) interpretation, the occurrence of lodicules in all true florets of the early grasses serves as evidence that most grasses have only subterminal flowers (see the previous section). Thus, the putative absence of lodicules in *Anomochloa* and *Streptochaeta*, neither of which has true florets, is perhaps best regarded as a plesiomorphic absence. The earliest recognizable lodicules, as interpreted from the present analysis (chars. 15–18), were three in number, unfused, apically membranous (unlobed, more or less lanceolate, and fleshy at the base), and heavily vascularized (except in *Pharus*, according to Judziewicz, 1987). Vascularization is reduced or lost within the PACC clade and in all Pooideae. In the PACC clade, above the point of divergence of *Aristida* from other members of the clade, the apical membranous portion is reduced or absent, giving the lodicule a truncate form and fleshy texture. Lodicules become fused in Meliceae, and are lost in a number of other taxa. Under Alternative Topology 1, lodicule number (char. 15) changes twice from three to two: once in the Ehrhartoideae and once in the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade. Under Alternative Topology 2 (i.e., late-diverging Ehrhartoideae), subfam. Ehrhartoideae is sister of the clade that consists of *Brachyelytrum*, Pooideae, and the PACC clade, and the change from three to two lodicules is a synapomorphy of this set of four lineages (Fig. 5). Where the reduction from three to two lodicules has occurred it has typically been by loss of the posterior lodicule (Clifford, 1961). The posterior lodicule appears to have been regained and lost again in early-diverging elements of Pooideae (Fig. 3, in the region between nodes 31 and 36).

The homology of lodicules with other organs in nongrasses is ambiguous. They may represent tepals, staminodes, stipules, ligules, reduced bracts, leaves, branch systems, or novel structures (Clifford, 1987). That the posterior lodicule develops above the anterior lodicules, rather than below them, as would be the case if they were all part of the same whorl, and that the posterior lodicule is sometimes suppressed, favors an interpretation that they are derived from stipules, leaves, or branches (Clifford, 1987). Under the latter interpretation (Clifford, 1987) lodicules would be absent from truly terminal flowers (which would not have paleas either), and thus their presence suggests that the flower is subterminal and subtended by a vestigial branch system (i.e., the lodicules). This again points to *Anomochloa* (if it lacks lodicules) as having terminal flowers (see previous section). However, it is not clear what is represented by the fringe of hairs below the staminal whorl in *Anomochloa*, or the large, fleshy, lanceolate bracts in this position in *Streptochaeta*. The possibility that these represent vestigial tepals is consistent with the interpretation of flowers in these taxa as terminal.

Lodicules are involved in the opening of florets at the time of flowering (Clayton, 1990). However, some grasses that lack lodicules also open at anthesis (e.g., *Nardus*). The posterior lodicule may not have been essential to this operation at certain stages of grass evolution, and its development therefore may not have been maintained. The large, indurate florets characteristic of many elements of Stipeae and relatives thereof may be difficult to force open, and re-expression of the third lodicule therefore may have been favored in these groups.

3. Stamen Number

Judging by the positions of stamens in alternating whorls, Clifford (1961) suggested that stamen number (char. 19) is reduced to three in the grasses from a putatively ancestral number of six, by loss of the inner whorl. Consistent with that suggestion, the presence of six stamens appears to be plesiomorphic in the grasses. This state changed to three stamens prior to the divergence of the PACC clade and Pooideae. This event occurred either just after the divergence of *Pharus* (under Alternative Topology 2) or just after the divergence of Ehrhartoideae (under Alternative Topology 1). The inner whorl of stamens was regained in some Bambuseae in either case, and in Ehrhartoideae (under Alternative Topology 2). In early-diverging genera not sampled in the present analysis stamen number has increased further; *Pariana* of Parianeae has 6–40 stamens (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992), and a few genera of Bambuseae may have as many as 120 stamens (Clayton & Renvoize, 1986).

4. Stigmatic Branching

A character that is particularly relevant to the evolution of wind pollination in grasses is the development of longer and higher orders of stigmatic branching (char. 22). Implications of this change in stigmatic structure for breeding system evolution are discussed below (section V.H). Here we discuss the character states and their distribution among taxa. Heslop-Harrison and Shivanna (1977) defined plumose stigmas as those with receptive cells dispersed on multiseriate branches. In their interpretation most stigmas in grasses are truly plumose, and those of *Flagellaria*, which have receptive cells concentrated in distinct ridges, zones or heads, are not. Stigmas of *Joinvillea* are similar to those of *Flagellaria*. Although Joinvilleaceae have been described as having "plumose" stigmas (Cronquist, 1981; Dahlgren et al., 1985), illustrations (Engler & Prantl, 1888; Dahlgren et al., 1985) show an absence of branches made up of series of receptive cells. Stigmas of Restionaceae, and the related families Anarthriaceae D. F. Cutler & Airy Shaw, Centrolepidaceae Endl., Ecdeiocoleaceae D.

F. Cutler & Airy Shaw, and Eriocaulaceae Desv., generally are more narrow and elongate in their primary axis (as in grasses) than those of *Flagellaria* or *Joinvillea* (see illustrations in Engler & Prantl, 1888; Black, 1960; Dahlgren et al., 1985). Although stigmas in these five families do have short lateral branches in some cases, illustrations of their stigmas either show branches that are not made up of series of receptive cells, or do not clearly show that they are. An illustration of *Baloskion* (in Black, 1960) falls into the latter category. For this reason, we scored stigmas of *Flagellaria* and *Joinvillea* as simple, and those of *Baloskion* as ambiguous. We further restrict the definition of "plumose" in our analysis and discussion to stigmas that have elongate branches and thus a nonlinear appearance (i.e., states 2 and 3 of char. 22). Thus, with simple stigmas also present in *Anomochloa*, *Streptochaeta*, and *Pharus*, stigmas appear to have been simple at the point of origin of the grasses.

The occurrence of simple stigmas in certain early-diverging herbaceous lineages has been interpreted as a reversal from plumose stigmas (Soderstrom, 1981: 44). However, the present analysis suggests the opposite. *Eremitis* has simple stigmas, as do the three earliest diverging lineages of grasses. Under either of the Alternative Topologies, broadly plumose stigmas arose twice after the divergence of Phareae, and were plesiomorphically simple in *Eremitis*, or were lost once and then regained in *Eremitis*. A factor that merits consideration at this point is the presumed monophyly of Parianeae and the nature of stigmas in other members of that tribe. The combination of a spiciform inflorescence with a fragile rachis, bearing verticils of 4–6 spikelets, the spikelets with single unisexual flowers, the pistillate ones disarticulating below the glumes, along with a set of other unifying features, is good evidence that Parianeae represent a natural group (Clayton & Renvoize, 1986; Hollowell, 1987). However, *Pariana* has stigmas that are distinctly broadly plumose, and introrse (Hollowell, 1987), the sparsely arranged primary branches originate on the inner side of the main axes and are not re-branched, and the receptive cells express papillae only at the branch tips (pers. obs.). The condition in *Pariana* may represent a novel state or an intermediate state between simple stigmas and the more frequent plumose condition in grasses. As such, it remains unclear whether the simple stigma in *Eremitis* is plesiomorphic or apomorphic within Parianeae.

In the phylogenetic structures resolved by simultaneous analysis of the two data sets, stigmas with branches made up of elongate series of receptive cells arise one or more times in the remainder of the grasses (Fig. 3, around node 5). Secondary stigmatic branching is well developed in a few groups of grasses and is synapomorphic for tribe Meliceae (Fig. 3, node 40), where secondary branching is highly developed and tertiary branching occurs. Stigmas revert to the simple state in *Nardus*, *Sesleria*, and *Sporobolus* and in many genera of the PACC clade and Pooideae not sampled in this study.

5. Fruit Characteristics

Embryo and caryopsis characters tend to be phylogenetically stable in the grasses. Although such characteristic grass features as spikelets and lodicules may not have been present in the earliest grasses (see above), the grass-type fruit, with a lateral and well-developed embryo (char. 25), is resolved as a synapomorphy of the grasses (Fig. 3, node 2). The four characters (chars. 26–29) of the embryo formula of Reeder (1957, 1962) all provide synapomorphies for the PACC clade and Pooideae, and for subclades within these two major groups. However, they were of little use in determining relationships among these clades and the earlier-diverging lineages, at least with the present sampling, for they are either optimizable at different nodes around the nexus of these lineages in most-parsimonious trees or they are apomorphies of lineages within the PACC clade or Pooideae. Epiblast occurrence (char. 26) is quite homoplasious (8 steps, CI = 0.12, RI = 0.46). Epiblasts are present in *Anomochloa* and absent in *Streptochaeta*. They are absent in *Ehrharta*, Arundinoids, *Uniola* L., and Panicoideae (except *Andropogon*, which was not sampled), but are present in other early-diverging lines, *Chasmanthium*, many Chloridoideae, and nearly all Pooideae (they are absent in *Bromus*, and are polymorphic in *Brachypodium* and Hordeeae). The absence of a scutellar tail (char. 27, 2 steps, CI = 0.50, RI = 0.96) is a synapomorphy of Pooideae or of *Brachyelytrum* plus Pooideae. A scutellar tail is present in all early-diverging lineages that have been studied, except *Pharus* and some Oryzeae, and it is variable in occurrence in *Brachyelytrum* and *Oryza*. A scutellar tail has been found to be present in all but two genera of the PACC clade studied. Mesocotyl internodes elongate (char. 28, 1 step, CI = 1.0, RI = 1.0) is a synapomorphy of the PACC clade, where it occurs in all but a few genera of Panicoideae (not sampled). The internodes are short or negligible among Pooideae and among the early-diverging lines in which they have been observed (except *Ehrharta*). Under Alternative Topology 2, the occurrence of embryonic leaf margins that do not overlap (char. 29, 3 or 4 steps, CI = 0.25–0.33, RI = 0.82–0.88) is a synapomorphy of the PACC clade plus Pooideae. Embryonic leaf margins overlap in embryos of taxa in the clade that consists of Centotheceae plus Panicoideae and in all lineages that diverge earlier than the point of divergence of Pooideae and the PACC clade other than *Anomochloa*, and *Potamophila* R. Br. of Oryzeae (not sampled).

A linear elongate hilum (char. 24) is plesiomorphic in the grasses. It is characteristic of all lineages that diverge before the point of divergence of Pooideae and the PACC clade, but variable within Pooideae and the PACC clade (7–8 steps, CI = 0.12–0.14, RI = 0.68–0.72). Hilum shape changes from long and linear to short relative to the caryopsis length and broad or punctiform within the PACC clade (Fig. 3, node 15) and then is reversed among some Arundinoids. It is also narrow and elongate in some genera of Panicoideae not sampled in this study. It also reverses from short to long within Pooideae within tribes Poeae and Agrostideae.

6. First Seedling Leaf

Absence of a blade on the first seedling leaf (char. 32) may be plesiomorphic in the Poaceae. The character state is not known for *Joinvillea* or *Anomochloa*, and the blade is absent in *Flagellaria* and present in *Baloskion* and other Restionaceae (B. Briggs, pers. comm.; H. P. Linder, pers. comm.). Among other early-diverging lineages, a blade on the first true leaf is known to occur only in *Pharus*, *Ehrharta*, *Streptogyna*, and *Zizania* L. (the latter two genera not sampled in the present analysis). The blade is absent for all genera of Bambuseae and early-diverging herbaceous lineages surveyed by Hoshikawa (1969), Soderstrom (1981), and Judziewicz and Soderstrom (1989). In Alternative Topology 1, gain of the blade represents a synapomorphy for the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade, and it is present in all taxa in this group for which the character has been observed (i.e., above node 13 in Fig. 3). Under Alternative Topology 2, in which subfam. Ehrhartoideae is the sister group of this clade, gain of the blade can be optimized parsimoniously as a synapomorphy of this clade, or as a synapomorphy of the larger clade that also includes Ehrhartoideae, in which case absence of the blade in *Oryza* and *Leersia* represents a loss. Further investigation of seedling leaf characters including presence/absence, angle of divergence, and width are needed (Kuwabara, 1961). Erect, narrow first seedling leaves may be a synapomorphy for Ehrhartoideae if that group is circumscribed to include *Ehrharta*, Oryzeae, and *Streptogyna*, or, as already noted, for this group plus *Brachyelytrum*, Pooideae, and the PACC clade.

7. Cross-Venation

As noted in Appendix 2, the potential for inconsistency in the scoring of this character is greater than with most others. If cross-venation is regarded as present only when it is frequent and regular in occurrence (i.e., tessellation), taxa with prominent but infrequent cross-venation must be scored as lacking cross-venation. On the other hand, if the rare to occasional presence of distinct cross-veins is regarded as sufficient for the recognition of cross-venation as present, additional taxa should be scored as having this feature. For these reasons, and because it appears that various authors have scored absence of the character somewhat inconsistently, the following statements should be regarded as tentative.

Presence of cross-venation of the leaf blade (char. 33) appears to be plesiomorphic in the grasses. Although we considered the character inapplicable for *Baloskion* and other Restionaceae, cross-venation is present in *Flagellaria*, *Joinvillea*, and the earliest-diverging grass lineages. It is characteristic of most other early-diverging lineages, but is absent from some Ehrhartoideae. Alternative Topology 1, with *Brachyelytrum* (which has cross-venation) sister of Pooideae, suggests that the loss of cross-venation arose independently in Pooideae and the PACC clade. Under Alternative Topology 2, loss of cross-venation can be interpreted as a synapomorphy of the clade that consists of Pooideae plus the PACC clade; however, the character still would be homoplasious by virtue of the occurrence of cross-venation within the PACC clade in five genera of Panicoideae, *Thysanolaena*, all genera of Centotheceae except *Chasmanthium*, and *Melanocenchrus* Nees of Chloridoideae, as well as within Pooideae, where it is known from *Phaenosperma*, *Pseudobromus* K. Schum. (neither of which was sampled), and a few other taxa. In this and in other respects, *Pseudobromus*, an African genus placed within *Festuca* by Clayton and Renvoize (1986) and Watson and Dallwitz (1992), is similar to *Brachyelytrum* (pers. obs.), which also has cross-venation, and it may be properly placed near that genus rather than in *Festuca*.

8. Microhairs

Multicellular microhairs (char. 34) can, but need not, be optimized as plesiomorphic in the Poaceae. They occur in Joinvilleaceae and are absent in Restionaceae, but the character is unobserved for Flagellariaceae (Appendix 2). Although multicellular microhairs have more than two cells in Joinvilleaceae and some early-diverging lineages (where they are bi- and multicellular), they are bicellular in most Poaceae. Bicellular microhairs are present in the Anomochlooideae and are widespread among other early-diverging lines but are absent in several of the tribes and genera in this region of the phylogeny: *Pharus* and Phareae [except *Suddia* Renvoize, which is excluded from the Phareae by Judziewicz (1987) and which was not sampled in the present study], *Ehrharta*, *Streptogyna*, and *Porteresia* (the latter two genera not sampled). In the PACC clade, they are absent in *Spartina* Schreb., *Distichlis* Raf., and *Uniola*, among taxa in the present sample, and sporadically elsewhere. In Alternative Topology 1 (*Brachyelytrum* sister of Pooideae) their absence is a synapomorphy within Pooideae for the clade that includes all members of the subfamily except *Nardus* and *Lygeum* (Fig. 3, node 31) or for the clade that includes *Brachyelytrum* and Pooideae if bicellular microhairs were lost initially and regained in the clade that consists of *Nardus* plus *Lygeum*. The absence of multicellular microhairs in *Brachyelytrum* is interpreted as an independent loss under Alternative Topology 2 (PACC clade sister of Pooideae), while under Alternative Topology 1 it can, but need not, be a synapomorphy of the clade that includes *Brachyelytrum* and Pooideae.

Bicellular microhairs with a short broad terminal cell relative to the basal cell, termed "chloridoid," occur in *Lygeum*, *Amphipogon*, and most Chloridoideae (except in *Eragrostis* Wolf in part, including the species sampled in this study). Those in *Lygeum* would appear to have arisen independently. The chloridoid microhairs in *Amphipogon* resemble those found in tribe Pappophoreae Kunth of Chloridoideae (Tateoka et al., 1959; Watson & Dallwitz, 1992), and chloridoid microhairs may be a synapomorphy of *Amphipogon* plus Chloridoideae.

9. Arm Cells

Arm cells (char. 36) are not known to occur among the nongrass taxa sampled in this analysis. Arm cells are present in all early-diverging lineages examined except for *Streptochaeta*, two genera of Phareae, a few of Olyreae, two genera of Bambuseae, most *Ehrharta*, and one genus of Oryzeae. This cell type is absent from *Brachyelytrum*, all Pooideae, and most members of the PACC clade (except *Phragmites* among the current sampling, and in a few other unsampled genera of Arundinoids, Chloridoideae, and Panicoideae). With the present sampling, loss of arm cells optimizes as a synapomorphy of the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade (Fig. 3, node 13) under either of the alternative topologies, but more extensive sampling within the PACC clade might alter that result. Lynn Clark (pers. comm.) notes that highly invaginated arm cells apparently occur only in Olyreae, Bambuseae, and Parianeae, and suggests that they may be a synapomorphy of this set of tribes.

10. Fusoid Cells

Fusoid cells (char. 37) have been considered a uniting feature of Bambusoideae s.l. (Clayton & Renvoize, 1986; also see Kellogg & Campbell, 1987). However, this assemblage is not resolved as monophyletic in the present study, and there is evidence that these cells occur outside the grasses, in *Joinvillea* (Smithson, 1957), so the presence of fusoid cells may be a plesiomorphy of the grass family. Within the grasses, loss of fusoid cells in Alternative Topology 1 (early-diverging Ehrhartoideae) is a parallel occurrence in Ehrhartoideae and in the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade, while in Alternative Topology 2 (late-diverging Ehrhartoideae), it is a synapomorphy of the clade that includes all four of these groups. Among early-diverging lineages, fusoid cells are absent in Phyllorhachideae (not sampled) and in two genera of Bambuseae (not sampled), and are variable in occurrence in *Ehrharta* and Oryzeae, though absent in all taxa sampled here. Fusoid cells are absent in *Brachyelytrum* and Pooideae but infrequently present in the PACC clade (in *Hakonechloa* Makino ex Honda, *Viguierella* A. Camus, *Homolepis* Chase, and *Streptostachys* Desv., none of which are sampled in the present study). Fusoid cells in some members of Panicoideae may be structurally different from those in other lineages (L. Clark, pers. comm.) and further investigation is warranted.

11. Photosynthetic Pathway

C_4 photosynthesis (chars. 38, 39) in the grasses is known only in members of the PACC clade. The results of the present analysis suggest that C_4 photosynthesis has originated three times, once each in *Aristida*, Chloridoideae, and Panicoideae. Some form of C_4 photosynthesis occurs in *Aristida*, a few other Arundinoids, all Chloridoideae reported in the literature

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A linear elongate hilum (char. 24) is plesiomorphic in the grasses. It is characteristic of all lineages that diverge before the point of divergence of Pooideae and the PACC clade, but variable within Pooideae and the PACC clade (7–8 steps, CI = 0.12–0.14, RI = 0.68–0.72). Hilum shape changes from long and linear to short relative to the caryopsis length and broad or punctiform within the PACC clade (Fig. 3, node 15) and then is reversed among some Arundinoids. It is also narrow and elongate in some genera of Panicoideae not sampled in this study. It also reverses from short to long within Pooideae within tribes Poeae and Agrostideae.

6. First Seedling Leaf

Absence of a blade on the first seedling leaf (char. 32) may be plesiomorphic in the Poaceae. The character state is not known for *Joinvillea* or *Anomochloa*, and the blade is absent in *Flagellaria* and present in *Baloskion* and other Restionaceae (B. Briggs, pers. comm.; H. P. Linder, pers. comm.). Among other early-diverging lineages, a blade on the first true leaf is known to occur only in *Pharus*, *Ehrharta*, *Streptogyna*, and *Zizania* L. (the latter two genera not sampled in the present analysis). The blade is absent for all genera of Bambuseae and early-diverging herbaceous lineages surveyed by Hoshikawa (1969), Soderstrom (1981), and Judziewicz and Soderstrom (1989). In Alternative Topology 1, gain of the blade represents a synapomorphy for the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade, and it is present in all taxa in this group for which the character has been observed (i.e., above node 13 in Fig. 3). Under Alternative Topology 2, in which subfam. Ehrhartoideae is the sister group of this clade, gain of the blade can be optimized parsimoniously as a synapomorphy of this clade, or as a synapomorphy of the larger clade that also includes Ehrhartoideae, in which case absence of the blade in *Oryza* and *Leersia* represents a loss. Further investigation of seedling leaf characters including presence/absence, angle of divergence, and width are needed (Kuwabara, 1961). Erect, narrow first seedling leaves may be a synapomorphy for Ehrhartoideae if that group is circumscribed to include *Ehrharta*, Oryzeae, and *Streptogyna*, or, as already noted, for this group plus *Brachyelytrum*, Pooideae, and the PACC clade.

(except *Eragrostis walteri* Pilg.), and in most Panicoideae. Among Arundinoids, it is reported in *Aristida* and *Stipagrostis* Ndes of tribe Aristideae, and in *Centropodia* and *Alloeochaete* C. E. Hubb. of tribe Arundineae sensu Clayton and Renvoize (1986). Barker et al. (1995) resolved *Centropodia* as sister group of tribe Pappophoreae of Chloridoideae, and on the basis of this placement *Centropodia* could be placed within Chloridoideae. Tzvelev (1989), without mentioning references, cites a few additional Arundinoid genera as C₄, but H. P. Linder, R. P. Ellis, and G. Davidse (pers. comm.), have confirmed that these genera are C₃. In Panicoideae, C₄ is constant within Saccharineae (i.e., Andropogoneae) and Eriachneae (Owhi) Eckardt-Boorsb., but is variable in occurrence in Paniceae and Arundinelleae Stapf and is absent in Hubbardieae C. E. Hubb. and Isachneae Benth. (Clayton & Renvoize, 1986; Hattersley & Watson, 1992). Thus it may have evolved more than once in Panicoideae. C₄ subtypes were of little significance as characters in the present study, in which sampling of C₄ groups is limited. However, the results are consistent with the hypothesis of Hattersley and Watson (1992) that the NAD-ME system originated before the PCK subtype in the Chloridoideae (Fig. 3, nodes 17 and 20). Other cladistic studies (Kellogg & Campbell, 1987; Barker et al., 1995; Clark et al., 1995) also indicate that Aristideae arose independently from the Paniceae and Chloridoideae. The structure resolved here supports suggestions that C₄ photosynthesis arose a minimum of three or possibly four times or more within the grass family (Brown, 1977; Clayton & Renvoize, 1986; Hattersley & Watson, 1992; Sinha & Kellogg, 1996).

12. Chromosome Numbers

Chromosome number diversity is extensive in Poales and in Poaceae. Chromosome number was not used as a character in the analysis because as a result of polyploidy, aneuploidy, dysploidy, and possible hybrid combinations, base chromosome numbers are ambiguous for many taxa (de Wet, 1954). In several early-diverging genera of the grasses, and in Pooideae, all or most species are polyploid and the scoring of base numbers would be unduly speculative. Although chromosome numbers were scored and were included in some provisional character analyses, the state of this character still was ambiguous at many nodes. For example, the plesiomorphic base number for Pooideae might be $x = 7, 8, 9, 10, 11, 12$, or 13, and that of Poaceae might be $x = 11$ or 12. The outgroups provide ambiguous evidence in this regard: The chromosome number of *Flagellaria* is $n = 19$, that of *Joinvillea* is $n = 18$, and those of Restionaceae s.l. have been interpreted as consistent with $x = 7, 8, 9, 11, 12$, and 13 (Dahlgren et al., 1985). *Joinvillea* and *Anomochloa* share the gametic chromosome number of $n = 18$ (Hunziker, 1989), and *Flagellaria*, *Diarrhena*, and *Miscanthus* Andersson share the gametic chromosome number $n = 19$, but it is not clear if these are base numbers. When chromosome numbers are overlaid on most-parsimonious trees, Olyreae are united by $x = 11$; Ehrhartoideae by $x = 12$; *Chasmanthium* and Arundinoids have $x = 12$ [except *Aristida* ($x = 11$), *Danthonia* ($x = 9$?), *Molinia* ($x = 9$), and possibly *Amphipogon* (x unknown)]; Chloridoideae are plesiomorphically $x = 10$; and within Pooideae, Brachypodieae and the "core" Pooideae are each united by $x = 7$.

E. SYNAPOMORPHIES OF VARIOUS GROUPINGS OF EHRHARTOIDEAE, POOIDEAE, BRACHYELYTRUM, AND THE PACC CLADE

In the consensus tree that summarizes most-parsimonious trees obtained by simultaneous analysis of both character sets, the polytomy at node 13 (Fig. 3) results from conflict between Alternative Topologies 1 and 2. In the former, the PACC clade is the sister group to Pooideae

plus *Brachyelytrum*; in the latter, *Brachyelytrum* is the sister group of Pooideae plus the PACC clade, and Ehrhartoideae is the sister group of the clade that includes all three of those taxa. Resolution of any group that includes Pooideae and the PACC clade but does not include Ehrhartoideae (or other early-diverging lineages, including Bambuseae) is in conflict with the resolution of a group that includes Pooideae and Ehrhartoideae (i.e., Oryzoideae) with Bambuseae, Olyreae, or Parianeae (i.e., the "BOP" clade resolved by Clark et al., 1995) but excludes the PACC clade. The structural synapomorphies of clades that are resolved by the present analysis, and that impinge on this question, are detailed in the following paragraphs. Character state transformations that are optimizable to other internodes are listed after unambiguous synapomorphies of the various groups.

Unambiguous synapomorphies of the clade that includes *Brachyelytrum*, Pooideae, and the PACC clade in all six trees with alternative topology 1 are the following: loss of pseudopetioles (char. 6), gain of awn or mucro (char. 10), loss of stylar fusion (char. 20), gain of lamina of first seedling leaf (char. 32), loss of arm cells (char. 36), and loss of fusoid cells (char. 37). Three additional characters may be synapomorphies of this group, but can be optimized equally parsimoniously elsewhere: presence of two lodicules (char. 15), embryonic leaf margins meeting rather than overlapping (char. 29), and loss of cross-venation in leaf blades (char. 33). There is only one unambiguous synapomorphy of this clade in the six trees with Alternative Topology 2, and it is one of the six that are unambiguous synapomorphies under Alternative Topology 1: loss of arm cells (char. 36). A potential synapomorphy of this group is gain of lamina of first seedling leaf (char. 32).

Unambiguous synapomorphies of the clade that includes Pooideae and the PACC clade (present only in Alternative Topology 2) are embryonic leaf margins meeting rather than overlapping (char. 29), and loss of cross-venation in leaf blades (char. 33); both of these character transformations are potential synapomorphies, in Alternative Topology 1, of the larger clade that also includes *Brachyelytrum*.

There are five unambiguous synapomorphies of the clade that includes Ehrhartoideae, *Brachyelytrum*, Pooideae, and the PACC clade (present only in Alternative Topology 2): loss of pseudopetiole (char. 6), gain of awn (char. 10), change in lodicule number from 3 to 2 (char. 15), loss of stylar fusion (char. 20), and loss of fusoid cells (char. 37). Two additional characters can, be but need not, be optimized on this internode: gain of disarticulation above the glumes (char. 12) and gain of lamina of first seedling leaf (char. 32).

Under Alternative Topology 1, in which Ehrhartoideae is not resolved as a close relative of *Brachyelytrum*, Pooideae, and the PACC clade, there are six structural characters that arise in parallel between these groups, either as unambiguous synapomorphies or as potential synapomorphies: loss of pseudopetiole (char. 6), gain of awn (char. 10), change in lodicule number from 3 to 2 (char. 15), loss of stylar fusion (char. 20), gain of lamina of first seedling leaf (char. 32), and loss of fusoid cells (char. 37). These six characters are elements of the syndrome of structural features that support a close relationship between Ehrhartoideae, *Brachyelytrum*, Pooideae, and the PACC clade (i.e., Alternative Topology 2), to the exclusion of Bambuseae and other early-diverging lines, and that are in conflict with Alternative Topology 1 as well as with the resolution of a BOP clade. Analyses that resolve relationships in conflict with these characters should account for parallelism in these characters.

F. PLACEMENT OF FIVE PROBLEMATIC TAXA WITHIN POOIDEAE

The distribution of character states in the present analysis, along with subsidiary character state data, provide evidence for the placement of *Anisopogon* in Pooideae, along with four addi-

tional orphan genera not sampled in this study. We suggest that *Anisopogon*, placed in Arundinoideae by Clayton and Renvoize (1986) and Watson and Dallwitz (1992), and *Danthoniastrum*, *Duthiea*, *Metcalfia*, and *Pseudodanthonia*, placed in Arundinoideae by Watson and Dallwitz and in Pooideae tribe Aveneae (i.e., Agrostideae) subtribe Duthieinae by Clayton and Renvoize, have characteristics generally diagnostic for Pooideae and not Arundinoideae. In all five of these genera, the species for which character scores are available have membranous, nonciliate ligules; absence of bicellular microhairs (except possibly *Duthiea*; see Watson & Dallwitz, 1992); two or three lodicules that are lanceolate, unlobed, and non- or weakly vascularized (including *Duthiea*, pers. obs., contra Clayton & Renvoize, 1986, and Watson & Dallwitz, 1992); long-linear hila; hairy ovaries; and small embryos. The first of these characters, membranous ligules without ciliate margins, is rare among Arundinoids (occurring only in *Arundo* L., *Dichaetaria* Nees ex Steud., *Elytrophorus* P. Beauv., *Hakonechloa*, *Monachather*, and *Thysanolaena*). Bicellular microhairs are present in most Arundinoideae but occur in Pooideae only in *Nardus* and *Lygeum*. If these five genera are excluded from the Arundinoids, taxa with three lodicules, or Pooideae-type lodicules (except in Aristideae), are absent in the PACC clade. Lanceolate, membranous-tipped, non- or weakly vascularized lodicules are both plesiomorphic and common in Pooideae, and the three-lodicule state is present among early-diverging lineages of the Pooideae (Stipeae and *Ampelodesmos*), while these lodicule characters (except the infrequent occurrence of weak vascularization) are rare or absent among Arundinoids. Long-linear hila are plesiomorphic and common in Pooideae, including the early-diverging members, and uncommon among Arundinoids. Hairy ovaries are frequent in Pooideae but rare among Arundinoids (present only in *Dregeochloa* Conert and *Pentameris* P. Beauv.). As in Pooideae (except *Cyathopsis* Stapf), embryos are small in *Anisopogon*, *Danthoniastrum*, *Duthiea*, *Metcalfia*, and *Pseudodanthonia* (pers. obs.), whereas embryos among Arundinoids are mostly large. Embryo formula characters, which are of major importance in distinguishing the PACC clade from the Pooideae, are known only for *Metcalfia*. That genus has formula F + FP (i.e., embryo mesocotyl internode negligible, epiblast present, scutellar tail absent, embryonic leaf margins overlapping), a pattern typical of Oryzeae, not unknown in Pooideae, and unrecorded within the PACC clade. A further piece of evidence favoring placement in Pooideae is the occurrence of large chromosomes of base chromosome number $x = 7$ in *Duthiea*, a combination of size and base number otherwise unknown from the PACC clade. Although most of the above features are homoplasious in both subfamilies, the presence of this suite of synapomorphic or plesiomorphic characteristics of the Pooideae, and absence of any characters diagnostic for the PACC clade, suggests that *Anisopogon*, *Danthoniastrum*, *Duthiea*, *Metcalfia*, and *Pseudodanthonia* should be recognized as early-diverging elements of Pooideae.

G. TAXONOMIC CONCLUSIONS

The analyses presented here suggest that among extant grasses, a clade consisting of *Anomochloa* and *Streptochaeta* diverged first from the lineage that includes all other grasses, and that *Pharus* was the next to diverge; further diversification resulted in one of two possible phylogenetic structures: 1) an "early-diverging" Ehrhartoideae, followed by Parianeae, Bambuseae, Olyreae, the PACC clade, and then *Brachyelytrum* from Pooideae; or 2) a clade consisting of Parianeae plus Bambuseae, followed by Olyreae, a "late-diverging" Ehrhartoideae, *Brachyelytrum*, and then the PACC clade from Pooideae. These alternatives are equally well supported by the combined data set. The second structure, however, is more strongly supported by the analysis of complex character structural data, as opposed to simple restriction site changes. Given the general correspondence between the phylogeny resolved by restric-

tion sites and by simultaneous analysis of both data sets, and those resolved by other molecular studies, we propose the following phylogenetic structure for the grasses:

Anomochlooideae (Pharoideae ((Parianeae Bambuseae Olyreae) (Ehrhartoideae (Brachyelytreae Pooideae (Aristidoideae (Chloridoideae [including some Arundinoids] (Arundineae s.str. (Thysanolaeneae Centotheceae Panicoideae))))))).

The present results thus are consistent with the recognition of Anomochlooideae and Pharoideae (Clark & Judziewicz, 1996). In light of the incongruence between the present analysis and that of *ndh*F concerning relationships among other major clades, it is reasonable to retain a Bambusoideae that is provisionally circumscribed to include Parianeae, Olyreae, and Bambuseae, until additional phylogenetic evidence becomes available. Clark et al. (1995) accepted subfam. Oryzoideae, and the present results are consistent with the recognition of that group with the name corrected to Ehrhartoideae. Acceptance of subfam. Ehrhartoideae would not affect the monophyly of other subfamilies if *Streptogyna* was also removed from Bambusoideae and placed in Ehrhartoideae (Clark et al., 1995). *Brachyelytrum* may be submerged in Pooideae (if future studies confirm its placement as sister of an already broadly circumscribed Pooideae) or recognized as a separate subfamily if confirmed to be the sister group of Pooideae plus the PACC clade. Either of these taxonomic placements would be compatible with results of the present analysis, but the former is consistent with the analyses of Kellogg and Linder (1995) and Clark et al. (1995), while the latter is not. *Phaenosperma* (according to Clark et al., 1995) and *Diarrhena* (present results) both appear to belong within Pooideae. Further, the present results agree with Clayton and Renvoize (1986) in the placement of certain orphan taxa such as *Ampeladesmos*, *Anisopogon*, *Lygeum*, *Nardus*, Stipeae, and Duthieinae in Pooideae.

The entire PACC clade (i.e., Aristidoideae Caro and all the names that follow it in the preceding list) could well be subsumed within a broadly defined Panicoideae, as proposed by Clark et al. (1995). However, an alternative approach, which would involve a less dramatic change to current classifications, would be to recognize Aristidoideae, to assign Centotheceae to Panicoideae, to apportion some of the remaining Arundinoids to Chloridoideae and Panicoideae, and to recognize one or more additional subfamilies that accommodate any monophyletic groups of Arundinoids that do not fall within the more broadly circumscribed Panicoideae and Chloridoideae. This proposal is consistent with the *rbc*L analysis of Barker et al. (1995) and with the *ndh*F analysis of Clark et al. (1995), which suggests that Panicoideae sensu Clayton and Renvoize (1986), Tzvelev (1989), or Watson and Dallwitz (1992), are polyphyletic unless they include, at minimum, Centotheceae and *Thysanolaena*, and that *Micraira* and *Amphipogon* can be accommodated within the Chloridoideae (Clark et al., 1995; and the present analysis, respectively). Despite the incongruous placement of *Donthania* in the present study, we suggest that the comprehensive analyses of Arundinoids by Verboom et al. (1994) and Barker et al. (1995) be followed (provisionally), in placing the Danthonioid taxa in the Chloridoideae.

H. BREEDING SYSTEMS IN GRASSES

1. Evolution of Wind Pollination in Grasses

The locations in the present phylogenetic trees of transformations in the degree of stigmatic branching, from simple in *Anomochloa*, *Streptochaeta*, Phareae, and Parianeae to plumose, are suggestive of corresponding changes among early grasses from insect to wind pollination. Plumose stigmas function more efficiently as traps for airborne pollen than do simple stigmas (Niklas, 1985), and they are clearly advantageous for wind pollination. Stigmatic surfaces are

simple and are distributed on short styles in *Joinvillea* and *Flagellaria*, the state is ambiguous in *Boloskion*, and the surfaces are simple or plumose in the Poaceae (see section V.D.4; Appendix 2, char. 22). The relatively simple style surface found in the earliest-diverging grasses in the present analysis is correlated with other features that suggest that the species possessing them are dependent, at least in part, upon insect pollination. Moreover, there is evidence that some degree of entomophily is present in some early-diverging lineages with plumose stigmas.

Insect pollination is documented in some early-diverging herbaceous lineages (*Olyra* L. and *Piresia* Swallen, of Olyreae, and *Pariana* and *Eremitis*, of Parianeae; Soderstrom & Calderón, 1971, 1979; Salgado-Labouriau & Rinaldi, 1990; Salgado-Labouriau et al., 1992) and is implicated for some species of *Chusquea*, *Bambusa* (Janzen, 1976), *Dendrocalamus* Nees, and *Schizostachyum* Nees, of Bambuseae (Chapman, 1990). Observations of insect pollination in bamboos have tended to be anecdotal, and further study is warranted. Although representatives of most of the early-diverging grass lineages appear to be wind pollinated (Soderstrom & Calderón, 1971), little is known of pollination modes in *Anomochloa*, *Streptochaeta*, or *Pharus*. However, the occurrence of simple stigmas and stamen filaments fused and exserted terminally from among the surrounding bracts in these three genera suggest insect rather than wind pollination (Soderstrom, 1981: 35).

Page (1978) found a correlation among grasses between degree of pollen exine sculpturing and the taxonomic distribution of states of this character. That correlation is still apparent when evaluated using the phylogeny of grasses resolved here. Nearly all of the early-diverging lineages compared in Page's study had grouped granules, and half of these had high surface relief. Although only two had separate granules, and none had separate granules and low relief, one-third of the members of the PACC clade and Pooideae had separate granules and two-thirds had low relief. Species known or suspected to be insect pollinated on other grounds had grouped granules (*Anomochloa*, *Streptochaeta*, *Leptaspis* R. Br. [Phareae], *Dendrocalamus*, *Olyra*) or high exine reliefs (*Olyra*, *Pariana*, *Piresia*). Species of Pooideae and the PACC clade tend to have widely spaced granules of low relief. Thus, a functional connection may exist between insect pollination and pollen with fused granules or high exine relief, and between wind pollination and pollen with low exine relief.

Joinvillea and *Flagellaria* have perfect flowers, occur in mesic tropical forests often in the shade, and probably are insect pollinated to some degree (Newell, 1969). Cronquist (1981) indicated that *Flagellaria* is apparently anemophilous, but did not comment on the pollination mode of *Joinvillea*. Newell (1969) reported ants as possible pollinators of *Flagellaria*, and suggested that bees and/or wind may pollinate *Joinvillea*. Species of Restionaceae are mostly monoecious or dioecious (including *Baloskion*), and they often inhabit wetlands and are wind pollinated (Black, 1960; Cronquist, 1981; Dahlgren et al., 1985). Thus, there is no compelling evidence from pollination mode in the closest relatives of grasses that wind pollination was fixed in the ancestor of the grasses, and some evidence to suggest that entomophily was plesiomorphic and possibly supplemented by wind pollination.

Relationships of taxa and taxonomic distribution of simple stigmas suggested by the present analysis, supplemented with data on floral emergence, insect visitation, and pollen sculpturing, suggest that the earliest grasses were at least partially entomophilous. It can further be suggested that grasses only became dependent on wind pollination some time after the divergence of *Anomochloa*, *Streptochaeta*, Phareae, and possibly Parianeae.

2. Evolution of Self-Incompatibility in Grasses

The distribution of monoecy, protogyny, and self-incompatibility in grasses, when compared with the phylogenetic structures resolved here, are suggestive of the possibility that

self-incompatibility evolved only once or twice in the grasses. Furthermore, an initial incompatibility system may have arisen in the ancestor of the clade that comprises *Brachyelytrum*, Pooideae, and the PACC clade, and separately in Ehrhartoideae; or, if these two clades are sister groups, it may have evolved in their most recent common ancestor.

It is possible that both protogyny and monoecy preceded the evolution of self-incompatibility. Protogyny is documented in several early-diverging herbaceous lineages: *Anomochloa* and *Streptochaeta* (Judziewicz & Soderstrom, 1989), *Pharus* and *Leptaspis* (Phareae; Judziewicz, 1987), and *Zizania* (Oryzeae; Conner, 1987). Monoecy is ubiquitous in species of Phareae, Olyreae, Parianeae, Phyllorachideae, and *Puelia* Franch. (Bambuseae, or given separate tribal status; Soderstrom & Ellis, 1987), and occurs in several genera of Oryzeae (Clayton, 1990).

The complex "S, Z incompatibility" system, called "the grass system," has been demonstrated only sporadically, and then only in genera of core tribes of the Pooideae (see review of pertinent literature in Chapman, 1990). A complex diallelic system such as this may be broken down easily, but it is unlikely to have evolved multiple times. Although the nature of the incompatibility system has not been determined in other tribes and subfamilies, self-incompatibility is widely documented in grasses. Outside of the core Pooideae, self-incompatibility is known in species of Meliceae and Stipeae of Pooideae, and in the PACC clade in Arundineae, Paniceae, Sacchareae (i.e., Andropogoneae), Chlorideae (i.e., Cynodonteae), and Eragrostideae (Conner, 1979, 1981). Given this wide distribution in the clade that comprises *Brachyelytrum*, Pooideae, and the PACC clade, it is reasonable to suggest that their most recent common ancestor was self-incompatible.

There is limited evidence regarding self-compatibility among early-diverging lines. Self-incompatibility is known in *Oryza* and *Ehrharta* (Conner, 1979), and suggested for *Phyllostachys* Siebold & Zucc. of Bambuseae (Chapman, 1990, and references therein). The suggestion of self-incompatibility in *Phyllostachys* may not be reliable, however, as many Bambuseae take up to three years from initiation of flowering to setting of mature fruit (L. Clark, pers. comm.). Self-compatibility is apparent in *Anomochloa*, *Streptochaeta*, and *Pharus* (L. Clark, pers. comm., from observations of seed set in greenhouse situations), *Eremitis* (Hollowell, 1987), *Zizania*, *Oryza*, and *Ehrharta* (Conner, 1979). Coincident with known occurrences of self-compatibility among early-diverging herbaceous lineages, given the relationships resolved here, it appears that several of these groups (Phareae, Parianeae, Olyreae, and possibly Ehrhartoideae) share the occurrence of unisexual florets as a synapomorphy. That the occurrence of unisexual flowers is negatively correlated with the occurrence of self-incompatibility (Conner, 1979; Chapman, 1996) suggests that most of these taxa may be self-compatible. The hypothesis that best fits the data on self-incompatibility in the context of grasses, just prior to the divergence of Ehrhartoideae from the clade that consists of *Brachyelytrum*, Pooideae, and PACC clade, if Ehrhartoideae are the sister group of that clade, or independently in each lineage if these are not sister groups.

I. BIOGEOGRAPHY

Grasses are widely believed to have evolved in Gondwana during the late Cretaceous (Clayton, 1975; Stebbins, 1981, 1987; Linder, 1987), and Clayton (1975) suggested that they had diversified to the tribal level by the end of the Cretaceous. However, as there are no confirmed grass fossils from the Cretaceous, a minimum age for the origin of grasses is Paleocene. According to Muller (1981), pollen of Poaceae has not been confirmed from earlier than

the Paleocene, but by the end of this epoch grass pollen occurred in Brazil, Africa, and Australia [see comments by Linder (1987) and Crepet and Feldman (1991) on pollen of grasses from the Cretaceous]. Grass pollen was widespread by the end of the Eocene but not abundant until the Oligocene (Muller, 1981). Only a few confirmed grass macrofossils date from the early Tertiary, in the Paleocene, Eocene, and Oligocene (Litke, 1968; Galbreath, 1974; Muller, 1981; Thomasson, 1987; Crepet & Feldman, 1991). Miocene and younger fossils have been found in abundance and often are referable to modern genera [Muller, 1981; Thomasson, 1987; Poinar & Columbus, 1992 (a corrected date for the latter authors' fossil was established by Iturralde-Vinent & MacPhee, 1996)].

Modern representatives of the earliest-diverging grass lineages detected in the present phylogenetic analysis are *Anomochloa* and *Streptochaeta*. If grasses did arise in Gondwana in the Cretaceous, representatives of these or earlier grass lineages have since died out on the African continent (or have yet to be discovered). If this is the case, the occurrence of the above and other early-diverging groups in northeastern South America may simply represent survival in a refugium and not the center of origin of the family (Soderstrom & Calderón, 1974; Soderstrom, 1981).

However, as these two genera are known only from the New World, and there are no confirmed Cretaceous grass fossils, it could also be postulated that grasses first arose in South America in the Paleocene. In any case, grasses could have been dispersed between South America and Antarctica/Australia via the land bridge that persisted between those continents well into the early Tertiary (Clayton, 1975; Stebbins, 1981). If grasses did originate in South America during the Paleocene, they may have been dispersed from South America to Eurasia and Africa via a North American land bridge, as has been postulated in the reverse direction for Leguminosae Juss. (Lavin & Luckow, 1993).

The earliest confirmed grass fossil was collected from North American strata assigned to the Paleocene/Eocene boundary (Crepet & Feldman, 1991), and more recently assigned to the early Eocene (S. Wing, pers. comm.). This fossil was reported to have racemose inflorescence fragments, spikelets with two glumes that are keeled, two florets (the bracts are presumed to be lemmas and paleas but are not well preserved), and a total of six exserted dorsifixed stamens. No evidence of gynoecia was found. Although the fossils could not be definitively assigned to any tribe of grasses, they were said to be "suggestive of Aveneae [i.e., Agrostideae, but the reference is to the two-flowered members of that tribe] . . . or Arundineae" (Crepet & Feldman, 1991: 1013). Given the ambiguity of the floret bract identification, and absence of evidence of gynoecia, these spikelets might have contained one floret with six stamens or two florets with three stamens each, and the floret or florets may have been bisexual or unisexual. We note that single-flowered, unisexual spikelets with six stamens are common among early-diverging herbaceous grass lineages, and that this combination of characteristics is not known in the Pooideae or the PACC clade. The associated impression fossils of slender roots, shoots, and base of the plant suggest that the plant was a herbaceous perennial (Crepet & Feldman, 1991: fig. 4). These vegetative parts suggest that the grass was a member of Streptogyneae, Olyreae, Ehrhartoideae, the PACC clade, Pooideae, or an immediate ancestor of these, and that it was not a member of any earlier-diverging extant lineage.

Paleontologists now believe that at the Cretaceous/Tertiary boundary, ca. 65 million years ago, many lineages went extinct as a result of a widespread inhospitable climate attributable to an impact event and/or volcanic activity (Alvarez et al., 1980, 1982; Hallam, 1987; Srivastava, 1994). The collapse of complex ecosystems may have set the stage for a rapid and widespread establishment of nonspecialist organisms with short generation times. Tropical and subtropical forest ecosystems did rebound in the Paleocene, but by the Eocene (or somewhat

later; S. Wing, pers. comm.) more arid and cooler climates were spreading, and these changes favored the emergence of cold- and drought-tolerant vegetation, including savanna (Wolfe, 1975, 1977, 1978; Stebbins, 1981). These vegetational shifts are correlated with the rise in South America of mammals with hypsodont teeth adapted to grazing (Stebbins, 1981). S. Wing (pers. comm.) notes that the timing of the rise of hypsodonts and of savanna in South America is more in line with that of North America than previously was thought, and thus was upper Oligocene to lower Miocene rather than lower or middle Eocene as reported by Stebbins. The available data are consistent with the hypothesis that the first grasses appeared in the earliest Tertiary, after forest landscapes were cleared by Cretaceous/Tertiary boundary events, survived and diversified in seasonally or aseasonally dry tropical and subtropical forests and wetland openings, and then emerged as dominants in the Oligocene and Miocene with the development of climatic conditions favorable to the evolution of savanna habitats.

VI. Acknowledgments

VII. Literature Cited

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VIII. Appendix 1: Restriction Site Character Data

Data matrix depicting occurrence of 364 mapped restriction sites among 75 exemplar taxa of Poaceae and related families (Table I). The total number of sites scored "missing" (i.e., not scored 0 or 1) is indicated for each taxon; "?" = site scored missing because unobserved; "\" = site scored missing because of uncertainty regarding homology (see text). The three delimited groups of characters for each restriction enzyme are those of the Large Single Copy (LSC) region, Inverted Repeat (IR) region, and Small Single Copy (SSC) region, respectively. The position of each site is keyed to the numbered nucleotides of the complete cpDNA genome sequence of *Oryza sativa* (Hiratsuka et al., 1989; Sugiura, 1989) and is provided, in thousands of base pairs, as a vertically oriented number with one decimal position (e.g., the first *Bam* HI site in the LSC, IR, and SSC regions are at locations 6.0, 99.9, and 101.8, respectively.

Appendix I

Restriction Site Character Data

Taxon	Total Missing	Bam HI			Bcl II			Cla I		
		1111111122222222222333333344445555666666677777777		11111111			11111	1111222233444445555555666777777	1	111111
		67014668890112345666801567804461267012259012 2357	9	00000111	11111122222233334444556677777	88888	00001	245781469145734235680112257577112349	8888990	011111
		049725936864931228270437645263136443096064355839	9	12579123	15745677800266036347802271135	13456	12491	165823041695227196172295258815291248	2466080	701233
			9	81783066	69401037146304600468611766804	04425	76856		5336037	733504
Flagellaria	270	\\\\\\\\\\\\\\\\\\\\\\\\\\\0101000\\\\\\\\\\\00\\\\\\111	0	10100000	?????????????????????????????	?????	?????	\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\	1\\\1\\	\\\\\\
Baloskion	285	\\\\\\\\\\\\\\\\\\\\\\\0001001000\\\\\\\\\\\\\\\\\\\\\\0	\	\\\\\\\\	?????????????????????????????	?????	?????	\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\	1\\\1\\	\\\\\\
Joinvillea	111	000\\11\\01101\\01\00011010000\\\\\\\\\\\100001111	0	10110000	?????????????????????????????	?????	?????	\0\\\\\110\0\01010101110010110110\	11101\\	\\\\\\
Anomochloa	99	\\\\\\\0\\01201\1012000110\0\\\\\\\\\\\\\\200002111	\	\11\000\	0\\\\\\\\\\\\\\10010000000001010	000\1	01010	\01\\0\\11110\0\\1000101100\\\001101	101010\	001111
Streptochaeta	101	\\\\\\\0\102101\101100011010\\0\\\\\1000110\00\111	0	10110000	?????????????????????????????	?????	?????	\01\\0\\11110\0001010111100101\01111	101110\	001110
Pharus	129	\\\1000\\0110101000000011010\\0\10110001100001111	0	\1100100	?????????????????????????????	?????	?????	????????????????????????????????????	???????	??????
Ehrharta	92	0001\1111010011101000011010\\\\\\0010\\\00000\\\1	0	\\\00000	?????????????????????????????	?????	?????	\01001000101011\\\\\\111100101\\\000	111111\	101110
Oryza	4	00010111101001110110001100000000000100011000000111	0	00110000	1100000011111100\0100000111111	01001	01010	001001001111011110010111100101001101	1110111	101111
Leersia	58	000\0\0\101001010110001100000000\01000110000\\01	0	\0110000	?????????????????????????????	?????	?????	001001001111\11110010111100101001101	111111\	101101
Eremitis	76	0\\1\00\\0110101001000\101011010001100\10000\110	0	\1110000	?????????????????????????????	?????	?????	\01001\\1111011110010101100101001101	111110\	\\\1\\
Bambusa	18	01000\0\\0110011\\100011010100110001001100001111	0	\1110000	10010011110111110010000111011	01100	0101\	\0100\\01111011111011111100101001111	101010\	101110
Pseudosasa	30	01000\0\\01100\\\\100011010110110011001100101111	0	\1110000	10010011110111110010000111001	01100	0101\	\0100\\01111011111011102100101001111	111010\	101110
Chusquea	61	000\\\0\10110101011000110101100000\000110000\111	0	\111000\	?????????????????????????????	?????	?????	\01001001111011111011111100101001111	111110\	101101
Guadua	65	0100010\10110101001000110101101000\0001100001011	0	\1110000	?????????????????????????????	?????	?????	\010010011110111\\\\\111100101001101	111110\	1\\111
Otatea	61	000\\10\10110101011000110101101000\00011000\111	0	\1110000	?????????????????????????????	?????	?????	\01001101111011111011111100101001101	111110\	\\\111
Lithachne	81	0101\\0\\011011100100010010000110111001100001111	0	\1110000	?????????????????????????????	?????	?????	\0100\\01100101\00010111100101001101	1111101	100\\\
Olyra	91	0\\1\1\\\011010101100011010\\\10\\\\\01100000111	0	\\110000	?????????????????????????????	?????	?????	\0100100111011110101111110010100\\\\	111110\	101110
Aristida	29	00000\0\\0110101011\\\110101000000101001110011111	0	\1110000	11\00000111110110100001001110	01101	0101\	00000000011101110100\\11\\0101\\1100	110111\	100100
Arundo	25	0000\\0110110101011000100101000\0111001110011111	0	\1110100	01\100111111111110100001101011	01101	0101\	\1100000\111011111010111010101011001	110111\	\\\110
Molinia	52	000\\\0110111101011000110101000000111001110011111	0	01110100	?????????????????????????????	?????	?????	\11001000121011011010111010101011001	110111\	100110
Phragmites	25	0000\\\\\011110101100010000110000101001100011111	0	\1110100	01\100111111110100100101101011	01101	0101\	1010010001200120110101110101011001	1101111	101100
Danthonia	32	11000\\\\\\11010101100010000110000101001100011111	0	10110100	010000111110111001000001\01011	01101	0101\	\\\\\\001111000011\10101010101011100	0201111	101\\\
Chasmanthium l	38	0\0\\\10100\0101\\\\\0011000100101\000001200110001111	0	\111\\\\	01000011111111110010000111111	01001	0101\	011000\0\111011\110111111100101011100	120111\	100110
Chasmanthium n	72	000\\\1010110101\\\\\001100011011011\\01100001111	0	\1110100	?????????????????????????????	?????	?????	\\\00000\11\011111010111100101011101	1\0111\	\\\\\\
Panicum	68	0\00\\0\\0010101010000110101100001110\01100001111	0	\1110000	?????????????????????????????	?????	?????	\1100001011101100\\001111001000\1101	110110\	110110
Pennisetum	33	0\00\\\\\\00101010100001101011010011000\100011111	0	\1110000	01\000111111111110000011111111	01001	0101\	0\0\\0\1011101101101\111\00101011100	110111\	110010
Miscanthus	30	0\000\0\\00001010100001101011000011000\100011111	0	\1110000	01\000111111111110100011011111	01001	0101\	\11\\0010111011\\\\001110001010\1101	1001111	100101
Amphipogon	48	\\\\\\\0\1011010101100011010\\\\\0011100\110011111	\	\1110100	010\\\\\0111111101000011011111	01101	0101\	001000\00111011101010111\\\101011101	1\1111\	100000
Eragrostis	28	0000000\\0010101010000100100000000111001101011111	\	\1110100	00\00111101110110101001100011	02101	0101\	001\\\\0010101111\\0011100\101011101	1\01111	1001\\
Uniola	65	00\\\0011001010101100010010000000111001101011111	0	\1110000	?????????????????????????????	?????	?????	00110000010101110\\\\111010101001101	120111\	\\\\\\
Zoysia	65	1000000\\01100010110001101010000000111001101011111	0	\1110000	?????????????????????????????	?????	?????	0110000001110111\\\\0111000111001101	120111\	100100
Distichlis	60	10000001101110101001000\10101000000111001101011111	0	\1110000	?????????????????????????????	?????	?????	01100000011101110\\\0111010111001100	110111\	100100
Spartina	29	1000000\\0110001001000\10101000000011100110101011	0	10110000	00\00110101111110101002101111	01201	0101\	011000\\011101110\\\0111010110001001	110111\	100100
Sporobolus	62	1100000\\0110001001000110101000000111001101001111	\	\1110000	?????????????????????????????	?????	?????	01100000\11101110\\10111010111001001	120111\	100100
Brachyelytrum	36	00\\\\\\\1011010101100001000\\000\\\\\\0100001111	0	\1110000	11010011111111110100000111011	01101	0001\	\01001\11111011101000111100\\1001101	011111\	101110
Lygeum	48	00\\\\\0\\\11011101\0000\\\10000\00101\1100001111	0	1111100\	010101\\\11011110100100011011	001\1	01001	\0100\11011101110\\0011100\\\\001101	111111\	001111
Nardus	58	011\\\00\0110111010000110100000\00101\1100001110	0	11000001	010\\\\\\111111110100100\11011	011\1	0101\	1\\00\\\11111111\\\\\\\11110\1010\\101	1001111	1011\\
Ampelodesmos	11	00000000101101010110000100011010000\0010111100001110	0	\1100001	110\\\10111011100100100111011	01101	01011	101\\\11011101011101\011111101001101	111111\	101101
Stipa	10	0000000\10110101011000010001101001010011000010111	0	\1100000	11010110111011100100100111011	01101	01010	\01\\\\001110111110\011111101001101	1111111	101101
Nassella	20	0000000\1011010101100001000110100101001000001111	0	\1110001	110101101110111\\100100111011	01101	01011	\01\\\\001\1011111000011101101000101	1111111	1011\\
Piptatherum	19	0000000\1011010101100001000\\\100101001100001111	0	\1110000	110101101110101\\100100111011	01101	11010	101\\\\0011101111100001111001001101	1111111	1011\\
Anisopogon	18	0000100010110101011000000000100100101001100000\111	0	\1110\01	11000111111001110100100111011	01101	11010	101\\\\11111011\11011111111101000101	111111\	101111
Brachypodium d	43	00\\\\0000110110001010110001000\\10\000100001110	\	\1110100	11000010011110110100101110011	011\1	01011	10101\\\1111011\11\00111111000101101	1111011	\\\\\\
Brachypodium p	24	000\1\000011011000101011000101000101000100001110	0	\1111001	11000010011110110100100110011	01101	01011	1010010\1111001\11100111100001101100	1011011	\\\\\\
Brachypodium s	42	000\1\000011011000101011000101000101000100001110	0	\\111001	11000010011110110100100110011	01101	0101\	101001\\1111011\11100111100001001100	1011011	\\\\\\
Schizachne	29	001110\\\010011100100000100100101000101000100001110	0	\\\11001	10000110111010100100100110111	11101	0101\	\01011\0111001100111011011\101001100	111111\	001101
Melica a	14	0001100\10100111001000001001001\0001\00100001100	0	\1010001	1101001011\011100100100111001	11101	01011	10100\\1111101101111011011\101001101	111111\	001101
Melica c	13	0011100\10100111001100001001001\0001000100001100	0	11010001	1101011011\011100100100111001	11101	01011	101011\1111101101111011011\101001101	111111\	001101
Glyceria s	16	1011100\\010011101110000100100001011000100001100	0	11010001	01010010011011100100100111001	11101	01010	101001011111011111111011011\101001101	111111\	000101
Glyceria d	24	1011000\101001110110000010010000101100010000 1100	0	\1010001	1100001001101110010\100110011	11101	0101\	1010\1\1111101101111011011\101001101	111111\	000101
Diarrhena	13	0011100010110101011000010001001001010011000 01100	0	\1\10001	11\\\\\\11\010100100100110011	01101	11011	101011111111101111\111111110001001101	111111\	101101
Bromus	13	0111100000110101001000110010101000010011000 01110	0	\1110000	11\00010111010101100101100020	11101	11010	1010101111111011101000111110000101101	111\01\	10\101
Boissiera	14	01111000001101010010001100101010000100110000 0010	0	\1110000	11\0101011101010\1001011\0010	11101	01010	1010110111111011100000111110\\0101101	0111011	101101
Triticum	10	011110000\110111001000100010101000010011000 00010	0	\1110000	11\0001011101010000001001\0010	11101	01010	1010111111111011101000111000000001101	0111112	100100
Elymus	11	011110000\11011100100000001010100001001100 001010	0	\1110000	11\000101110101001001011\0010	111\1	01020	1010111111111011101000111100000001101	0111111	100100
Peridictyon	17	011110000\11011100100000000101010000100110000 1010	0	\1110000	11\000101110\\1001001011\0010	11101	01010	1010111111111011101000111100000001101	011111\	1\\100
Anthoxanthum	23	01101\\\\011\111001\\\1\0010101000010011000 01010	0	\1110000	110010101110101111\0100110011	00111	01110	100001110111\11110001111100000001101	1111020	000101
Phalaris	17	011010000\11\101\\1000110010000\\\11\\1100011100	1	10110001	10000110111010100100100110011	00111	01110	101001110111\11101000111110000001101	1111110	100101
Amphibromus	14	0110100000110101001000110000000\\\1100110000\110	1	10110001	10001010111010111100100110011	01101	01110	101001110111\11111001111110000001101	1111110	100101
Ammophila	10	011010000011\1010010001100000001\\\11\01100001110	1	10110001	10001010111010101100100110011	01101	01110	10111110111\111100\\111110000001101	1111110	100101
Calamagrostis	7	011010000111\10100100011001000100111001100001110	1	10110001	10001010111010101200100110011	01101	01110	10111110111\111100\0111110000001101	1111110	100101
Agrostis	21	01101\\00111\10100100111001000100111001100001010	1	10110001	10\\\\\\\11010101100100110011	01101	01110	101111110111\111100\0111110000001101	1111110	100111
Deschampsia	5	0110100001110101001001110010001\\\01001100001010	1	10110001	10000010111010101100100110011	01101	01110	101111110111011110000111110000001101	1101110	100111
Arrhenatherum	8	011\100000110101001000110010001000\01001000001010	1	10110001	11001010111010101100100010011	01101	01010	1010011101110110110001111100000001101	1111110	\\\101
Avena	16	01101000\011\101001000110010001001110011000 01110	1	10110001	10001010111000001100100110011	01101	01010	101001110111\111110\0111110000001101	1111110	100101
Koeleria	10	0110100000110101001000110010001\\\\\1\\1100001110	1	\1110001	10001010111010101100100010011	01101	01010	1010011000110111100001111\0000001101	1\11110	1001\1
Trisetum	14	0010\0000011\10100100011001\\0100111\11100001110	1	10110001	10000010111010101100100010011	01101	01010	101001010011\111110\1111100000001101	1111110	100101
Sesleria	8	011010000\\\00011010001000000001001110011000 01110	1	10110001	10001010111010100100100110011	01101	01010	10101111011011110000111110000001101	0111111	10\101
Poa	11	011000100011\10110100010000000001001110011000 01010	1	10110000	00000010111010100100100110011	01101	11110	\01011111111\111100\0111110000001101	0111111	100101
Puccinellia	11	011010000\1101010010001100000 0\\\11\\1100001110	1	10110000	10001010111010101100100110011	01101	01110	101001101111011110000111110000001101	011111\	100101
Catabrosa	15	\11010000\11\0010010001100000 0\10011000110010111 0	1	10110000	10001010111000101100100010011	01101	01110	101011101111\111100\0111110000001101	011111\	100101
Festuca	18	0111000000011\10100100010000000001100011001 0\110	1	10110000	10101010111010101100100110011	01101	01010	101001101101\110110\0111110000001101	0111111	100101
Vulpia	19	\110\0000011\1011010001000000000\\\10\\1100001110	1	10110000	10100010111010101100100\0011	01101	00000	101011101101\111100\0111110000001101	0111111	100101
Lolium a	14	1100100000\11\1010010001100000000\\\10\\1100001110	1	10110010	10101010011010100100100110011	01101	01110	101001101101\111100\0111110000001101	0111111	100101
Lolium p	21	11001000001101010010001100000000001100011000\1110	1	10110010	11101010011010100100100110011	01101	01110	100001101101\11\\00\0111110000001101	0111111	100101

Appendix 1
Restriction Site Character Data

Taxon	*Bgl II*			*Hind III*			*Kpn I*		
	11122222233333444444555556666667777777 2334457813605768011681245780366800129014899 19281774244350225149461419145066627572824327	8889999 7893559 1993027	111111 000111 136133 383628	11222334444445555556677777777 136928367682235691256890701234586 6272293703170840740264314772056900	889 348 736	11111 00001 12351 97113	11122223334566677 246837990383035736 064649182724932390	899 558 139	11 00 27 42
Flagellaria	\\			0000\\\\\\0000\\0\0000011010000000	001	011\0	\\\\\\\\\\\\\\\\\\	100	00
Baloskion	00100100\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\	0101000	\\\\\\	\\\\\\0100\\00\\011000001\10000\\\	\01	01100	\\\\\\\\\\\\\\\\\\	000	00
Joinvillea	00100100000\00001101001\\\\\\\\\\\\\\\\\\\\\	0000\\\	\\\\\\	0000000100001100010000011011010000	001	0\010	\\\0001100100000100	100	00
Anomochloa	0100010000000000111\00100101\\\\\\\\\110\000	0101001	\\\\\\	000000011\0011000\10\0011010000001	001	01100	000000\100100100\\	101	00
Streptochaeta	00000110010\\0001111001\\\\\\\\\110011\\0101	1101000	\\\\\\	0000000111\01100110000011011010001	011	0\\10	0\\\\0110010010100	101	00
Pharus	00000100010\\000111\0110\\\\00\\110010101000	1101000	100101	00000001100011000\0010011110\10000	011	0101\	\00\\\110010000100	101	00
Ehrharta	0000010000000000111\\\0001\11001\1\\0\\\1001	1101010	101001	000000011\\1110011000\001100101000	011	00110	110011110010001110	101	10
Oryza	00000100000000001111011001010001110011001001	1101001	101001	0000000110001100110000011110011000	011	01100	011001110010100100	111	10
Leersia	00000100000\0001101011001010001110011001001	1101001	101101	0000000110001100110000011110011000	011	00100	110001110010000100	111	10
Eremitis	0000010001000100111\01100101\\\1110110101111	1101001	101001	0000000110001100110101011110010000	011	01110	010010110010001100	101	00
Bambusa	001001000000000011\0011001111001110011101111	1101001	101\\\	0000000110001100110010011110010000	011	01110	110000110010000100	101	10
Pseudosasa	001001000000000011\1011001111001110011101111	1101001	111001	1000000110001100110010011110010000	011	0\100	100000110010000100	101	10
Chusquea	0010001000001010110101100011001110011101111	1101001	111001	0000000110001100110001011110010000	011	01110	110000110010000100	101	10
Guadua	0010010000001000110101100111\\\\111001100111	1101001	101001	0000000110001100110001011110010000	111	01110	110000110010000100	101	10
Otatea	00100100000010001101011001111001110011001111	1101001	101001	0000000110001100110001011110010000	111	01110	110000110010000100	101	10
Lithachne	000001000000\0001010\\\\\\111001110011001111	1101001	101001	0\00010110001\00\\0011011100010000	011	01100	11001\\10010000000	101	0\
Olyra	00100100000000000\101\01100111\\\11100111011\1	1001001	1\\0001	000000110\\\\\\\\\\\\\\11110010000	011	\\\\\	110011\1001000\\00	101	10
Aristida	00100100000\\1\\111\01100111\\\1110011001111	1001001	100101	00000000100011001100010111100010\\	011	01100	100000010010000100	101	00
Arundo	00100100000\\\\\\101\011000110001010011001000	1101001	001001	0000000110101100110001011110011000	011	01100	110000110010001100	101	00
Molinia	0010010000000\\101\011001110001111011001111	1101001	001001	0000000110011100110001011110011000	011	01100	110000110010001100	101	00
Phragmites	0010010000000\\101\011001110001111011001111	1101001	001000	0000000110001100110001010110011000	011	01100	110000110010001100	101	00
Danthonia	010001000\\\\\\001111011001110001111011001111	1101001	001000	0000000110011100110001010110111000	011	01100	110000110000001100	101	0\
Chasmanthium l	001000\0000\\0\0\\\\\\11001110000110011000001	1101001	001000	0000000110001100110001011110011000	011	01100	110000110010001100	101	00
Chasmanthium n	001000\0000\\0\0111\111001011001010011001111	1101001	001001	0000000110001100110001011110011000	111	01100	110000110010001100	101	00
Panicum	0\\\\\00000\0000111\111001111001110011001111	1101001	000001	000000\110001100110000010110011000	011	01100	101\\0110010001100	101	00
Pennisetum	00100100000\000\\111011001011100001100110\\1	1101001	101001	000000011000110011000001111\011100	011	0\\00	111000110010001100	101	\0
Miscanthus	000001000001100\011\011001011000010001000\\1	1101001	001001	0000000110101101010000011110011100	011	01100	110000110010001100	101	00
Amphipogon	00100100000\\1\\111\0110011100001110011001\1	1100001	001001	100000011000110011000101111001\000	011	11100	100000110010001100	001	00
Eragrostis	0010010000000000111011100111\\\010001100\\\1	1001001	001001	00000001100011000\0000011110111000	011	11100	100000110010001100	101	00
Uniola	00100100000000\0111\11100111\\\0100011001100	1101001	001001	0000000110001100010000011110011000	011	11100	100000110010001100	101	00
Zoysia	0010010000\\\1\\111\111001\\\\\0100011001100	1101001	001001	0000001110001100010000011110011000	011	00100	110000010011000000	101	00
Distichlis	0010010000\\00\\111\11100111\\\0110001101111	1101001	001001	0000000010001110010000011110011000	011	11100	010000110010001100	101	00
Spartina	0010010000\\00\\111\111001\1\\\0110001000\10	1100001	000\01	0000000110001110\10000011110011000	011	10100	11000011001110\\00	101	01
Sporobolus	001001\000\\00\\111\111001\1\\\0110001101110	1101001	001001	0000000110001100010000011110011000	011	10100	11000011001100\\00	101	01
Brachyelytrum	001001000\0\\0001110011001011001110001101110	1101001	001001	000000011000110011000101111\\\\000	011	01100	000001110010000100	101	00
Lygeum	0010010000\001001101101\111100\\\\\\11100000	110101\	101001	1\0\100111001100110000011110000000	011	01100	1001001100101001\\	101	00
Nardus	00000100\\\\\\\\\\\0111\111101\\\\\\11100001	1111001	001000	1000100110011101110001011110100000	011	01110	100100110000100100	101	00
Ampelodesmos	00100100010000101110011001111011110011001111	1111001	101001	1\00000110001100110010011110\10000	011	01100	100000111010000110	101	00
Stipa	00100100010000101110001001111001110011001111	1011001	101001	1000000110001100110010011110110000	011	01100	110000111010000110	101	0\
Nassella	10100100010000101110111001111001110011001111	1011001	101001	1000000110001100110010011110110000	011	01100	110000111010000110	101	00
Piptatherum	001001000\\0001011100110011110101100110011\1	1011001	100001	1\00000110001100110010011110110000	011	01100	11000011\010000111	101	00
Anisopogon	001001000100101011100111\1111\\11100110011\1	1011001	100001	1000000110001100110100011110010000	011	01100	100000110010000110	101	00
Brachypodium d	000001000\\\\0\\\0000110\\111000110011001111	1011001	101001	1010000110001100110000011110010000	011	\\\10	100000110010000110	101	00
Brachypodium p	000001000000\\00010100110\\111000110011001111	1011001	100011	1011000110001100100000011110010000	011	00110	100000110010000110	101	00
Brachypodium s	000001000\\\\000101\0110\\\\\\\011\\\1001111	1011001	001011	1011000110001100100000001110010000	011	\\\10	100000\10010000110	101	00
Schizachne	101001\00\\01010111\0111\\\\\\\\1000110011\\	1011001	001010	1000000110011110110000\11110010010	010	00101	100000010010010111	100	00
Melica a	101001010100001011100111011100\\1100110011\\	1011001	101001	10000001100111100110000011110010000	010	00101	100000010010010111	100	00
Melica c	101001010100001011100110011100\\1100110011\\	1011001	101001	10000001100111100110000011110010000	010	00101	100000010010010111	100	00
Glyceria s	101001000100001011000110011100\\1100110011\\	1011001	101001	1000000110011110110000011110010010	011	00101	110000010010010110	100	00
Glyceria d	10100100000\001010000111\\\100\\110001000\\\	1011001	101001	1000001110011110110000011110010010	011	00101	110000010010010110	100	00
Diarrhena	00100100000001010111001\\\\111100011000100\\\	1011001	1\1001	1000000110001100110000011110010000	011	01100	100000110010000110	101	00
Bromus	001001000\\0011010100100\\111000110001001101	1011001	101001	1010000110001100110000011110010000	001	01100	110000110010001010	101	00
Boissiera	001001000\\0011010100100\\111000110001001101	1011001	101001	101\000110001100110000011110010000	001	01100	100000110010001010	101	00
Triticum	001001000000000101010\00\\111000110001001001	1011001	101001	1000000110001100110000011110010000	001	01000	110000110010001010	101	00
Elymus	001001000000000101010\00\\111100110001011101	1011001	101001	1000000110001100110000011110010000	001	01100	110000110010001010	101	00
Peridictyon	001001000000000101010\00\\111000110001011101	1011001	101001	1000000110001100010000011110010000	001	01100	110000110010001010	101	00
Anthoxanthum	0010010000000001010100100\\111000110001001101	1011001	101001	1000000110011001101001111110010000	011	01100	100000100110100010	101	00
Phalaris	0011110010100010110\1011\1111\00110101001111	1011001	101001	1000000110001100110100011110010000	011	11100	100000100110100010	101	00
Amphibromus	001111001010001011001011\1111\0011\\\1001111	1011001	101001	1000000110001100110100111110010000	011	01100	1000001000100\0010	101	00
Ammophila	001011001\\10010111001111\111000110\\1001111	1011001	101001	1000000110001100110100111110010000	011	01100	100000100010000010	101	00
Calamagrostis	001\11001\\11010111\0111111111001110101001111	1011001	101001	1000000110001100110100111110010000	011	01100	100000100010010010	101	00
Agrostis	001011001\\110101110011111111001110101001111	1011001	101001	1000000110001100110100111110010000	011	01100	100000100010000010	101	00
Deschampsia	001\11001\\1101110100111111111001110101001111	1011001	101001	1000000110001100110100111110010000	011	00100	100000100010000010	101	00
Arrhenatherum	000011001\\1101110100111111111001110101001111	1011001	101001	1000000110001100110100111110010000	011	01100	100000100010000010	101	00
Avena	001011001\\100101110011111111001110101001111	1011001	101001	1000000110001100110101111110010000	011	01100	100000100010000010	101	00
Koeleria	001011001\\10011100\0011111111000110001001100	1011001	101001	1000000110001100110110111110010000	011	01100	100000100010000010	101	00
Trisetum	001011001\\1001010100011111111000110001001101	1011001	101001	1000000110001100110100111110110000	011	01100	100000100010000010	101	00
Sesleria	00101100101000101010011111111000110001001101	1011001	101001	1000000110001100110000011110010000	011	01100	100000100010000010	101	00
Poa	0010010011000010111010111111010001\\01001001	1011101	101001	1100000110001100110000011110010000	011	01100	100000100010000010	101	00
Puccinellia	00100100110000101010101111111000010101001001	1011101	101011	1000000110001100010010011110010000	011	01100	10000\\\\000001010	101	00
Catabrosa	00000000110000101010101111101\00100101001001	1011101	101011	1000010110001100110010111110010000	011	01100	10000\\\\000001010	101	00
Festuca	0010110011001010111010111111000011\\01001001	1011101	101011	1100000110001100110000011110010000	011	01100	100000100010000011	111	00
Vulpia	00101100110010\1111010111111000011\\01001001	1011101	101011	1100000110001100110000011110010000	011	01100	100000100010000010	101	0\
Lolium a	00101100110\00111\\\10101111110011\\01001001	1011101	101011	1000000110001100110000011110000000	011	01100	100000100010000010	101	00
Lolium p	001011001\\\00\11\\\10111111110011\\01001001	1011101	101011	1000000110001100110000011110000000	011	01100	100000100010000010	101	00

Appendix I
Restriction Site Character Data

```
Taxon                        Pac I                    Pvu II

              111111122333444555567777  111
              170245883725924922459437 9 99 001        334555567 89  111
              243860176512824904844065 5 78 343        7259115855 08  001
                                                        71740577996 99  242
                                                                       010
Flagellaria   1\\\\\\\\\\\\\\\\\\\\\\\\ \\\\\\ 
Baloskion     \\\\\\\\\\\\\\\\\\\\\\1001 00 \\\       ?????????? 00 ???
Joinvillea    110000000100010\\\\\\\\\\ 00 \\\        ?????????? 00 ???
Anomochloa    01011\0000100010002000000 01 110        00000010000 10 000
Streptochaeta 010100000010\010\\\\00000 01 110        01000100000 10 000
Pharus        010000000\0010\\00100000  01 \0\        11000100000 10 000
Ehrharta      00010000011\00\\\1101000  01 110        10000010000 10 000
Oryza         01000000011001100110010000 01 100       10001010000 10 000
Leersia       0100\\0001100010\\11001000 01 110       10000010001 10 000
Eremitis      0100\\00011000\\\\11001000 01 110       10000010001 10 000
Bambusa       0101\0001100010\110010000 01 110        10000010000 10 000
Pseudosasa    010100000110001\100010000 01 110        10001010000 10 000
Chusquea      01011100011\0010\\10010000 01 110        10001010000 10 000
Guadua        0101\\00011\0010\\1001100 01 110        10000010000 10 000
Otatea        0101\\00011\0010\\1001000 01 110        10000010000 10 000
Lithachne     00\\000001100000\\\01000  01 110        10000010000 10 000
Olyra         0000\\0001100001\\\01000  01 110        10001010000 10 000
Aristida      01011100001\\000\\12001000 01 110       10001010000 10 000
Arundo        0100\\0001100010\11011000 11 010        10000010100 10 000
Molinia       010011000110001001011000  01 110        10000010100 10 100
Phragmites    0100\\00011000\\11001000  11 110        10000010100 10 000
Danthonia     0100\\0001100010\\\\11001 11 110        10000010100 10 100
Chasmanthium 1 0100\\0001100010\10001000 11 110       10000010100 10 100
Chasmanthium 2 010010000110001001101000  11 110       10000010100 10 101
Panicum       01001100011000\\11001000  11 110        10001010100 10 10\
Pennisetum    0100\\0001100010\11001000 11 110        10001010100 10 100
Miscanthus    0100\\0001100010\11001000 11 110        10001010100 10 100
Amphipogon    01001\0001100010\10000000 11 110        10001010100 10 100
Eragrostis    0101\\0001100010\10000000 11 110        10011101\0 10 \\\
Uniola        0000\\00011000010010000\\ 01 110        10000010100 10 100
Zoysia        0000\\0001100010\12000000 01 110        10000010100 10 \\\
Distichlis    0000\\00011000010010000   01 110        10000010100 10 001
Spartina      0100\\0001100010\12000000 01 110        10000010100 10 101
Sporobolus    010011000110001\11000000  01 110        10000010100 10 101
Brachyelytrum 0\\0\\0001100010\11000000 01 110        10000010100 10 101
Lygeum        0100\\0001100100\\\\11000 01 110        10000010100 10 101
Nardus        01000000011000\\\\\00     01 010        10000010000 10 00\
Ampelodesmos  010100001100010122110000  01 010        10000100000 10 000
Stipa         01010000011000101\\011 01 010           10000010100 10 000
Nassella      0101\\0001100\11000000    01 100        00000010000 10 000
Piptatherum   01010000011000\\11000000  01 100        00000010000 10 000
Anisopogon    010100000110001\\1001000  01 100        00000010000 10 000
Brachypodium d 010100000110001\11001000 01 110        00000010000 10 000
Brachypodium p 0101\\0001001010\\11001000 01 110      00000010000 10 \\\
Brachypodium s 00010000010010\\\\01000  01 010        10001000000 10 000
Schizachne    0001000001001010\\\01000  01 010        10001000000 10 000
Melica a      0100\\00010010112110100   01 010        10000010000 10 000
Melica c      0100\\0001000100110100    01 100        00000010000 10 000
Glyceria s    0100\\00011000101110100   01 100        00000010000 10 000
Glyceria d    010\\00011000101110100    01 100        00000000010 10 000
Diarrhena     0100\\0001100010\110\1000 01 110        00001000000 10 000
Bromus        010100000110011011110\    01 110        00001000000 10 0\\
Boissiera     00010000001000101110\     01 110        00000010000 10 000
Triticum      0010000000100010\0000000  01 110        10010000000 10 000
Elymus        00010010001000100\0000000 01 110        10010000000 11 00\
Peridictyon   0001001000100010\\0000000 01 110        10010000000 11 000
Anthoxanthum  000100100\100010\\0000000 01 110        10010000000 11 000
Phalaris      0100000011000\11001000    01 110        10010000000 11 00\
Amphibromus   010000001101010\110010000 01 110        10010000000 11 000
Ammophila     01000000010110\11001000   01 110        00010001000 10 000
Calamagrostis 010000001101010\110010000 01 110        00010001000 10 000
Agrostis      010000001101010\11001000  01 110        00010000\000 10 000
Deschampsia   0100000011101010\11001000 01 110        00010000000 10 010
Arrhenatherum 00000001101010\11001000   01 110        00010000000 10 010
Avena         0100000101101010\11001000 01 110        00010000000 10 010
Koeleria      010000011110010\11001010  01 110        10010000000 10 010
Trisetum      010000011110010\11001010  01 110        10010000000 10 010
Sesleria      \\\0000111101010\11001010 01 110        10000000000 10 000
Poa           01000001110010\11011010   01 110        10001000100 10 000
Puccinellia   0100000000110011\11001000 01 110        10001000000 10 000
Catabrosa     010000000110010\11001000  01 110        00000000010 10 000
Festuca       010000000110010\11001000  01 111        00010000010 10 000
Vulpia        0010000001110010\11001000 01 111        00000000010 10 000
Lolium a      00100000010100001\1000    01 110        00110000000 10 000
Lolium p      00000000011000\\\1100      01 110        00110000000 10 000
              00000000011000\\11001000  01 110        00010000000 10 000
                                                       00010000000 10 000
```

```
              Sal I                        Sma I

                        1 1                                            1
              1112223334467777 8890 1     11112222223344455666677778 89  1
              4560574587820568 1961 1     71259122356271484900591268 0 08  1
              3360422521336491 1350 2     8314720068885594210683125 83 89  5
Flagellaria   \\\\\\\\\\\\\\\\ 001  0     \\\\\\\\\\\\\00000000\\000 01  0
Baloskion     \\\\\\\\\\\\\\100 0010 0    1\\000\\\0000000101000\\001 01  \
Joinvillea    0001011101000100 0010 0     1\\000\\\0000000101000\\001 01  \
Anomochloa    0001011101000100 0110 0     0\\\\\\\\\\\001001\\\\001 11  \
Streptochaeta 0001011101000100 0110 0     0\\\\\\\\\\\001001\\\\001 \2  0
Pharus        0001000101000100 0110 1     0000002\00000\\\\0010000010 11  1
Ehrharta      0001011101000100 0110 1     0000000\\\\\11000\00000 10  0
Oryza         0001001001000100 0110 1     010000\\\00000100000110000 10  0
Leersia       0001011101000100 1110 \     0\\000\\\00\001000000000 11  1
Eremitis      0001011101000100 0110 0     011000\\\00000101001000010 11  1
Bambusa       0001011101000100 0110 0     011000\\\00000101001000010 11  1
Pseudosasa    0001011101000100 0110 0     0\\000\\\00000010\011000010 11  1
Chusquea      0001011101000100 0110 0     0\\000\\\00000010\011000010 11  1
Guadua        0001011101010100 0110 0     0\\0001100000010\01010000 10  0
Otatea        0001011101000100 0100 0     0\\0001\00000010\0011000000 11  1
Lithachne     0001011101000100 0110 0     011000\\0000010\0011000010 11  1
Olyra         0001011101000100 0110 0     0\\000\\\00000010010011000 11  0
Aristida      0001010101000100 0110 0     0\\000\\\0000100100010011 11  0
Arundo        0001011101000101 0110 0     000000\\\00\0100\0011000010 11  0
Molinia       0001011101000001 0110 0     0\\000\\\00000100100100000 11  1
Phragmites    0001011111000100 0110 1     0\\000\\\00000100100110000 11  1
Danthonia     0001011101000100 0110 0     \\\0001\\001001001000000 \1  1
Sporobolus    0011011101010100 0110 0     000000\\\001010010\0100000 11  1
Brachyelytrum 0011011101010100 0110 0     000000\\\001010010\0100000\\ 11  1
Lygeum        0011011101010100 0110 0     000002\0010110010010000000 11  1
Nardus        0011011101010100 0110 0     000002\001110010010000000 11  1
Ampelodesmos  0001011101000100 111\ 1     0000001010100001000000000 11  1
Stipa         0001011101000100 0111 1     0\\1001000001001001000000 11  1
Nassella      0001011101000100 0111 1     001001000000\0\0011000000 11  1
Piptatherum   0001011101000100 0111 0     000000100010010101101000 11  1
Anisopogon    0101011101000100 0111 0     000000110010001010011000 01  1
Brachypodium d 0001011101000100 0111 0    000000001001010101001000 11  1
Brachypodium p 0001011101000100 0111 0    000000000\\00100011000000 11  1
Brachypodium s 0001011101000100 0111 0    0\\0001\00010\0\0011000010 \1  1
Schizachne    0001011101000100 0111 0     0\\0001\000100\0\0011000010 11  1
Melica a      0001011101000100 0111 0     0\\0001\0000100010\001000 10  1
Melica c      0001011101000100 0111 0     0\\00010000010\10\1000010 10  1
Glyceria s    0001001011000000 0111 0     000010100000110011000100 11  0
Glyceria d    0001011101100000 0111 0     0000101000000011\0011000100 11  0
Diarrhena     0001011101100100 0111 0     0000101000100011\0011000100 11  0
Bromus        0001011101100100 0111 0     0001010010001\0011000010 11  1
Boissiera     0001011101000100 0111 0     001010001001010\0011000010 11  1
Triticum      1001011101000100 0111 0     0010100010000100\011000010 11  1
Elymus        1001011101000100 0111 0     0000000100001\0011010010 11  1
Peridictyon   1001011101000100 0111 0     0000000100010\0011010010 11  0
Anthoxanthum  0001011101000100 1111 0     0000011101101000\\11000000 11  1
Phalaris      0001011101000100 1111 0     1000010001010\0011000000 11  1
Amphibromus   0001011101000100 1111 0     0000011001101000\0011000000 11  1
Ammophila     0001011101000100 1111 1     0000011001101000\0011000000 11  0
Calamagrostis 0001011101000100 1111 1     0000021001101000\0011000000 11  0
Agrostis      0001011101000100 1111 0     0000021001101000\0011\0000 11  0
Deschampsia   0001011101000100 1111 0     000010100110000\01011000 10  0
Arrhenatherum 0001111101000101 1111 0     0000011001010000\021000000 01  1
Avena         0001111101000100 1111 0     0000011011101000\011100000 01  1
Koeleria      0001011101000100 0111 0     000010100100000\01011000 01  1
Trisetum      0001011101001100 0111 0     0000001000100000\1011000000 01  1
Sesleria      0001011101000100 0111 0     000001\00000000\0011000000 11  1
Poa           0001011101001110 0111 0     0000001\00000000\001\\1000 11  1
Puccinellia   0000011101001100 0111 0     00000\1000100000\0011001000 11  0
Catabrosa     0000011101001100 0111 0     00000010001\0000\0011001000 11  0
                                          00000010001\0000\0011001000 11  0
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IX. Appendix 2: Structural Characters and States

Forty-two structural characters were scored for 75 exemplar taxa of Poaceae and related families (Table I), and notes on scoring are given where different from that of Watson and Dallwitz (1992) or where Watson and Dallwitz provide no report; where scoring differs from that of Watson and Dallwitz, their scoring is noted prior to that used in the analysis. Abbreviations: "C&R" = Clayton & Renvoize, 1986; "DCY" = Dahlgren et al., 1985; "H&W" = Hattersley & Watson, 1992; "W&D" = Watson & Dallwitz, 1992; "nr" = no report in Watson & Dallwitz, 1992 (implicit for taxa in families other than Poaceae); "pers. obs." = personal observation of specimens at the L. H. Bailey Hortorium; "-" = inapplicable; "?" = unobserved; "\" = homology ambiguous or observed state intermediate between recognized states. Multiple states [in brackets] signify polymorphism or subset ambiguity in multistate characters, where one or more states are determined to be absent (e.g., [01] for a character with states 0, 1, and 2, signifies polymorphism of states 0 and 1 OR indeterminant homology where state 2 is determined to be absent, but discrimination between states 0 and 1 has not been made). Guadua is included in Bambusa, and Eremitis in Pariana, by Watson and Dallwitz. Information on Baloskion is to be found in the primary literature under Restio, except when provided by H. P. Linder or B. Briggs. All multistate characters are scored as unordered. Four individual numbers (or ranges) following each character description represent results of optimization of the character on 12 most-parsimonious trees obtained by simultaneous analysis of restriction site and structural data (see text); the four numbers are number of steps on most-parsimonious trees, number of extra steps beyond minimum required if character were consistent with trees, consistency index, and retention index, respectively. Additional steps implied by polymorphism within terminals not included in calculation of steps or CI.

CULM

1: Perennating and branching woody culms: 0 = absent; 1 = present. NOTE: See Soderstrom (1981: 16) for a strict definition of "woody" versus "herbaceous" in Bambusoid grasses. 2, 1, 0.50, 0.80.
  Flagellaria = \. Stems perennate, but whether vegetative stems branch or are lignified is uncertain (pers. obs.).
  Baloskion (*Restio* = [01]; DCY). *Restio tetraphyllus* = 0 (Black, 1960).
  Joinvillea = 0 (Newell, 1969).
  Eremitis (W&D 1). *Eremitis* = 0, persisting alive for one year, or two at maximum, non-branching (V. Hollowell, pers. comm.).

2: Culm internodes: 0 = solid; 1 = hollow. NOTE: Occurrence of a small pore is considered intermediate. 11, 10, 0.09, 0.09.
  Flagellaria = 0 (DCY; pers. obs.).
  Baloskion = 1 (B. Briggs, pers. comm.).
  Joinvillea = 1 (DCY; pers. obs.).
  Aristida (W&D [01]). *Aristida purpurea* = 0 (Ebinger & Carlen, 1975; Brown et al., 1959).
  Danthonia (nr). *Danthonia californica* = 1 (pers. obs.).
  Eragrostis (W&D [01]). *Eragrostis curvula* = \, small pores (Brown et al., 1959).
  Eremitis (nr). *Eremitis* = 1 (V. Hollowell, pers. comm.).
  Leersia (W&D [01]). *Leersia virginica* = 1 (Ebinger & Carlen, 1975).

  Nassella (nr). *Nassella viridula* = 1, included in *Stipa* in Hitchcock, 1969.
  Panicum (W&D [01]). *Panicum virgatum* = 1 (Ebinger & Carlen, 1975).
  Pennisetum (W&D [01]). *Pennisetum alopecuroides* = 0 (Ebinger & Carlen, 1975).
  Spartina (W&D [01]). *Spartina pectinata* = 1 (Ebinger & Carlen, 1975).
  Sporobolus (W&D [01]). *Sporobolus giganteus* = 0 (Holmgren & Holmgren, 1977).
  Uniola (nr). *Uniola paniculata* = \, culms solid or with a small pore (Brown et al., 1959), or hollow (Ebinger & Carlen, 1975).

LEAF

NOTE: Characters 4 through 6 are inapplicable for *Baloskion* (B. Briggs, pers. comm.).

3: Leaf sheath margins: 0 = free; 1 = fused at least ¼ of length. 5, 4, 0.20, 0.60.
  Flagellaria indica = 1 (pers. obs.), but the genus is polymorphic (pers. obs., contra DCY).
  Baloskion = 0 (pers. obs.).
  Joinvillea = 0 (DCY; pers. obs.).
4: Adaxial ligule type: 0 = membrane (with or without fringe of hairs); 1 = fringe of hairs only. 4, 3, 0.25, 0.62.
  Flagellaria = -, no ligules (pers. obs.).
  Joinvillea = 0, when present (DCY; pers. obs.).
  Aristida (W&D [01]). *Aristida purpurascens* = [01], either a minute fringed collar or a fringed membrane (Gould, 1975).
  Ehrharta (W&D [01]). *Ehrharta calycina* = 0, membranous, not ciliate (pers. obs.).
  Panicum (W&D [01]). *Panicum virgatum* = 0, a fringed membrane (Gould, 1975).
  Pennisetum (W&D [01]). *Pennisetum alopecuroides* = 1, ciliate with a very short collar (pers. obs.).
  Sporobolus (W&D [01]). *Sporobolus giganteus* = [01], either a minute fringed collar or a fringed membrane (Gould, 1975).
  Zoysia (W&D [01]). *Zoysia japonica* = [01], densely ciliate on the margin, but the membranous portion is variable in occurrence (pers. obs.).
5: Abaxial (contra-) ligule: 0 = absent; 1 = present. 1, 0, 1.00, 1.00.
  Flagellaria = 0 (pers. obs.).
  Joinvillea = 0 (pers. obs.).
  Bambusa (nr). *Bambusa* = 1 (Davidse et al., 1994), *Bambusa multiplex* = 1 (Judziewicz, 1990; pers. obs.).
  Chusquea (nr). *Chusquea* = 1 (Soderstrom & Calderón, 1978: fig. 2).
  Eremitis (nr). *Eremitis* = 0 (V. Hollowell, pers. comm.).
  Guadua (nr). *Guadua* = 1 (Judziewicz, 1990).
  Olyra (nr). *Olyra latifolia* = 0 (pers. obs.).
  Oryza (nr). *Oryza sativa* = 0 (pers. obs.).
  Pharus (nr). *Pharus latifolius* = 0 (pers. obs.).
  Stipa (W&D [01]). *Stipa barbata* = 0 (Bor, 1968; Martinovský, 1980).
6: Pseudopetiole: 0 = absent; 1 = present. 1-2, 0-1, 0.50-1.00, 0.90-1.00.
  Flagellaria = [01] (pers. obs.).
  Joinvillea = 1 (pers. obs.).

SPIKELET

NOTE: Spikelet characters 7–13 are inapplicable or ambiguous except when grass-type spikelets or florets are present. The three nongrass genera do not have grass-type spikelets or florets. Pseudospikelets in *Bambusa* and *Guadua* are possibly homologous to each other, and grass-type florets are evident. However, pseudospikelets in *Anomochloa* and *Streptochaeta* are neither alike nor of the Bambuseae form, and the homology of any or all of their floral bracts with those of typical grass spikelets or florets is ambiguous (C&R; Judziewicz & Soderstrom, 1989).

7: Pedicel of spikelet: 0 = absent; 1 = present. 5, 4, 0.20, 0.31.
   Amphipogon (W&D equivocal, not truly sessile). *Amphipogon strictus* = 1, spikelets subsessile (Black, 1960).
   Chasmanthium (W&D [01]). *Chasmanthium latifolium* = 1, pedicels present, *Chasmanthium nitidum* = 1, spikelets subsessile (Hitchcock, 1951).
   Eremitis (W&D refer to a false spike). *Eremitis* = 1, never sessile (V. Hollowell, pers. comm.).
8: Proximal female-sterile florets in female-fertile spikelets: 0 = absent; 1 = present. 7, 6, 0.14, 0.45.
   Leersia and *Oryza* = \, homology of the vestigial bracts below the single fertile floret is ambiguous, as these may represent sterile florets or glumes (Núñez, 1968; Clifford, 1987).
   Ehrharta = 1.
9: Number of female-fertile florets per female-fertile spikelet: 0 = two or more; 1 = one. 13, 12, 0.07, 0.57.
   Melica (W&D [01]). *Melica cupanii* = 1, *Melica altissima* = [01] (Davis, 1985).
10: Awn or mucro on fertile or sterile lemma: 0 = absent; 1 = present. 13–14, 12–13, 0.07–0.08, 0.45–0.50.
   Ehrharta (W&D [01]). *Ehrharta calycina* = 1 (pers. obs.).
   Panicum (W&D [01]). *Panicum virgatum* = 0 (Gould, 1975).
11: Awn attachment: 0 = terminal / subterminal; 1 = from a sinus; 2 = dorsal. NOTE: Character 11 is inapplicable for taxa scored 0 for character 10, and is considered applicable for taxa polymorphic for character 10. 6, 4, 0.33, 0.69.
   Ampelodesmos (W&D 1). *Ampelodesmos mauritanicus* = [01], awn terminal or from a very short sinus (Tutin, 1980; pers. obs.).
   Amphipogon (description by W&D does not clearly translate to our states). *Amphipogon strictus* = [01], ambiguous, but not dorsal (pers. obs.).
   Anisopogon (W&D 1). *Anisopogon avenaceus* = 1, three awns, the central from a distinct sinus in our interpretation (Black, 1960).
   Arundo (W&D [012]). *Arundo donax* = [01], apical or subapical from a minute to short sinus (Gould, 1975).
   Bromus (W&D [012]). *Bromus inermis* = 0, awnless or with a short, almost terminal awn (i.e., with a minute flange of tissue between the apex and awn; pers. obs.).
   Ehrharta (W&D [01]). *Ehrharta calycina* = 0, terminal (pers. obs.).
   Guadua (W&D *Guadua* mucronate). *Guadua* = 0, apiculate or in one species with a 3–5 mm awn (Davidse et al., 1994).
   Schizachne (W&D awned from just below a sinus). *Schizachne* = [12], variable (Hitchcock, 1969).

Stipa, *Nassella*, and *Piptatherum* (W&D 0). The awn in Stipeae is interpreted as from a sinus when lateral lobes are present. *Stipa barbata* = [01] (Bor, 1968), and *Nassella viridula* = [01], lobes to 1.5 mm present or absent (Hitchcock, 1969), *Piptatherum miliaceum* = 0, no lobes evident (pers. obs.).
12: Disarticulation above glumes: 0 = absent; 1 = present. 8, 7, 0.12, 0.30.
13: Germination flap in lemma: 0 = absent; 1 = present. 5, 4, 0.20, 0.33.
   Calamagrostis (nr). *Calamagrostis* = 0 (Johnston & Watson, 1981).
   Eremitis (nr). *Eremitis* = 0 (V. Hollowell, pers. comm.).
   Oryza (nr). *Oryza* = 1 (Johnston & Watson, 1981).
   Phragmites (nr). *Phragmites* = 0 (Johnston & Watson, 1981).

FLOWER

NOTE: Characters 14–18 are scored as ambiguous for taxa that have tepals rather than lodicules, and characters 15–18 are scored as inapplicable for taxa that are scored 0 for character 14. Character 14 is scored as ambiguous in *Streptochaeta* and *Anomochloa*, as the homology of structures sometimes called lodicules in those taxa is ambiguous. Reporting and application of lodicule characters 17 and 18 by W&D is inconsistent with the literature and available illustrations for our taxa (e.g., lodicules in Stipeae reported as fleshy or membranous, heavily vascularized). We observed lodicules of as many taxa as possible from specimens and original literature (Jirasek & Jozífova, 1968; Tzvelev, 1977).

14: Lodicules: 0 = absent; 1 = present. 3, 2, 0.33, 0.50.
   Aristida (W&D [01]). *Aristida purpurea* = 1 (Gould, 1975; Holmgren & Holmgren, 1977).
15: Lodicule number: 2 = two; 3 = three; 4 = four; 5 = five; 6 = six. 4–5, 3–4, 0.20–0.25, 0.63–0.72.
   Nassella (W&D 2 "in material seen"). *Nassella viridula* = 2 (Hitchcock, 1969, where it is included in *Stipa*).
   Stipa (W&D 3 or rarely 2). *Stipa* = [23], three or very rarely two lodicules (Bor, 1968; Tzvelev, 1977).
16: Fusion of anterior pair of lodicules: 0 = free; 1 = fused. 1, 0, 1.00, 1.00.
   Glyceria (W&D 1 for whole genus). *Glyceria* = [01], variable; *G. declinata* = [01], free or fused in *G. fluitans*, a close relative (Jirasek, 1969; Jirasek & Jozifova, 1968); *G. striata* = [01], free or possibly fused only near the base (Hitchcock, 1969).
   Schizachne (W&D 1). *Schizachne* = [01], free or fused (Hitchcock, 1969).
17: Distally membranous portion of lodicule: 0 = absent; 1 = present. 2, 1, 0.50, 0.93.
   Eremitis (nr). *Eremitis* = 1 (V. Hollowell, pers. comm.).
   Nassella (W&D fleshy). *Nassella viridula* = 1 (Hitchcock, 1969).
   Panicum (W&D 0). *Panicum virgatum* = [01], ambiguous, rudimentary (pers. obs.).
   Stipa (W&D fleshy or membranous). *Stipa barbata* = 1 (Bor, 1968).
18: Lodicule vascularization: 0 = very faint to absent; 1 = prominent. 2, 1, 0.50, 0.95.
   Anisopogon (nr). *Anisopogon avenaceus* = 0 (pers. obs.).
   Brachyelytrum (W&D 0). *Brachyelytrum* = 1 (Macfarlane & Watson, 1980; Campbell et al., 1986; pers. obs.).
   Danthonia (nr). *Danthonia californica* = 1 (pers. obs.).
   Eremitis (nr). *Eremitis* = 1 (V. Hollowell, pers. comm.).
   Panicum (nr). *Panicum virgatum* = 1 (pers. obs.).

Piptatherum (W&D 1). *Piptatherum miliaceum* = 0 (pers. obs. for this species; Tzvelev, 1977, for other species).

Stipa (nr). *Stipa barbata* = 0 (Bor, 1968).

19: Stamen number: 1 = one; 2 = two; 3 = three; 4 = four; 5 = five; 6 = six. 10–11, 6–7, 0.36–0.40, 0.36–0.45.

Flagellaria = 6 (DCY).

Baloskion (*Restio* = [123]; DCY). *Restio tetraphyllus* = 3 (H. P. Linder & B. Briggs, pers. comm.).

Joinvillea = 6 (DCY).

Anthoxanthum (W&D [23]). *Anthoxanthum odoratum* = 2 (Tzvelev, 1977; Tutin, 1980).

Diarrhena (W&D [123]). *Diarrhena obovata* = [23] (Great Plains Flora Association, 1986).

Ehrharta (W&D [346]). *Ehrharta calycina* = 6 (Black, 1960).

Eremitis (W&D = 10–40). *Eremitis* = 2 (V. Hollowell, pers. comm.; C&R), and *Pariana* = 6–30 (C&R).

Glyceria (W&D [23]). *Glyceria striata* = 2 (Hitchcock, 1969). *G. declinata* = 3, (Holub, 1980; Tzvelev, 1977).

Leersia (W&D [1236]). *Leersia virginica* = [12] (Fernald, 1950).

Vulpia (W&D [123]). *Vulpia alopecuros* = 3 (Stace, 1980).

20: Styles fused at least at base: 0 = absent; 1 = present. NOTE: The solitary style in some taxa (see character 21) can be interpreted as the product of fusion or reduction in number, and those taxa are scored as ambiguous for character 20. 8–9, 7–8, 0.11–0.12, 0.50–0.56.

Flagellaria = 0 (DCY).

Baloskion = 1 (B. Briggs, pers. comm.).

Joinvillea = [01], variable within the species, sometimes fused for a short distance (DCY).

Anomochloa (nr). *Anomochloa* = \ (Clifford, 1987: 27; Judziewicz & Soderstrom, 1989).

Eremitis (W&D [01]). *Eremitis* = \ (V. Hollowell, pers. comm.).

Nardus and *Lygeum* (W&D 1). Both = \ (Clifford, 1987).

21: Number of stigmas: 1 = one; 2 = two; 3 = three; 4 = four. 7, 5, 0.28, 0.44.

Flagellaria = 3 (DCY).

Baloskion (*Restio* = [123]; DCY). *Restio tetraphyllus* = 2 (Black, 1960).

Joinvillea = 3 (DCY).

Eremitis (W&D 2). *Eremitis* = 1 (V. Hollowell, pers. comm.).

Lithachne (W&D 1). *Lithachne humilis* = 2 (Judziewicz, 1990; pers. obs.).

Peridictyon (nr). *Peridictyon* inferred to be = 2, no reports to the contrary found in *Elymus* (in which it was formerly included), or for the tribe (C&R; Tutin, 1980).

22: Highest order of stigmatic branching present: 1 = simple (unbranched, or with branches composed of single elongate papillate receptive cells, or with very short branches composed of a few papillate receptive cells, but in the latter case the stigmas linear in outline); 2 = primary (branches well developed, composed of series of dispersed papillate receptive cells, secondary branches absent or minimally developed, stigmas lanceolate or broader); 3 = secondary (secondary to tertiary branches well developed, branches composed of series of dispersed papillate receptive cells). NOTE: In the present study only stigmas with state 2 or 3 are called plumose. This character is not recorded by W&D. Major general references are Kunth, 1835; Nees, 1843; Tzvelev, 1977; Heslop-Harrison & Shivanna, 1977. Specific references for Bambusoids

are Camus, 1913; Clark & Londoño, 1991; Judziewicz, 1987; Judziewicz & Soderstrom, 1989; McClure, 1973; Soderstrom, 1980; Soderstrom & Calderón, 1978; Soderstrom & Zuloaga, 1989. 5, 3, 0.40, 0.72.

Flagellaria = 1 (DCY; Engler & Prantl, 1888; Heslop-Harrison & Shivanna, 1977).

Baloskion (*Restio* = [12]; DCY). *Restio tetraphyllus* has minimal primary branching (Black, 1960), and B. Briggs (pers. comm.) refers to it as plumose. We recognize it as ambiguous with regard to states 1 and 2, and regard state 3 as absent.

Joinvillea = 1 (DCY; Engler & Prantl, 1888). Both Cronquist (1981) and DCY report stigmas of *Joinvillea* as plumose, but the stigmas are simple, without well-developed primary branches evident in illustrations (DCY; Engler & Prantl, 1888; see also Heslop-Harrison & Shivanna, 1977).

Eremitis (nr). *Eremitis* = 1, (V. Hollowell, pers. comm.).

FRUIT AND EMBRYO

NOTES: Four embryo characters that refer to parts of the typical grass-type embryo (26–29) are inapplicable for the three nongrass genera, which lack the grass-type embryo (i.e., have state 0 of character 25). Because W&D indicate that data provided for *Piptatherum* for embryo characters may refer to *Oryzopsis* Michx., *Piptatherum* was left unscored for characters 26–31 unless data were specifically available under that name.

23: Number of ovules per pistil: 1 = one; 2 = two; 3 = three. 2, 0, 1.00, 1.00.

Flagellaria = 3, one ovule per locule and 3 locules (DCY).

Baloskion = 2, two locules, one ovule per locule (Black, 1960).

Joinvillea = 3, one ovule per locule and 3 locules (DCY).

24: Hilum: 0 = linear-long, >⅓ length of grain; 1 = nonlinear, <⅓ length of grain, elliptical or broader to punctiform. NOTE: linear-short, <⅓ length of grain, is considered ambiguous. 7–8, 6–7, 0.12–0.14, 0.68–0.72.

Amphipogon (W&D short). *Amphipogon* = 1, punctiform (Black, 1960).

Aristida (W&D long-linear or short). *Aristida purpurea* = 0, long-linear (pers. obs.).

Arundo (W&D short). *Arundo donax* = 1, short, broadly obovate, 1/5 length of grain, sub-basal (pers. obs.).

Calamagrostis (W&D short). *Calamagrostis* = 0, long-linear (Nees, 1843; pers. obs.).

Chasmanthium (W&D short). *Chasmanthium latifolium* = 1, narrowly elliptical, 1/5 length of grain, basal to sub-basal (pers. obs.).

Danthonia (W&D usually long-linear). *Danthonia californica* = 0, long-linear (pers. obs.).

Distichlis (W&D short). *Distichlis stricta* = 1, punctiform, sub-basal or basal (pers. obs.).

Eremitis (nr). *Eremitis* = 0 (V. Hollowell, pers. comm.).

Pennisetum (W&D short). *Pennisetum alopecuroides* = 1, elliptical small, 1/5 length of grain (pers. obs.).

Phragmites (W&D short). *Phragmites* = \, ⅓ length, narrowly elliptical (Bor, 1968; Tzvelev, 1977).

25: Embryo position and structure: 0 = embedded, simple; 1 = lateral, grass-type. NOTE: The grass-type embryo is lateral, peripheral to the endosperm, and differentiated in fruit (Reeder, 1957; Cronquist, 1981; DCY). Although presence of this type of embryo is not explicitly recorded by W&D, state 1 is inferred for all grasses for which they record embryo characters. 1, 0, 1.00, 1.00.

Flagellaria, Joinvillea, and *Baloskion* = 0, central, undifferentiated in fruit (DCY).

26: Embryo epiblast: 0 = absent; 1 = present. 8, 7, 0.12, 0.46.

Bambusa (nr). *Bambusa* = 1 (Kinges, 1961; Yakovlev, 1950: fig. 63),

Brachypodium (W&D [01]). *Brachypodium sylvaticum* = 0 (Mlada, 1977: pl. I); *B. pinnatum* = 1 (Mlada, 1977: pl. II); *B. distachyon* = [01] (scored as in W&D).

Elymus (W&D [01]). *Elymus trachycaulus* = 1 (Mlada, 1977: pl. V).

Guadua (nr). *Guadua* = 1 (Reeder, 1962),

Lygeum (nr). *Lygeum* = 1 (Kennedy, 1899: pls. 25 & 26).

Vulpia (nr). *Vulpia hispanica* = 1 (*Nardurus* [Bluff, Nees, Schauer] Rchb. in Decker, 1964).

27: Embryo scutellar tail: 0 = absent; 1 = present. 2, 1, 0.50, 0.96.

Anthoxanthum (W&D 0). *Anthoxanthum odoratum* = [01], polymorphic (Kennedy, 1899: figs. 29 & 51; Mlada, 1977: pl. IV).

Avena (W&D 0). *Avena sativa* = [01], a distinct notch present (Yakovlev, 1950) or absent (Mlada, 1977: pl. VII).

Brachyelytrum (W&D 0). *Brachyelytrum erectum* = [01], present (Kennedy 1899: fig. 43; Campbell et al., 1986) or absent (Reeder, 1957).

Diarrhena (W&D 1). *Diarrhena* = [01], present (Macfarlane & Watson, 1980) or absent (Reeder, 1957).

Oryza (W&D 1). *Oryza sativa* = 0 (Yakovlev, 1950), and *Oryza* = 0 (Mlada, 1977: pl. X; Kennedy, 1899: fig. 27; Reeder, 1957). Tateoka (1964) reports tail absent in *O. sativa* and other species of sect. *Sativa* but present in some other sections. C&R (p. 7) describe the *Oryza*-type embryo as lacking a scutellar tail.

Vulpia (nr). *Vulpia hispanica* = 0 (*Nardurus* in Decker, 1964).

28: Embryo mesocotyl internode: 0 = negligible; 1 = elongate. 1, 0, 1.00, 1.00.

Vulpia (nr). *Vulpia hispanica* = 0 (*Nardurus* in Decker, 1964).

29: Embryonic leaf margins: 0 = meeting; 1 = overlapping. 3–4, 2–3, 0.25–0.33, 0.82–0.88.

Avena (W&D 0). *Avena* = \, *A. sativa* and *A. byzantina* C. Koch illustrated as somewhat overlapping (Mlada, 1977: pl. VII).

Diarrhena (W&D 1). *Diarrhena* = [01], meeting (Reeder, 1957) or overlapping (Macfarlane & Watson, 1980; W&D).

Puccinellia (W&D 0). *Puccinellia distans* = [01], *P. distans* subsp. *sevangeana* (Grossh.) Tzvelev = 1 (Mlada, 1977: pl. II).

Triticum (W&D 0). *Triticum* = \, *T. durum* Desf., *T. monococcum* L., and *T. polonicum* L. illustrated as somewhat overlapping (Mlada, 1977: pls. V & VI).

Vulpia (nr). *Vulpia hispanica* = 0 (*Nardurus* in Decker, 1964).

30: Endosperm lipid: 0 = absent; 1 = present. NOTE: Liquid and semi-liquid endosperm are indicative of the presence of lipid, but "semi-solid" and solid states do not imply absence of lipid (Terrell, 1971; Rosengurtt et al., 1972). 3, 2, 0.33, 0.83.

Baloskion = 0 (B. Briggs, pers. comm.).

Ampelodesmos (nr). *Ampelodesmos* = 0, lipid absent (Rosengurtt et al., 1972).

Brachyelytrum (W&D 1 "liquid"). *Brachyelytrum* = ?. We regard the report of "liquid" endosperm to be erroneous; specimens at BH have hard endosperm. Although Macfarlane and Watson (1980) report the endosperm as "not hard," they do not say "liquid." "Not hard" may be interpreted as semi-solid, so there is no positive evidence of endosperm lipid in this genus.

Diarrhena (nr). *Diarrhena* = 0, lipid absent (Rosengurtt et al., 1972).

Lithachne (nr). *Lithachne* = 0, lipid absent (Rosengurtt el al., 1972).

Lygeum (nr). *Lygeum* = 0, lipid absent (Rosengurtt el al., 1972).

Nassella (nr). *Nassella* = 0, lipid absent (Rosengurtt el al., 1972).

31: Endosperm starch grain syndromes: 0 = *Triticum*-type (simple only, dimorphic in size, round or lenticular, free); 1 = *Festuca*-type (highly compound grains present, with or without simple grains); 2 = *Andropogon*-type (simple and compound together, the latter consisting of few granules); 3 = *Panicum*-type (simple only, uniform in size, small to medium, angular or sometimes smooth walled, densely packed); 4 = *Brachyelytrum*-type (simple only, large). NOTE: W&D report starch grains as "simple only" (= [034]) or "compound" (= [12]). Scoring here follows Tateoka's (1962) classification with one exception. He scored *Brachyelytrum* as having simple *Panicum*-type grains, but emphasized a major size difference. We recognize *Brachyelytrum*-type as a separate state (see also Campbell et al., 1986). Additional reports come from Pammel, 1898; Yakovlev, 1950; and Tzvelev, 1977. 8, 4, 0.57, 0.72.

Flagellaria = 1 (Tillich, 1996).

Baloskion = 1 (Yakovlev, 1950: 160).

Anisopogon (W&D simple only). *Anisopogon* = 1 (Tateoka, 1962). There is only one species, and we follow the original report.

Brachyelytrum (W&D simple only). *Brachyelytrum* = 4.

Chasmanthium (nr). *Chasmanthium* = 3 (Tateoka, 1962).

Danthonia (W&D compound). *Danthonia* = [12], mostly *Festuca*-type, but a few species exhibit *Andropogon*-type (Tateoka, 1962).

Distichlis (W&D simple only). *Distichlis* = [034], from the report by W&D states 1 and 2 can be eliminated.

Eremitis (nr). *Eremitis* = 1 (V. Hollowell, pers. comm.).

Festuca (W&D 1). *Festuca ovina* = 1. *Festuca* generally has *Festuca*-type (Tateoka, 1962), but *F. paradoxa* Desv. has *Triticum*-type (Pammel, 1898). The latter is a member of an unusual North American section of the genus (though clearly *Festuca* s.str.) that Tateoka apparently did not sample.

Miscanthus (W&D compound). *Miscanthus* = 2 (Tateoka, 1962).

Nassella (W&D compound). *Nassella viridula* = [12], from the report by W&D states 0, 3, and 4 can be eliminated.

Panicum (W&D [13]). *Panicum* = [13], Tateoka (1962) reported 30 species with *Panicum*-type, two species with *Festuca*-type.

Pennisetum (W&D simple). *Pennisetum* = 3 (Tateoka, 1962).

Pharus (nr). *Pharus* = 1, compound only (Yakovlev, 1950).

Piptatherum (nr). *Piptatherum* = 1, included in *Oryzopsis* by Tateoka (1962).

Pseudosasa (nr). *Pseudosasa* = 3 (Tateoka, 1962). It should be noted that *Arundinaria* Michx. has *Festuca*-type (Pammel, 1898).

Sporobolus (W&D compound). *Sporobolus* = [13], *Panicum*-type in *S. cryptandrus* (Pammel, 1898: pl. xix, fig. vii), or *Festuca*-type (Tateoka, 1962).

Stipa (W&D report as simple only, or compound). *Stipa* = [0134]. Among Stipeae, Tateoka (1962) scored eight species of *Stipa*, and eight species of other genera, *Oryzopsis, Piptochaetium, Achnatherum* P. Beauv., and *Orthoraphium* Nees, as *Festuca*-type. However, given W&D's report, only the *Andropogon*-type can be eliminated for *Stipa*.

Zoysia (W&D compound). *Zoysia* = [12]. According to Tateoka (1962) this is compound, but the granules are few in number as in *Danthonia*. Tateoka scored *Zoysia* as *Festuca*-type but stressed intermediacy to *Andropogon*-type.

SEEDLING

32: Lamina of first seedling leaf: 0 = absent; 1 = present. 4, 3, 0.25, 0.57.
Flagellaria = 0, lacks a first blade (Jacques-Felix, 1988: fig. 3; Tillich, 1996).
Baloskion = 1 (H. P. Linder & B. Briggs, pers. comm.).
Pharus (nr). *Pharus* = 1, "the first blade is expanded, large, ovate" (Soderstrom, 1981: 23, 24, 26).
Bambusa (nr). *Bambusa* = 0 (Hoshikawa, 1969).
Eremitis (nr). *Eremitis* = 0 (V. Hollowell, pers. comm.).
Miscanthus (nr). *Miscanthus* = 1 (Hoshikawa, 1969).

VEGETATIVE ANATOMY

NOTE: Vegetative leaf anatomy characters 33, 36, and 37 are inapplicable for *Baloskion* (B. Briggs, pers. comm.).

33: Cross-venation of leaf blades: 0 = absent or obscure, or if distinct, then rare or occasional; 1 = present, distinct, more frequent than occasional. NOTE: The two states recognized for this character are intended to discriminate the regular occurrence of cross-venation from rare or accidental occurrences. In four cases we have assigned state 1 to species of genera recognized by W&D as lacking cross-venation (*Ehrharta*, *Lithachne*) or being variable for this character (*Bambusa*, *Brachyelytrum*). It is possible that these differences represent variation among observers in the interpretation of frequency and prominence of cross-veins, and reevaluation of other taxa may be warranted. 2–3, 1–2, 0.33–0.50, 0.81–0.90.
Flagellaria = 1 (pers. obs.).
Joinvillea = 1 (pers. obs.).
Bambusa (W&D [01]). *Bambusa multiplex* = 1 (pers. obs.).
Brachyelytrum (W&D [01]). *Brachyelytrum erectum* = 1 (Campbell et al., 1986; pers. obs.).
Ehrharta (W&D 0). *Ehrharta calycina* = 1 (Renvoize, 1985a); *E. erecta* also has cross-veins in mature leaves (pers. obs.).
Lithachne (W&D 0). *Lithachne humilis* = 1 (pers. obs.).
34: Multicellular microhairs: 0 = absent; 1 = present. 4, 3, 0.25, 0.90.
Baloskion = 0 (H. P. Linder & B. Briggs, pers. comm.).
Joinvillea = 1, often several-celled (Smithson, 1957).
Diarrhena (W&D [01] for microhairs). *Diarrhena* = 0. Bicellular microhairs lacking; unicellular microhairs are reported as possibly present, but rare, in one species (Scholz, 1982; Renvoize, 1985b).
Stipa and *Piptatherum* (W&D [01] for microhairs). All Stipeae = 0 for bicellular microhairs. Unicellular microhairs are reported as present, but rare, in a few species (Scholz, 1982; Renvoize, 1985b).
Molinia (W&D 0). *Molinia caerulea* = 1, (Jirasek, 1970).
35: Occurrence of a broad, short terminal cell, often with a longer basal cell in microhair, the walls of the terminal and basal cells similar in thickness: 0 = absence; 1 = presence. NOTE: Tateoka et al. (1959) distinguished hairs of this form as "Chloridoid-type" as they are mainly restricted to subfamily Chloridoideae. This type of hair is contrasted with "Panicoid-type" microhairs, which have relatively longer and thin-walled ter-

minal cells and are widespread among non-Chloridoid grasses. This distinction has been recognized in subsequent studies (Johnston & Watson, 1976; C&R; W&D, p. 28, #309). This character is inapplicable for taxa scored 0 for character 34. 2, 1, 0.50, 0.83.

36: Arm cells: 0 = absent; 1 = present. 4, 3, 0.25, 0.72.
Flagellaria = 0 (Smithson, 1957).
Joinvillea = 1, slight lobing possibly present (Smithson, 1957).
Diarrhena (W&D 1). *Diarrhena* = 0. Soderstrom and Ellis (1987) report arm cells as absent, Metcalfe (1960) does not mention them (voucher, *W. G. Dore 646*, is *D. americana* P. Beauv. or *D. obovata*), and Macfarlane and Watson (1980) report them as absent. We have not found a source for the report by W&D, and consider it erroneous.
Streptochaeta (W&D, p. 880, "without arm cells, or at least without conspicuous arm cells, in the material seen"). *Streptochaeta* = 0. The genus has been examined in at least three studies and found wanting arm cells. Arm cells are not mentioned by Judziewicz and Soderstrom (1989), Soderstrom (1981), or Metcalfe (1960) or Metcalfe's discussion of Page's (1947) work on the genus.
37: Fusoid cells: 0 = absent; 1 = present. 2–3, 1–2, 0.33–0.50, 0.81–0.90.
Flagellaria = 0 (Smithson, 1957).
Joinvillea = 1 (Smithson, 1957).

BIOCHEMISTRY

NOTE: Our primary source for photosynthesis subtype data was H&W.

38: Carbon fixation pathway: 0 = C₃; 1 = C₄ NADP-ME classical-type; 2 = C₄ NADP-ME *Aristida*-type; 3 = C₄ NAD-ME. 4, 1, 0.75, 0.85.
Baloskion = 0 (H. P. Linder & B. Briggs, pers. comm.).
Aristida (W&D 1). *Aristida* = 2 (H&W).
Distichlis (nr). *Distichlis* = 3 (H&W).
Eragrostis (W&D [03]). *Eragrostis curvula* = 3 (Hattersley, 1987).
Panicum (W&D [0123]). *Panicum virgatum* = 3 (Hattersley, 1987).
Spartina (W&D 3). *Spartina* = 3 (H&W).
Sporobolus (W&D 3). *Sporobolus* = 3 (H&W).
Uniola (nr). *Uniola* = 3, "NAD-ME or PCK" (H&W).
Zoysia (W&D 3). *Zoysia* = 3 (H&W).
39: Carbon fixation PCK: 0 = absent; 1 = present. NOTE: PCK-type carbon fixation is recognized as a subtype of NAD-ME by H&W, who indicate that taxa with the PCK subtype exhibit both PCK and NAD-ME pathways, while other taxa exhibit only the NAD-ME pathway. Character 39 therefore is applicable only to taxa with state 3 for character 38. 1, 0, 1.00, 1.00.
Distichlis (nr). *Distichlis* = 0 (H&W).
Eragrostis (W&D 0). *Eragrostis curvula* = 0 (Hattersley, 1987). *Eragrostis* species can be C₃, NAD-ME, or NAD-ME and PCK (H&W). PCK occurs among the annual species (H&W).
Panicum (W&D [01]). *Panicum virgatum* = 0 (Hattersley, 1987).
Spartina (W&D 1). *Spartina* = 1 (H&W).
Sporobolus (W&D [01]). *Sporobolus* = [01] (H&W).

Uniola (nr). *Uniola* = \, indeterminate, "NAD-ME or PCK" (H&W).
Zoysia (W&D 1). *Zoysia* = 1 (H&W).

CHLOROPLAST GENOME STRUCTURE

40: 6.4 kb inversion in the chloroplast genome relative to the arrangement in *Nicotiana*: 0 = absent; 1 = present. NOTE: Most scores are from Doyle et al. (1992), who used the polymerase chain reaction (PCR) to test for the occurrence of this inversion among a variety of exemplar monocots. The present restriction site mapping confirms presence of this inversion in additional grass species and in *Joinvillea*. 1, 0, 1.00, 1.00.

Baloskion = 0, determined by PCR (Jane Doyle, pers. comm.).

41: *trn*T inversion in the chloroplast genome relative to the arrangement in *Nicotiana*: 0 = absent; 1 = present. NOTE: Most scores are from Doyle et al. (1992); new scores are listed below. 1, 0, 1.00, 1.00.

Anisopogon, Anomochloa, Brachyelytrum, Lygeum, Molinia Schrank, and *Poa* L. = 1, determined by PCR (V. Tharp & J. Davis, pers. obs.).

42: 15 bp *ndh*F insertion in the chloroplast genome at *Oryza sativa* position 101951: 0 = absent; 1 = present. NOTE: Scores are from Clark et al. (1995). 2, 1, 0.50, 0.83.

X. Appendix 3: Structural Character Data

Data matrix (see facing page) for 42 structural characters (Appendix 2) as scored for 75 exemplar taxa of Poaceae and related families (Table I). Polymorphisms and subset ambiguities (see text) are signified as follow: A = [01]; B = [02]; C = [03]; D = [12]; E = [13]; F = [23]; G = [34]; H = [034]; I = [123]; J = [234]; K = [0134]. "-" = character inapplicable for a taxon; "?" = character state unobserved for a taxon; "\" = observed state is intermediate between recognized states, or there is uncertainty regarding homology of the observed state (see text and Appendix 2).

Appendix 3
Structural Character Data

Taxon	Character Number
	1 2 3 4 123456789012345678901234567890123456789012
Flagellaria	\01-0A-------\\\\\\6031370----77017-000-000
Baloskion	010----------\\\\\\312D270----011-0---0-0??
Joinvillea	010001-------\\\\\\6A31370----???110\10-100
Anomochloa	000101\\\0-\\\\\\\\4\11101110071?110110-110
Streptochaeta	010101\\\\-\\\\\\\\6131010101?10110010-110
Pharus	0000011010-07130176111011A0101110-110-110
Ehrharta	0A0000111101012011602210101010111110A00-1-1
Oryza	01000A1\1A011120116A221010010010010100-110
Leersia	0100001\1A010120A1D023101001010017A00-170
Eremitis	0100011010-00130112\11101110171011010-110
Bambusa	110011\\\0-\\130116132101110??70110110-111
Pseudosasa	110011100A0171301101131071107?110110-1??
Chusquea	1000111110-101301\13122010110107?A10110-171
Guadua	110011\\\10\\1301161321012101017A10110-171
Otatea	1100111001017301131271011101?7A10110-171
Lithachne	0100021010-0113101131?101110107010110-111
Olyra	0100011010-1113011312F101110107010110-111
Aristida	000A001910112011302210101010110110-111
Arundo	110000100AA1012001302211011071?7010000-111
Molinia	010100100A01712A0130221010110011010000-111
Phragmites	010100110A010120013132\1101100110010-111
Danthonia	0101001001110120A130221010110D01000-111
Chasmanthium 1	0100001100-10120011122\1111110310010000-111
Chasmanthium n	0100001100-101300111221111111111031010000-111
Panicum	0100001110-01120A1302211011101E10100030171
Pennisetum	010A00111A001A20773A2211101110310100001-1??
Miscanthus	000000111110012001F0221110111721021010001-1??
Amphipogon	0101001011A111200031221110110710??10100-1??
Eragrostis	0\01001010-1013001302211111001101A0030111
Uniola	0\01001100-17120013127121011071101??1011003\17?
Zoysia	000A0000110070----FA221111111000D1011003171
Distichlis	0000001000-17120073022111121100H70110031?1
Spartina	0101000010-170----312221111100110A10031??
Sporobolus	000A001010-10A2001I02D11111100E1021003A1?1
Brachyelytrum	000000101101712011302210011A0174110-000-111
Lygeum	000000\000-1?0----1\12101100000110121000-11?
Nardus	010000000110170-----3\11110100001101010000-1??
Ampelodesmos	0000001002A171301030221010100007100-000-1??
Stipa	0100001011A101F01030J2101010000E100-000-1??
Nassella	0100001011A101201030?210110000C100-000-1??
Piptatherum	01000101A010130103022012177701000-000-1??
Anisopogon	0100001011101301030F210177777?1700-000-117
Brachypodium d	010000100101712017102210A0000010-000-1??
Brachypodium p	01000010010171201030221011000000100-000-1??
Brachypodium s	010000100101712010302210100000010-000-1??
Schisachne	011000100101200A00030231011001007?000-000-1??
Melica s	01100010A0-00121002310110001?00-000-1??
Melica c	0110001010-00121003023101101000001100-000-1??
Glyceria s	0110001000-1012A0020231011100001100-000-1??
Glyceria d	0110001000-1012A0030231101100001100-000-1??
Diarrhena	01000010A0-1712010F0221011A0A01100-000-171
Bromus	01100010OAAB1012010300221011000000100-000-171
Boissiera	01100010012171201030221010000000100-000-1??
Triticum	010000000A010130103022101100000700-000-1??
Elymus	01000000A010130103022101100000100-000-1??
Paridictyon	010000000A010130103022101100100\00100-000-1??
Anthoxanthum	01000000101712017302710?7?7??0700-000-1??
Phalaris	01000011112170----20221111A0011100-000-1??
Amphibromus	0100001110-00120103A221A1100011100-000-1??
Ammophila	01000010012101201030271117?7711100-000-1??
Calamagrostis	01000010112101201030221011100011100-000-1??
Agrostis	01000010112101201030221011100011100-000-1??
Deschampsia	010000100121712010302211100011100-000-1??
Arrhenatherum	01000011112101201030221011100011100-000-1??
Avena	01000010012101201030221011A0\11100-000-1??
Koelaria	010000100A2171201030221111000011100-000-171
Trisetum	010000100121712010302211110011100-000-1??
Sesleria	011000100101712010312D1111100011100-000-1??
Poa	0110001000-1012010302211110001100-000-1??
Puccinellia	01\0001000-1012010302211110001100-000-111
Catabrosa	01100010-1012010302211100A01100-000-1??
Festuca	010000100101201030221111100001100-000-1??
Vulpia	01000010010121010302?101100001100-000-1??
Lolium s	010000100101712010302210110001100-000-1??
Lolium p	010000100A0101201030221011000001100-000-1??
	010000000AA1712010302210110001100-000-1??

The Botanical Review
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———— & D. R. Brooks. 1981. Advances in cladistics. The New York Botanical Garden, Bronx, New York.

Gifford, E. M. & A. S. Foster. 1988. Morphology and evolution of vascular plants. Ed. 3. W. H. Freeman, New York.

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Gómez, Pedro Sánchez, Juan Guerra Montes, Ernesto Coy Gómez, Antonio Hernández González, Santiago Fernández Jiménez, and Antonio Félix Carrillo López. 1997. Flora de Murcia—Claves de Identificación de plantas vasculares. ISBN 84-8958-20-2. Promociones y Publicaciones Universitarias (S. A. Marqués de Campo Sagrado, 16.08015 Barcelona).

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Nayar, N. M., and T. A. More. 1998. Cucurbits. ISBN 1-57808-003-7. Science Publishers (P.O. Box 699, May St., Enfield, NH 03748). Price: $75.00 cloth.

Page, C. N. 1997. The Ferns of Britain and Ireland. 2nd ed. ISBN 0-521-58380-2 cloth; 0-521-58658-5 paper. Cambridge University Press. Price: $125.00 cloth; $64.95 paper.

Pushpangadan, P., K. Ravi, and V. Santhosh. 1998. Conservation and Economic Evaluation of Biodiversity. Volumes 1 & 2. ISBN 1-57808-002-9. Science Publishers. Price: $110.00 cloth.

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