

KEYNOTE LECTURE

An Updated Tribal and Subtribal Classification of the Bamboos (Poaceae: Bambusoideae)

Bamboo Phylogeny Group¹

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Abstract

The Bambusoideae (bamboos), comprising 1,439 described species in 115 genera, is one of 12 subfamilies of Poaceae (grass family), and it is the only major lineage of the family to diversify in forests. The bamboos are ecologically and economically important, but they remain understudied relative to other grasses, especially with respect to morphology, and an updated, phylogeny-based classification for the Bambusoideae has not previously been available. In this paper, a compilation of described bamboo diversity by tribe and subtribe is presented, phylogenetic studies of bamboos are reviewed, and the basis for the revised classification presented here is discussed, with putative synapomorphies indicated in the text and descriptions. The taxonomic treatment includes descriptions of the subfamily, the three tribes, and all accepted subtribes, and included genera are listed as appropriate.

Keywords

Arundinarieae, bamboo classification, Bambuseae, Bambusoideae classification, Olyreae.

List of Abbreviations

AFLPs – amplified fragment length polymorphisms; ESTs – expressed sequence tags; GBSSI – granule-bound starch synthase subunit I; g – genera; in prep. – in preparation; ITS – internal transcribed spacer; pers. comm. – personal communication; RAPDs – random amplification of polymorphic DNA; RFLPs – random fragment length polymorphisms; spp – species; SSRs – simple sequence repeats; unpubl. data – unpublished data; # – number.

Introduction

The Bambusoideae (bamboos) is one of 12 currently recognized subfamilies of Poaceae (grasses), receiving strong bootstrap support in comprehensive molecular analyses of the family [Grass Phylogeny Working Group (GPWG) 2001; Duvall et al. 2007; Bouchenak-Khelladi et al. 2008; GPWG II 2012; Wu and Ge 2012]. A putative structural synapomorphy for the subfamily is the presence of strongly asymmetrically invaginated arm cells in the foliage leaf chlorophyll (Zhang and Clark 2000). The bamboos are notably the only major lineage of grasses to diversify in forests (Zhang and Clark 2000; Judziewicz and Clark 2007; Sungkaew et al. 2009) and the complex morphology and unusual flowering behavior of most bamboos are likely the result of adaptations to this habitat or the retention of ancestral states, as is the case with their broad, pseudopetiolate leaves with fusoid cells in the mesophyll (Clark 1997; Judziewicz et al. 1999).

Bambusoideae are worldwide in distribution (see Maps, Bamboo Biodiversity), occurring between 46° N and 47° S latitude, with an altitudinal range from sea level to 4,300 m (Judziewicz et al. 1999). Estimates of total diversity vary from source to source, but our compilation reveals 1,439 described species in 115 genera (Table 1). Three tribes reflecting the three main lineages of Bambusoideae are currently recognized (Sungkaew et al. 2009): Arundinarieae (temperate woody bamboos, 533 species), Bambuseae (tropical woody bamboos, 784 species) and Olyreae (herbaceous bamboos, 122 species). New species and new genera in all of these tribes continue to be discovered and described and phylogenetic analyses in some cases support generic recircumscriptions (e.g., Fisher et al. 2009).

Table 1. Diversity of Bambusoideae by tribe and subtribe and by region for Bambuseae.

Taxon	Number of genera	Number of species
Arundinarieae	28	533
Bambuseae	66	784
Neotropical	19	377
Arthrostylidiinae	13	172
Chusqueinae	1	160
Guaduinae	5	45
Paleotropical	47	407
Bambusinae	28	264
Hickeliinae	8	33
Melocanninae	10	88
Racemobambosinae	1	22
Olyreae	21	122
Buergersiochloinae	1	1
Parianinae	2	36
Olyrinae	18	85
Total for subfamily	115	1,439

Woody bamboos possess culm leaves (leaves modified for the protection and support of the tender young shoots), complex vegetative branching, an outer ligule (contraligule) on the foliage leaves, usually gregarious monocarpy (with flowering cycles ranging from a few years to 120 years), and bisexual flowers (Judziewicz et al. 1999; GPWG 2001; Judziewicz and Clark 2007). Herbaceous bamboos usually lack differentiated culm leaves and outer ligules and have restricted vegetative branching, usually nearly continuous or seasonal flowering, and unisexual spikelets (Judziewicz et al. 1999; Judziewicz and Clark 2007). All Olyreae, except for the New Guinea endemic *Buergersiochloa*, also have crenate (olyroid) silica bodies (Soderstrom and Ellis 1987; Zhang and Clark 2000; Clark et al. 2007).

Woody bamboos, which colonize forest gaps and edges, are an important element in tropical and temperate forests, especially in mountainous regions (Soderstrom and Calderón 1979; Li and Xue 1997; Judziewicz et al. 1999; Zhou et al. 2011). These bamboos may be canopy or understory dominants, and they may form nearly mono-dominant stands that can cover extensive areas (Numata 1979; Wong 1991, 1995, 2004; Judziewicz et al. 1999; Franklin and Bowman 2004). Woody bamboos also are important and sometimes dominant in high altitude grasslands in both tropical and subtemperate montane systems (Soderstrom and Calderón 1979; Soderstrom et al. 1988; Judziewicz et al. 1999; Judziewicz and Clark 2007). As a function of their colonizing ability or status as understory dominants, woody bamboos appear to play a key role in the ebb and flow of forest dynamics, while over the long term, the gregarious, monocarpic flowering of woody bamboos permits the forest to reoccupy previously disturbed sites (Wong 1991; Widmer 1997; Judziewicz et al. 1999; Martins et al. 2004). Flowering and death of woody bamboos may also affect nutrient uptake, soil fertility and water relations in forests (e.g., Takahashi et al. 2007; Ishii et al. 2008; Marchesini et al. 2009) and these bamboos affect the regeneration of other forest species in various ways (e.g., Oliveira-Filho et al. 1994; Caccia et al. 2009; Larpkern et al. 2010; Montti et al. 2011). Bamboos can play an important role in carbon sequestration, especially as the extent of bamboo forests is increasing in some parts of the world (Zhou et al. 2011 and references cited therein).

Although much remains to be learned about the ecology of woody bamboos, the ecology of herbaceous bamboos is even more poorly studied. Olyreae usually occupy the forest understory and may even become dominant (Poulsen and Balslev 1991; Judziewicz et al. 1999); some occur in savannas or wet cliff faces associated with waterfalls (Zuloaga and Judziewicz 1991; Judziewicz et al. 1999; Judziewicz and Sepsenwol 2007) and *Ekmanochloa* is a serpentine endemic (Zuloaga et al. 1993). A few species, especially of *Lithachne* or *Olyra*, may become weedy (Judziewicz et al. 1999; Judziewicz and Clark 2007). The association of gall midges and other insects with the showy inflorescences of *Pariana* species suggests the possibility of insect pollination (Soderstrom and Calderón 1971), but this remains to be confirmed. The hardened female floret characteristic of Olyreae may be an adaptation for dispersal by granivorous birds; in some taxa, a swollen, oil-containing internode attached to the female floret presumably functions as an elaiosome for ant dispersal (Davidse 1987; Judziewicz et al. 1999). Olyreae exhibit their greatest species diversity from 7–10° N and 12–18° S, with minimal diversity near the equator and their greatest endemism in the Atlantic forests of Brazil (Soderstrom et al. 1988). Many species of Olyreae are endangered due to the continuing loss of these forests (Oliveira and Clark 2009).

The often extensive biomass of woody bamboos, coupled with their unique life form, not surprisingly provide an important resource for many other organisms. The giant panda is by far the best known animal that depends on bamboo (Schaller 1994; Dierenfeld 1997), but there are also bamboo lemurs (Mutschler and Tan 2003; Ravaloharimanitra et al. 2011), bamboo rats (Medway 1964, 1969; Emmons

1997), bamboo birds (Judziewicz et al. 1999; Lentino and Restall 2003; Areta and Bodrati 2008), and even a bamboo bat (Ridley 1908; Medway 1969; Ades 1999). Many invertebrates take advantage of the sheaths and hollow stems for shelter (Brailovsky 1988; Kovac 1993; Conover 1994; Louton et al. 1996; Hidalgo et al. 2012), thus attracting larger animals to this food source. Fungi also use bamboo as a host (Judziewicz et al. 1999; Higgins et al. 2010). And the periodic gregarious flowering of woody bamboos can produce massive amounts of fruit that are particularly attractive to birds and small mammals (Judziewicz et al. 1999; Areta et al. 2009), especially rodents (Jaksic and Lima 2003; Singleton et al. 2010).

The increasing economic importance of woody bamboos in housing construction (especially in earthquake-prone regions) but also as a material for flooring, furniture and other household items, food (new shoots), fencing, scaffolding, and as ornamentals is well known and growing (McClure 1966; Bahadur 1979; Wong 1989; Judziewicz et al. 1999; Yang et al. 2004). Woody bamboos are also increasingly viewed as a sustainable resource for developing countries, where the bulk of bamboo diversity is found (Bystriakova et al. 2003, 2004). Technology for *in vitro* propagation of woody bamboos has been commercially developed, allowing mass production for use in reforestation or other projects (Agro Vitro 2012; Oprins Plant 2012). And despite their reputation for invasiveness, many bamboos are of conservation concern due to destruction of their forest habitats (Bystriakova et al. 2003, 2004). The massive gregarious flowering and fruiting of certain bamboos can have negative effects on local human populations through rodent outbreaks and subsequent crop losses and increased incidence of rodent-borne diseases (Jaksic and Lima 2003; Sage et al. 2007; Singleton et al. 2010).

The Bamboo Phylogeny Group was formed in 2005 to address the need for a robust, global phylogeny of the Bambusoideae and an updated tribal, subtribal, and generic classification based on the phylogenetic results (BPG 2006). A comprehensive analysis across the subfamily with extensive sampling has yet to be achieved, but much has been learned through intermediate phylogenetic analyses of various lineages based on both plastid and nuclear data (Table 2). We here present a compilation and review of the phylogenetic findings to date and a revised and updated tribal and subtribal classification of the Bambusoideae based on a synthesis of these results. A separate manuscript by the BPG is in preparation, in which a rigorously tested phylogenetic analysis of plastid sequences is presented for representatives of all tribes and subtribes of Bambusoideae.

Review of Bamboo Phylogeny and Classification

Table 2. Prior published molecular/morphological phylogenetic analyses focused on Bambusoideae. These are not included and the number of taxa does not include outgroups.

Authors	Year	# Taxa (Focus)	Data Used	Findings
Friar and Kochert	1994	1 g, 20 spp (<i>Phyllostachys</i>)	nuclear RFLPs	Support for division of <i>Phyllostachys</i> into two major groups; utility of RFLPs for species-level problems.
Takahashi et al.	1994	4 g, 21 spp (<i>Sasa</i> and allies)	allozymes	Support for intersectional hybrids between species of <i>Sasa</i> and intergeneric hybrids between species of <i>Sasa</i> and <i>Sasamorpha</i> or <i>Sasa</i> and <i>Pleioblastus</i> .
Watanabe et al.	1994	16 g, 19 spp (Asiatic woody)	plastid RFLPs	Support for monophyly of each of the temperate and paleotropical

		bamboos)		woody bamboos; aspects of morphological evolution.
Gielis et al.	1997	1 g, 42 spp (<i>Phyllostachys</i>)	RAPDs	Support for <i>Phyllostachys</i> section <i>Heteroclada</i> ; utility and reliability of RAPDs in identifying genotypes within <i>Phyllostachys</i> .
Kelchner and Clark	1997	13 g, 35 spp (Bambusoideae)	<i>rpl16</i> intron, indels	Support for monophyly of Olyreae, temperate Bambuseae, tropical Bambuseae, and Chusqueinae.
Kobayashi	1997	31 g, 32 spp (Bambusoideae)	plastid RFLPs	Support for monophyly of the temperate bamboos.
Guala et al.	2000	19 g, 21 spp (woody bamboos)	<i>ndhF</i> (3' end)	Polyphyly of <i>Apoclada</i> confirmed, with <i>A. simplex</i> (type species) in the Guaduinae and the other two species forming a clade in the Arthrostylidiinae.
Hodkinson et al.	2000	4 g, 15 spp/1 g, 23 spp (<i>Phyllostachys</i>)	ITS, AFLPs	Support for monophyly of <i>Phyllostachys</i> and its major subgeneric groups; utility of AFLPs for phylogenetic reconstruction among closely related species.
Loh et al.	2000	4 g, 15 spp (Bambusinae)	AFLPs	Most species with unique bands; possible polyphyly of <i>Bambusa</i> and distinctness of <i>Thyrsochloa</i> .
Zhang and Clark	2000	24 g, 24 spp (Bambusoideae)	<i>ndhF</i> , indels, morphology	Asymmetrically invaginated arm cells as a synapomorphy for Bambusoideae; molecular support for monophyly of the subfamily and 3 major clades (Olyreae, temperate woody and tropical woody).
Guo et al.	2001	3 g, 23 spp (temperate woody)	ITS	Non-monophyly of <i>Yushania</i> , <i>Fargesia</i> ; support for some species groupings within alpine bamboos.
Guo et al.	2002	7 g, 31 spp (temperate woody)	ITS	Putative support for monophyly of the <i>Thamnocalamus</i> group of the temperate woody bamboos and position of <i>Chimonocalamus</i> as sister to the remainder of this group; support for monophyly of <i>Ampelocalamus</i> .
Nayak et al.	2003	6 g, 12 spp	RAPDs	Two clusters recovered but no correspondence to taxonomic groupings.
Guo and Li	2004	8 g, 31/33 spp (temperate	ITS, GBSSI	Support for monophyly of <i>Ampelocalamus</i> and

		woody)		<i>Chimonocalamus</i> ; polyphyly of <i>Thamnocalamus</i> and the <i>Thamnocalamus</i> group.
Barkley et al.	2005	11 g, 42 spp (mainly temperate woody)	EST-SSRs	Used transfer markers from maize, wheat, sorghum and rice to assess genetic diversity of the USDA bamboo germplasm collection; accessions clustered \pm according to taxonomy; utility in identification of contaminated plots.
Sun et al.	2005	3 g, 21 spp	ITS	Polyphyly of <i>Bambusa</i> .
Zhuge et al.	2005	3 g, 17 spp (<i>Arundinaria</i> and related genera)	ITS, <i>trnL-trnF</i>	Moderate support for what are now recognized as the <i>Arundinaria</i> and <i>Phyllostachys</i> clades within the temperate woody bamboos.
Sun et al.	2006	2 g, 15 spp (<i>Bambusa</i> s.l.)	RAPDs	Recovery of a core of thorny <i>Bambusa</i> species; subgenus <i>Leleba</i> polyphyletic.
Clark et al.	2007	27 g, 46 spp (Chusqueinae, Hickeliinae)	<i>rpl16</i> intron, morphology	Support for monophyly of Bambusoideae, Bambuseae (moderate), Olyreae, Chusqueinae, and Madagascan Hickeliinae; possible paraphyly of <i>Neurolepis</i> ; aspects of morphological evolution.
Das et al.	2007	4 g, 15 spp (<i>Bambusa</i> , <i>Dendrocalamus</i> , <i>Pseudobambusa</i> , <i>Gigantochloa</i>)	RAPDs, vegetative morphology	Relationships among the 15 species based on allelic polymorphism data consistent with Gamble (1896); demonstration of potential use of RAPDs for evaluation of phylogenetic relationships.
Ramanayake et al.	2007	4 g, 9 spp (<i>Bambusa</i> , <i>Dendrocalamus</i> , <i>Gigantochloa</i> , <i>Arundinaria</i>)	RAPDs	RAPDs useful in determining the genetic diversity among species, even among putatively closely related species; <i>Arundinaria</i> (temperate) distant from the remainder (paleotropical).
Yang et al.	2007	8 g, 26 spp (paleotropical woody)	GBSSI, <i>trnL-F</i> spacer	Support for monophyly of an alliance of <i>Melocanna</i> , <i>Schizostachyum</i> , <i>Cephalostachyum</i> and <i>Pseudostachyum</i> (= Melocanninae); generic realignments of some species.
Bouchenak-Khelladi et al.	2008	25 g, 25 spp (Bambusoideae) + 80 g, 80 spp (other Poaceae)	<i>rbcL</i> , <i>matK</i> , <i>trnL-F</i>	Sister relationship of Pooideae + Bambusoideae; paraphyly of Bambuseae (woody bamboos).
Hisamoto et al.	2008	9 g, 20 spp	FT homolog	Support for monophyly of

		(Bambusoideae, mainly temperate woody)		Bambuseae (woody bamboos), the <i>Phyllostachys</i> and <i>Arundinaria</i> clades within temperate bamboos, neotropical and paleotropical clades within tropical woody bamboos.
Peng et al.	2008	25 g, 43 spp (temperate woody)	ITS, GBSSI	Support for monophyly of the temperate woody bamboos; non-monophyly of traditional subtribes and many genera; support for inclusion of <i>Menstruocalamus</i> and <i>Qiongzhuea</i> in <i>Chimonobambusa</i> .
Ruiz-Sanchez et al.	2008	12 g, 25 spp (neotropical woody)	<i>rpl16</i> intron, <i>trnH-psbA</i> spacer, morphology	Support for monophyly of Guaduinae including 2 spp of <i>Aulonemia</i> and support for monophyly of constituent genera; diagnostic features for Guaduinae.
Sharma et al.	2008	6 g, 21 spp (1° Bambusinae + <i>Phyllostachys</i> , <i>Sasa</i>)	SSRs	Support for monophyly of <i>Phyllostachys</i> and groupings of <i>Bambusa</i> + <i>Dendrocalamus</i> and <i>Melocanna</i> + <i>Ochlandra</i> ; rice genomic SSRs and sugarcane EST-SSRs can be transferable to bamboo (to 44.8% and 75% respectively).
Yang et al.	2008	17 g, 53 spp (paleotropical woody)	ITS, GBSSI, <i>trnL-F</i> , indels	Support for monophyly of Bambusinae and Melocanninae, but Hickeliinae not sampled; <i>Dinochloa</i> sister to remaining Bambusinae; fruit evolution.
Fisher et al.	2009	2g, 22 spp (Chusqueinae)	<i>ndhF</i> , <i>trnD-T</i> , <i>trnC-rpoB</i> , <i>rps16-trnQ</i> , <i>rpl16</i> intron, indels	Confirmed monophyly of Chusqueinae, <i>Chusquea</i> s.s., <i>Euchusquea</i> clade and <i>Chusquea</i> subg. <i>Rettbergia</i> ; confirmed paraphyly of <i>Neurolepis</i> ; submerged <i>Neurolepis</i> into <i>Chusquea</i> .
Sungkaew et al.	2009	33 g, 52 spp (Bambusoideae)	<i>matK</i> , <i>rps16</i> intron, <i>trnL</i> spacer, <i>trnL-F</i> spacer, <i>atpB-rbcL</i> spacer	Confirmed paraphyly of woody bamboos; Melocanninae as sister to the remaining paleotropical woody bamboos; recognition of three tribes: Arundinarieae, Bambuseae, Olyreae.
Goh et al.	2010	9 g, 24 spp (Bambusinae)	GBSSI, <i>rps16-trnQ</i> , <i>trnC-rpoB</i> , <i>trnH-psbA</i> and <i>trnD-T</i>	Non-monophyly of <i>Bambusa</i> ; climbing Southeast Asian genera are distinct from the core <i>Bambusa</i> group.

Hodkinson et al.	2010	27 g, 41 spp (Arundinarieae)	<i>trnL-F</i> , ITS	Support for monophyly of Arundinarieae and polyphyly of its subtribes; lack of internal resolution due to recent, rapid radiation.
Lewis et al.	2010	4 g, 15 spp (temperate and paleotropical woody)	Vegetative morphological characters	Four clusters detected, with only Cluster IV (<i>Dendrocalamus strictus</i> and <i>D. membranaceus</i>) corresponding to any current phylogenetic groupings.
Ruiz-Sanchez and Sosa	2010	1 g, 7 spp (<i>Otatea</i>)	ITS, <i>atpF-atpH</i> , <i>psbKpsbI</i> , <i>trnL-rpl32</i>	Molecular data showed non-monophyly of most entities and conflicted with morphological data; species delimitations based on total evidence.
Triplett and Clark	2010	28 g, 82 spp (1 st 4 markers)/16 g, 21 spp (all 12 markers) (temperate woody)	<i>rps16-trnQ</i> , <i>trnC-rpoB</i> , <i>trnD-trnT</i> , <i>trnT-trnL</i> + <i>ndhF</i> (3' end), <i>atpI-atpH</i> , <i>psaA-ORF170</i> , <i>rpl32-trnL</i> , <i>trnH-psbA</i> , <i>trnK-rps16</i> , <i>trnV-ndhC</i> , <i>trnG</i> intron	Confirmed monophyly of Arundinarieae and support for 6 major clades within the tribe; polyphyly of morphologically-based subtribes; restriction of <i>Arundinaria</i> to N. Am. taxa; evidence for possible role of hybridization within the tribe.
Triplett et al.	2010	1 g, 3 spp (<i>Arundinaria</i> s.s.)	<i>trnT-trnL</i> spacer, AFLPs	Support for three entities in <i>Arundinaria</i> s.s. and a sister relationship between <i>A. tecta</i> and <i>A. appalachiana</i> ; natural, reciprocal hybridization among the three species.
Zeng and Zhang et al.	2010	26 g, 148 spp (temperate woody)	<i>atpI-H</i> , <i>psaA-ORF170</i> , <i>rpl32-trnL</i> , <i>rpoB-trnC</i> , <i>rps16-trnQ</i> , <i>trnD-T</i> , <i>trnS-G</i> , <i>trnT-L</i>	Confirmed monophyly of Arundinarieae and polyphyly of traditional subtribes; support for 10 major clades within the tribe; low molecular divergence within the tribe.
Yang et al.	2010	8 g, 62 spp (core Bambusinae)	GBSSI, <i>psbA-trnH</i> , <i>rpl32-trnL</i> , <i>rps16</i> intron	Monophyly of Bambusinae, <i>Melocalamus</i> , <i>Thyrsostachys</i> supported; 2 main clades (<i>Bambusa</i> s.l. and <i>Dendrocalamus</i> + <i>Gigantochloa</i> + <i>Oxytenanthera</i> + <i>Neosinocalamus</i>) recovered.
Zhou et al.	2010	38 g, 44 spp (woody bamboos)	Ty1- <i>copia rt</i> , ITS	ITS tree largely congruent with other analyses; Ty1- <i>copia rt</i> tree

				incongruent with this ITS tree; <i>Ty1-copia</i> retroelements widespread and abundant in Bambusoideae and present in multiple copies.
Pattanaik and Hall	2011	1 g, 10 spp (<i>Dendrocalamus</i>)	AFLPs	Evidence for polyphyly of <i>Dendrocalamus</i> ; no support for previous infrageneric classifications of the genus.
Wu and Ge	2012	3 g, 3 spp Bambusoideae, 19 spp other grasses	76 chloroplast protein-encoding genes	Support for (Bambusoideae + Pooideae) Ehrhartoideae.

Subfamily Bambusoideae

The bamboo subfamily (Bambusoideae) traditionally included what are now recognized as the “true” bamboos as well as a number of other taxa now classified as subfamilies or tribes within other subfamilies of grasses (e.g., Clayton and Renvoize 1986; Soderstrom and Ellis 1987). A number of molecular analyses (e.g., Clark et al. 1995; GPWG 2001) unequivocally demonstrate the polyphyly of the traditionally circumscribed Bambusoideae and Zhang and Clark (2000) and the GPWG (2001) provide the narrower circumscription of the subfamily that is currently accepted and consistently supported in all analyses that have sufficient taxon sampling (e.g., Bouchenak-Khelladi et al. 2009; Sungkaew et al. 2009; GPWG II 2012). Detailed reviews of the classification history of the Bambusoideae prior to GPWG (2001) are available in Clark et al. (1995), GPWG (2001) and Judziewicz and Clark (2007).

Tribe Olyreae

The more narrowly drawn Bambusoideae are considered to include two main groups, the woody bamboos (as one or more tribes) and the herbaceous bamboos (Olyreae) (GPWG 2001; Clark et al. 2007; Sungkaew et al. 2009). In all analyses, the olyroid lineage is well supported with molecular data but no unequivocal morphological synapomorphies for it have been identified (Zhang and Clark 2000; GPWG 2001). Herbaceous bamboos have often been classified into three tribes (Buergersiochloaeae, Parianeae, Olyreae) (e.g., Soderstrom and Ellis 1987) based primarily on morphological data but these are now usually treated as three subtribes (Buergersiochloinae, Parianinae and Olyrinae) within the Olyreae (Judziewicz and Clark 2007). To date, phylogenetic relationships within the Olyreae have not been rigorously examined, although preliminary data support these three lineages and indicate the probable paraphyly of *Pariana* and probable polyphyly of *Olyra* (GPWG 2001; de Oliveira et al., in prep.).

Woody bamboos

In earlier phylogenetic analyses, the woody bamboos (as the tribe Bambuseae) are well supported as monophyletic based on morphological characters but receive moderate support at best from molecular data (Kelchner and Clark 1997; Zhang and Clark 2000; Clark et al. 2007). Within woody bamboos, three or four moderately to well supported clades (North Temperate clade, Paleotropical clade, and one or two Neotropical clades) forming a polytomy have usually been recovered (Watanabe et al. 1994; Kelchner and Clark 1997; Kobayashi 1997; Zhang and Clark 2000; Clark et al. 2007; Ramanayake et al. 2007). The most recent analyses based on multiple molecular data sets and more thorough sampling across the subfamily strongly support two lineages of woody bamboos that are

paraphyletic to the Olyreae or form a trichotomy with it (Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; BPG, in prep.). Although alternate hypothesis testing is unable to reject monophyly of the woody bamboos (BPG, in prep.), it is likely that temperate and tropical bamboos will each continue to be recognized as a tribe whatever the ultimate resolution of branching order. Sungkaew et al. (2009, Table 1) summarize the subtribal classifications in use for woody bamboos.

Tribe Arundinarieae

The temperate woody bamboos (North Temperate clade) or Arundinarieae exhibit a more or less typical Laurasian distribution pattern (Judziewicz and Clark, 2007; Map 5, Bamboo Biodiversity). The longest known flowering cycles in bamboos, up to 120 years, are found in members of this clade. All Arundinarieae for which data are available are tetraploids with a chromosome complement of $2n = 48$ (Soderstrom 1981). Many also have leptomorph (running) rhizomes, but no consistent morphological synapomorphy has been identified for this clade. Two or three subtribes have traditionally been recognized (e.g., Dransfield and Widjaja, 1995; Ohrnberger 1999; Li 1997; Guo and Li 2004) to accommodate the morphological diversity of the temperate bamboos: Arundinarieae, Shibataeinae and Thamnocalaminae. The temperate bamboo clade is consistently robustly supported in all phylogenetic analyses to date (Kelchner and Clark, 1997; Kobayashi, 1997; Zhang and Clark, 2000; Ní Chonghaile 2002; Guo et al., 2001, 2002; Guo and Li 2004; Zhuge et al. 2005; Bouchenak-Khelladi et al. 2008; Hisamoto et al. 2008; Peng et al. 2008; Sungkaew et al. 2009; Hodkinson et al. 2010; BPG, in prep.), but with relatively little internal resolution. Two recent studies, Triplett and Clark (2010) and Zeng and Zhang et al. (2010), both with extensive sampling across the clade and based on multiple plastid markers, recover six and ten well supported lineages, respectively, within the temperate woody bamboos. The three subtribes are highly polyphyletic, and the two most diverse lineages in both analyses are the *Arundinaria* clade and the *Phyllostachys* clade. Triplett et al. (2010) present evidence that hybridization within the temperate bamboos may be more widespread than previously thought.

Tribe Bambuseae

The tropical woody bamboos or Bambuseae are widespread in both the Paleo- and Neotropics (Judziewicz and Clark, 2007; Maps 3 and 4, Bamboo Biodiversity). All Bambuseae, with one apparent diploid exception in the neotropical genus *Chusquea*, are either tetraploid or hexaploid with base chromosome numbers of mainly $x = 10$ or $x = 12$ (Soderstrom 1981; Judziewicz et al. 1999; Li et al. 2001). All exhibit pachymorph culm bases (= pachymorph rhizomes) although some members of *Chusquea* also have leptomorph rhizomes (Judziewicz et al. 1999). Two well supported neotropical lineages, the Chusqueinae clade (Clark et al. 2007; Fisher et al. 2009) and the Arthrotyliidiinae + Guaduinae clade (Ruiz-Sanchez et al. 2008), may associate in a weakly to moderately supported neotropical clade sister to the paleotropical clade (Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; BPG, in prep.), but the two neotropical clades are paraphyletic to the paleotropical clade in other trees (Zhang and Clark 2000; Clark et al. 2007). The relatively strongly supported paleotropical clade includes four currently recognized subtribes (Bambusinae, Melocanninae, Hickeliinae, and Racemobambosinae) distributed throughout Southeast Asia, northern Australia, India, Africa, and Madagascar (Soderstrom and Ellis 1987; Dransfield and Widjaja 1995; Ohrnberger 1999). Evidence of hybridization has been documented in both neotropical (Clark et al. 1989) and paleotropical taxa (Goh et al. 2011; Wong and Low 2011) but how prevalent this might be in the Bambuseae is not yet known.

Neotropical woody bamboos

Chusqueinae is strongly supported as a monophyletic lineage and is diagnosed by the apparent synapomorphies of bi-papillate subsidiary cells in the foliar stomatal apparatus and a uniform spikelet structure of four glumes and one female-fertile floret with no rachilla extension (Clark et al. 2007; Fisher et al. 2009; BPG, in prep.). Within the *Chusqueinae*, four major lineages are robustly supported with these sister relationships based on plastid sequence data (Fisher et al. 2009): *Neurolepis* II + [*Neurolepis* I + (*Euchusquea* clade + *Rettbergia*)]. Non-monophyly of *Neurolepis* led Fisher et al. (2009) to submerge this genus under *Chusquea*.

Analyses of *Arthrostylidiinae* and *Guaduinae*, the other two neotropical subtribes of *Bambuseae*, always recover taxa of each in one moderately to robustly supported clade (Zhang and Clark 2000; Clark et al. 2007; Ruiz-Sanchez et al. 2008; Sungkaew et al. 2009), but only more recent analyses with more extensive sampling support the monophyly of each subtribe (Ruiz-Sanchez et al. 2008; Tyrrell et al., in review; BPG, in prep.). Although a formal morphological analyses remains to be completed, the *Arthrostylidiinae* + *Guaduinae* clade may be diagnosed by the presence of refractive papillae, although these also occur in *Melocanninae* (Soderstrom and Ellis 1987; Ruiz-Sanchez et al. 2008). The *Arthrostylidiinae* is robustly supported as monophyletic based on plastid sequence data (Tyrrell et al., in review) and is also supported by the presence of intercostal sclerenchyma and simple midribs in the foliage leaf blades (Soderstrom and Ellis 1987). A green, waxless stripe along one margin of the abaxial leaf blade surface is characteristic of *Arthrostylidiinae* but not unique to it (Tyrrell et al., in review). The *Guaduinae* have an unusual foliar micromorphology in which the blades are amphistomatic and with papillae overarching the stomates, especially on the adaxial surface (Soderstrom and Ellis 1987; Ruiz-Sanchez et al. 2008). In contrast to the *Arthrostylidiinae*, foliage leaf blades of *Guaduinae* lack intercostal sclerenchyma and have the complex midribs typical of most woody bamboos (Soderstrom and Ellis 1987).

Paleotropical woody bamboos

The paleotropical woody bamboos receive strong support in analyses of plastid sequence data as a monophyletic lineage (Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; BPG, in prep.), but no morphological synapomorphy has been identified for this clade. The *Melocanninae* are consistently robustly resolved as sister to the remaining paleotropical woody bamboos in recent analyses (Sungkaew et al. 2009; BPG, in prep.; Chokthaweeapanich et al., unpubl. data) and the subtribe is supported by the possible synapomorphies of a glabrous ovary with a long, slender, hollow style and an S-shaped keel in the foliage leaf blade (Soderstrom and Ellis 1987). The results of Yang et al. (2007, 2008) suggest that some generic realignments within *Melocanninae* will be necessary, but further analyses are required. Within the remaining paleotropical woody bamboos, *Hickeliinae* is supported as monophyletic based on plastid sequence data and the putative synapomorphy of adaxially projecting midribs (Soderstrom and Ellis 1987; Clark et al. 2007; BPG, in prep.) but its position relative to *Racemobambos*, *Bambusinae*, and sometimes other clades (e.g., *Neololeba* + *Cyrtochloa* or *Dinochloa* + *Sphaerobambos*) remains ambiguous due to lack of resolution or incomplete sampling (Yang et al. 2007, 2008; Goh et al. 2010; BPG, in prep.). Molecular data also do not support the placement of *Greslania* in *Hickeliinae* (Clark et al. 2007; Chokthaweeapanich et al., unpubl. data). Monophyly of *Bambusinae*, the most diverse of the four currently recognized subtribes of paleotropical woody bamboos, has not been rigorously tested but *Vietnamosasa* and *Neomicrocalamus* (both previously classified in *Racemobambosinae*) are supported as members of core *Bambusinae* (Yang et al. 2008; Sungkaew et al. 2009). Not surprisingly, given the economic importance of these taxa, most phylogenetic studies of *Bambusinae* have focused on *Bambusa*, *Dendrocalamus* and *Gigantochloa*, the core genera of the subtribe (e.g., Nayak et al. 2003; Sun et al. 2005, 2006; Das et al.

2007; Goh et al. 2010; Yang et al. 2010; Pattanaik and Hall 2011). Relationships among these genera and other putative members of the Bambusinae, as well as circumscriptions of a number of constituent genera, are controversial and require much additional work before these issues can be resolved (Goh et al. 2010).

Basis for an Updated Classification

The recognition of three tribes within the Bambusoideae is clearly supported by the molecular phylogenetic results (Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; BPG, in prep.). Although a formal morphological analysis is not yet available, putative synapomorphies have now been identified for the three tribes. These need to be further tested, but for now, Arundinarieae is diagnosed by basipetal branch development and a chromosome number of $2n = 48$, Bambuseae by acropetal or bidirectional branch development, and Olyreae by unisexual, often strongly dimorphic, 1-flowered spikelets with no rachilla extension, although all but the earliest diverging lineage (*Buergeriochloa*) also share cross-shaped silica bodies in the costal zone and crenate (olyroid) silica bodies in the intercostal zone.

Members of what is now recognized as the Arundinarieae were traditionally classified in up to three subtribes, the Arundinariinae, Shibateinae and Thamnocalaminae, based on the presence or absence of pseudospikelets and rhizome structure. The evident polyphyly of all three subtribes has caused them to be abandoned in favor of the recognition of numbered lineages (Triplett and Clark 2010; Zeng and Zhang et al. 2010). Branching order among the 10 current lineages is largely unresolved, so until more data are available, we simply list the genera for the tribe without reference to subtribes or lineages.

Within the Bambuseae, the three neotropical subtribes as delimited by Judziewicz et al. (1999) are supported by molecular phylogenetic analyses, and each has at least one morphological synapomorphy, so we continue to recognize these three. Among the paleotropical subtribes, the Melocanninae, Hickeliinae and Bambusinae remain largely as circumscribed by Soderstrom and Ellis (1987), with the addition of a number of more recently described genera mainly in the Bambusinae and Hickeliinae and the placement of *Greslania* in the Bambusinae. The Racemobambosinae here is restricted to *Racemobambos*, based on recent molecular results indicating that *Neomicrocalamus* and *Vietnamosasa* fall within the Bambusinae (Yang et al. 2008; Sungkaew et al. 2009). Morphological synapomorphies have not yet been identified for either the Bambusinae or the Racemobambosinae. As Goh et al. (in prep. and pers. comm.) suggest, it may be necessary to recognize one or more additional subtribes segregated from the Bambusinae once the major lineages of paleotropical woody bamboos are more fully understood.

Our subtribal treatment of Olyreae is consistent with Judziewicz and Clark (2007) and the few phylogenetic analyses including sampling across the diversity of this tribe (BPG, in prep.). A more comprehensive phylogenetic analysis is in progress (de Oliveira et al., in prep.) and will provide more insight into the evolution of the herbaceous bamboos.

Taxonomic Treatment

The subfamily description is modified from GPWG (2001). Potential synapomorphies for tribes or subtribes are underlined within the descriptions. Genera are listed alphabetically within each tribe or subtribe, and the number of species for each genus is given in parentheses after the genus name. Two

electronic databases are available with more detailed information on bamboo genera: GrassBase (www.kew.org/data/grasses-db/) and Grass Genera of the World. (www.delta-intkey.com/grass).

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

Plants perennial (possibly rarely annual in Olyreae), rhizomes (leptomorph) present or absent, herbaceous or woody, of temperate and tropical forests, tropical high montane grasslands, riverbanks, and sometimes savannas or swamps. Culms hollow or solid; aerial branching often present. Leaves distichous; outer (abaxial) ligule absent (Olyreae) or present (Arundinarieae, Bambuseae); adaxial ligule membranous or chartaceous, fringed or unfringed; sheaths often auriculate or fimbriate or both; blades usually relatively broad, pseudopetiolate, venation parallel; mesophyll non-radiate, an adaxial palisade layer absent, fusoid cells large and well developed in at least shade leaves, arm cells usually well developed and strongly asymmetrically invaginated; Kranz anatomy absent, photosynthetic pathway C_3 ; midrib complex or simple; adaxial bulliform cells present; stomates with dome-shaped, triangular or parallel-sided subsidiary cells; bicellular microhairs present, panicoid-type; papillae common and abundant. Synflorescences spicate, racemose or paniculate, completing development of all spikelets in one period of growth and subtending bracts and prophylls usually absent, or pseudospikelets with basal bud-bearing bracts producing two or more orders of spikelets with different phases of maturity and subtending bracts and prophylls usually present. Spikelets (or spikelets proper of the pseudospikelets) bisexual (Arundinarieae, Bambuseae) or unisexual (Olyreae), consisting of 0, 1, 2 or several glumes and 1 to many florets; lemma lacking uncinata macrohairs, if awned, the awns single; palea well developed; lodicules usually 3 (rarely 0 to 6 or many), membranous, vascularized, often ciliate; stamens usually 2, 3 or 6 (2 to 40 in *Pariana*, 6 to 120 in *Ochlandra*); ovary glabrous or hairy, sometimes with an apical appendage, haustorial synergids absent, styles 2 or 3, sometimes very short but close, stigmas 2 or 3. Caryopsis with hilum linear (rarely punctate), extending its full length (rarely less than full length); endosperm hard, without lipid, containing compound starch grains; embryo small, epiblast present, scutellar cleft present, mesocotyl internode absent, embryonic leaf margins overlapping. First seedling leaf blade absent. Base chromosome numbers: $x = 7, 9, 10, 11$, and 12.

Included Tribes: Arundinarieae, Bambuseae, Olyreae.

Arundinarieae Nees ex Asch. & Graebn., Syn. Mitteleurop. Fl. 2, 1: 770. 1902. Type: *Arundinaria* Michx.

Rhizomes (leptomorph) and culm bases well developed, some taxa lacking leptomorph rhizomes. Culms woody, usually hollow; culm development occurring in two phases, first, new, unbranched shoots bearing culm leaves elongate to full height, second, culm lignification and branch development with production of foliage leaves occur; branch development basipetal; aerial vegetative branching complex, usually derived from a single bud per node (multiple, subequal buds per node in *Chimonocalamus* and *Chimonobambusa*). Culm leaves usually well developed with expanded sheaths and well developed to reduced blades. Foliage leaves with an outer ligule; sheaths often bearing fimbriae and/or auricular appendages at the summit; blades pseudopetiolate, articulated, deciduous; epidermal silica cells lacking cross-shaped or crenate silica bodies. Flowering usually cyclical, gregarious and monocarpic. Synflorescences bracteate or not, determinate (spikelets) or indeterminate (pseudospikelets). Spikelets (or spikelets proper of the pseudospikelets) bisexual with 1 to many bisexual florets; glumes (0-1) 2-4; lemmas multinerved, similar in texture to the glumes; paleas several-nerved with an even number of nerves, bicarinate. Caryopsis basic, uncommonly baccate (e.g., *Ferrocalamus*); hilum linear. Base chromosome number $x = 12$; $2n = 48$.

Included genera: *Acidosasa* C. D. Chu & C. S. Chao ex P. C. Keng (11) (including *Metasasa* W. T. Lin), *Ampelocalamus* S. L. Chen, T. H. Wen & G. Y. Sheng (13), *Arundinaria* Michx. (3), *Bashania* P. C. Keng & Yi (2), *Chimonobambusa* Makino (37) (including *Menstruocalamus* T. P. Yi, *Oreocalamus* Keng, *Qiongzhusa* Hsueh & Yi), *Chimonocalamus* Hsueh & Yi (11), *Drepanostachyum* P. C. Keng (10), *Fargesia* Franchet (90) (including *Borinda* Stapleton, *Sinarundinaria* Nakai), *Ferrocalamus* Hsueh & P. C. Keng (2), *Gaoligongshania* D. Z. Li, Hsueh & N. H. Xia (1), *Gelidocalamus* T. H. Wen (9), *Himalayacalamus* P. C. Keng (8), *Indocalamus* Nakai (23), *Indosasa* McClure (15), *Oligostachyum* Z. P. Wang & G. H. Ye (15) (including *Clavinodum* T. H. Wen), *XPhyllosasa* Demoly (1), *Phyllostachys* Sieb. & Zucc. (51), *Pleioblastus* Nakai (40) (including *Nipponocalamus* Nakai, *Polyanthus* C. H. Hu), *Pseudosasa* Makino ex Nakai (19), *Sarocalamus* Stapleton (3), *Sasa* Makino & Shibata (40), *Sasaella* Makino (13), *Sasamorpha* Nakai (5), *Semiarundinaria* Makino ex Nakai (10) (including *Brachystachyum* Keng), *Shibataea* Makino ex Nakai (7), *Sinobambusa* Makino ex Nakai (10), *Thamnocalamus* Munro (4), *Yushania* P. C. Keng (80) (including *Burmabambus* P. C. Keng, *Butania* P. C. Keng, *Monospatha* W. T. Lin).

Bambuseae Kunth ex Dumort., Anal. Fam. Pl.: 63. 1829. Type: *Bambusa* Schreb.

Rhizomes (leptomorph) and culm bases well developed, leptomorph rhizomes occurring only within *Chusquea*. Culms woody, usually hollow (solid in most *Chusquea* and a few species of other genera); culm development occurring in two phases, first, new, unbranched shoots bearing culm leaves elongate to full height, second, culm lignification and branch development with production of foliage leaves occur; branch development acropetal or bidirectional; aerial vegetative branching complex (but absent in *Glaziophyton*, *Greslania* and two clades within *Chusquea*), usually derived from a single bud per node (multiple, subequal buds per node in *Apoclada*, *Filgueirasia*, *Holttumochloa*; multiple, dimorphic buds in most of *Chusquea*). Culm leaves usually well developed with expanded sheaths and well developed to reduced blades, sometimes poorly differentiated from foliage leaves (e.g., *Aulonemia*, two clades within *Chusquea*) or absent. Foliage leaves with an outer ligule; sheaths often bearing fimbriae and/or auricular appendages at the summit; blades usually pseudopetiolate, articulate, deciduous; epidermal silica cells lacking cross-shaped or crenate silica bodies. Flowering usually cyclical, gregarious and monocarpic. Synflorescences bracteate or not, determinate (spikelets) or indeterminate (pseudospikelets). Spikelets (or spikelets proper of the pseudospikelets) bisexual with 1 to many bisexual florets; glumes (0-) 1-4 (-6), sometimes very reduced; lemmas multinerved, similar in texture to the glumes; paleas several-nerved with an even number of nerves, bicarinate. Caryopsis usually basic, sometimes baccate (e.g., *Alvimia*, *Dinochloa*, *Melocanna*, *Ochlandra*, *Olmecca*, at least one species of *Guadua*) or nuroid (e.g., *Actinocladum*, *Merostachys*); hilum linear. Base chromosome numbers $x = 10, (11), \text{ and } 12; 2n = (20) 40, (44), 46, 48, 70, 72$.

Neotropical Woody Bamboo Subtribes

Arthrostylidiinae Bews, World's Grasses: 96. 1929. Type: *Arthrostylidium* Rupr.

Rhizomes (leptomorph) absent. Culm bases sympodial, pachymorph, necks short to somewhat elongated; internodes of the aerial culms usually hollow, sometimes thick-walled, rarely septate (*Glaziophyton*), all subequal or sometimes very short internodes alternating in various combinations with elongated internodes; nodes of aerial culms without a patella. Aerial branching usually well developed and derived from a single bud per node; thorns absent. Culm leaves usually well developed (absent in *Glaziophyton*); margins of the sheath and blade more or less continuous or distinct; sheaths usually bearing fimbriae or fimbriate auricles; oral setae absent; blades erect or reflexed. Foliage leaf

sheaths usually bearing fimbriae or fimbriate auricles at the summit, oral setae absent; blades with a simple, abaxially projecting midrib; intercostal sclerenchyma usually present; adaxial epidermis lacking stomates and papillae or these infrequent and poorly developed; abaxial epidermis usually with a green stripe along the narrow-side margin, with stomates common and papillae usually well developed on at least some long cells; stomatal apparatus with papillae absent from the subsidiary cells but usually overarched by papillae from adjacent long cells. Synflorescences usually ebracteate, indeterminate (pseudospikelets) or determinate (spikelets), paniculate or racemose; prophylls present or absent. Spikelets (or spikelets proper of the pseudospikelets) consisting of 2-3 glumes, 1 to many female-fertile florets, and a rachilla extension bearing a rudimentary floret; palea keels wingless. Stamens (2) 3 (6), filaments free. Ovary glabrous, with a short style; stigmas 2 (3). Caryopsis basic, uncommonly baccate (*Alvimia*) or nuroid (*Actinocladum*, *Merostachys*). Base chromosome number $x = 10$; $2n = 40$ (but only 2 counts available for the subtribe).

Included genera: *Actinocladum* Soderstr. (1), *Alvimia* Soderstr. & Londoño (3), *Arthrostylidium* Rupr. (32), *Athroostachys* Benth (1), *Atractantha* McClure (6), *Aulonemia* Goudot (40) (including *Matudacalamus* F. Maekawa), *Colantheria* McClure & E. W. Sm. (7), *Elytostachys* McClure (2), *Filgueirasia* Guala (2), *Glaziophyton* Franch. (1), *Merostachys* Spreng. (48), *Myriocladus* Swallen (12), *Rhipidocladum* McClure (17).

Chusqueinae Bews, World's Grasses: 96. 1929. Type: *Chusquea* Kunth.

Neurolepidinae Soderstr. & R. P. Ellis in Soderstr. et al., Grass Syst. Evol.: 238. 1987. Type: *Neurolepis* Meisner.

Rhizomes (leptomorph) sometimes present. Culm bases sympodial, pachymorph, necks short; internodes of the aerial culms usually solid, all subequal; nodes of the aerial culms without a patella. Aerial branching usually well developed and derived from a multiple, dimorphic bud complement, absent in two clades (= *Neurolepis*) but a single bud per node often present in these taxa; thorns absent. Culm leaves usually well developed (sometimes not well differentiated in the *Neurolepis* clades); margins of the sheath and blade usually distinct; fimbriae or fimbriate auricles absent; oral setae absent; blades usually erect, rarely reflexed. Foliage leaf sheaths usually bearing cilia at the summit, rarely well developed fimbriae present, oral setae absent, auricles absent; blades with a complex, abaxially projecting midrib; intercostal sclerenchyma absent; adaxial epidermis lacking stomates and papillae or these infrequent and poorly developed; abaxial epidermis usually lacking a green stripe along the narrow-side margin, with stomates common and papillae usually well developed on at least some long cells; stomatal apparatus bearing two or more papillae per subsidiary cell and also often overarched by papillae from adjacent long cells. Synflorescences usually ebracteate, determinate (spikelets), paniculate or rarely racemose; prophylls absent. Spikelets consisting of 4 glumes and 1 female-fertile floret, rachilla extension absent; palea keels lacking wings. Stamens (2) 3, filaments free. Ovary glabrous, with a short style; stigmas 2. Caryopsis basic. Base chromosome number $x = 10$ (11, 12); $2n = (20) 40$ (44, 48).

Included genus: *Chusquea* Kunth (160) (including *Neurolepis* Meisn., *Rettbergia* Raddi, *Swallenochloa* McClure).

Guaduinae Soderstr. & R. P. Ellis in Soderstr. et al., Grass Syst. Evol.: 238. 1987. Type: *Guadua* Kunth.

Rhizomes (leptomorph) lacking. Culm bases sympodial, pachymorph, necks short to elongated; internodes of the aerial culms hollow to solid, all subequal; nodes of the aerial culms without a patella. Aerial branching well developed and derived from a single bud per node (1-4 subequal buds per node

in *Apoclada*); thorns absent or present (*Guadua*). Culm leaves well developed; margins of the sheath and blade continuous or nearly so, uncommonly distinct; sheaths often bearing fimbriae or fimbriate auricles at the sheath summit; oral setae usually present (absent in *Guadua*); blades erect or reflexed. Foliage leaf sheaths often with fimbriae or fimbriate auricles at the summit; oral setae present; blades with a complex, abaxially projecting midrib; intercostal sclerenchyma absent; adaxial epidermis usually with abundant stomates and well developed papillae, rarely these lacking or infrequent and poorly developed; abaxial epidermis usually lacking a green stripe along the narrow-side margin, with stomates present and abundant (absent in *Apoclada*) and papillae absent to well developed; stomatal apparatus with papillae absent from the subsidiary cells but usually overarched by papillae from adjacent long cells. Synflorescences bracteate or not, indeterminate (pseudospikelets) or determinate (spikelets), paniculate; prophylls present or absent. Spikelets (or spikelets proper of the pseudospikelets) consisting of (0-) 1 to 4 (-7) glumes, 1 to many female-fertile florets, and a rachilla extension bearing a rudimentary floret; palea keels wingless to prominently winged. Stamens 3 or 6, filaments free. Ovary glabrous or hairy, with a short style; stigmas 2 or 3. Caryopsis basic, uncommonly baccate (*Olmecca* and *Guadua sarcocarpa*). Base chromosome number $x=12$; $2n = 46$ or 48.

Included genera: *Apoclada* McClure (1), *Eremocaulon* Soderstr. & Londoño (4) (including *Criciuma* Soderstr. & Londoño), *Guadua* Kunth (27), *Olmecca* Soderstr. (5), *Otatea* (McClure & E. W. Sm.) C. E. Calderón & Soderstr. (8)

Paleotropical Woody Bamboo Subtribes

Bambusinae J. S. Presl in K. B. Presl, Rel. Haenk. 1: 256. 1830. Type: *Bambusa* Schreb.

Rhizomes (leptomorph) lacking. Culm bases sympodial, pachymorph, necks short to slightly elongated; internodes of the aerial culms hollow or solid, all subequal; nodes of the aerial culms with or without a patella. Aerial branching well developed and derived from a single bud per node (multiple buds in *Holttumochloa*); thorns usually absent, sometimes present (*Bambusa*). Culm leaves well developed; margins of the sheath and blade continuous or distinct; sheaths bearing fimbriae or fimbriate auricles at the summit or neither; oral setae present or absent; blades erect or reflexed. Foliage leaf sheaths often with fimbriae or fimbriate auricles at the summit; oral setae present or absent; blades with a complex or simple, abaxially projecting midrib; intercostal sclerenchyma absent; adaxial epidermis with or without stomates, with or without papillae; abaxial epidermis usually lacking a green stripe along the narrow-side margin, usually with abundant stomates and well developed papillae; stomatal apparatus with papillae absent from the subsidiary cells but usually overarched by papillae from adjacent long cells. Synflorescences bracteate or not, indeterminate (pseudospikelets) or less commonly determinate (spikelets), paniculate; prophylls present or absent. Spikelets or spikelets proper of the pseudospikelets consisting of (0-) 1 to several glumes, 1-10 or more female-fertile florets and sometimes a rachilla extension bearing 1-3 rudimentary florets; palea keels wingless to prominently winged. Stamens 6, filaments free or fused. Ovary glabrous or hairy, usually with a short style; stigmas 1, 2 or 3. Caryopsis basic or baccate (*Cyrtochloa*, *Dinochloa*, *Melocalamus*, *Sphaerobambos*). Base chromosome number $x = 10$ or 12; $2n = 48, 70, 72$.

Included genera: *Bambusa* Schreber (100) (including *Dendrocalamopsis* Q. H. Dai & X. L. Tao, *Isurochloa* Buse, *Leleba* Rumphius ex Nakai, *Lingnania* McClure, *Neosinocalamus* P.C. Keng, *Tetragonocalamus* Nakai), *Bonia* Balansa (5) (including *Monocladus* Chia, H. L. Fung & Y. L. Yang), *Cyrtochloa* S. Dransf. (5), *Dendrocalamus* Nees (41) (including *Klemachloa* R. N. Parker, *Sinocalamus* McClure), *Dinochloa* Buse (31), *Fimbribambusa* Widjaja (2), *Gigantochloa* Kurz ex

Munro (30), *Greslania* Balansa (4), *Holttumochloa* K. M. Wong (3), *Kinabaluchloa* K. M. Wong (2), *Maclurochloa* K. M. Wong (1), *Melocalamus* Benth. (5), *Mullerochloa* K. M. Wong (1), *Neololeba* Widjaja (5), *Neomicrocalamus* P. C. Keng (5) (including *Microcalamus* Gamble), *Oreobambos* K. Schumann (1), *Oxytenanthera* Munro (1), *Parabambusa* Widjaja (1), *Phuphanochloa* Sungkaew & Teerawat. (1), *Pinga* Widjaja (1), *Pseudobambusa* Nguyen (1), *Pseudoxytenanthera* Soderstr. & Ellis (12), *Soejatmia* K. M. Wong (1), *Sphaerobambos* S. Dransf. (3), *Temochloa* S. Dransf. (1), *Temburongia* S. Dransf. & K. M. Wong (1), *Thyrsostachys* Gamble (2), *Vietnamosasa* Nguyen (3).

Hickeliinae A. Camus, Compt. Rend. Acad. Sci. 179: 480. 1924. Type: *Hickelia* A. Camus.

Nastinae Soderstr. & R. P. Ellis in Soderstr. et al., Grass Syst. Evol.: 238. 1987. Type: *Nastus* A. L. Juss.

Rhizomes (leptomorph) lacking. Culm bases sympodial, pachymorph, necks short to elongated; internodes of the aerial culms usually hollow or rarely solid, all subequal along the aerial culms. Aerial branching well developed and derived from a single bud per node (multiple buds in *Nastus productus*), central branch dominant; thorns absent. Culm leaves well developed; margins of sheath and blade usually discontinuous; sheaths bearing fimbriae or fimbriate auricles or neither; oral setae absent; blades erect or reflexed. Foliage leaf sheaths with fimbriae or fimbriate auricles present or absent; oral setae absent; blades with a complex, adaxially projecting midrib; intercostal sclerenchyma and fiber-like epidermal cells sometimes present; adaxial epidermis lacking stomates and papillae or these infrequent and poorly developed; abaxial epidermis usually lacking a green stripe along the narrow-side margin, with stomates common and papillae usually well developed on at least some long cells; stomatal apparatus with papillae absent from the subsidiary cells but usually overarched by papillae from adjacent long cells. Synfloresences determinate (spikelets), bracteate or ebracteate, paniculate, racemose or capitate; prophylls usually absent. Spikelets consisting of 4-6 glumes and 1 female-fertile floret; rachilla extension present or absent, if present well developed or much reduced bearing a rudimentary or reduced floret; palea usually 2-keeled (without keels when rachilla extension absent), keels wingless. Stamens 6, filaments usually free. Ovary glabrous or hairy, with long or short style; stigmas 3. Caryopsis basic, sessile or stalked (*Cathariostachys*). Base chromosome number and ploidy level unknown.

Included genera: *Cathariostachys* S. Dransf. (2), *Decaryochloa* A. Camus (1), *Hickelia* A. Camus (4) (including *Pseudocoix* A. Camus), *Hitchcockella* A. Camus (1), *Nastus* Juss. (20) (including *Chloothamnus* Büse, *Oreiochloa* Gamble), *Perrierbambus* A. Camus (2), *Sirochloa* S. Dransf. (1), *Valiha* S. Dransf. (2).

Melocanninae Benth., J. Linn. Soc. London 19: 31. 1881. Type: *Melocanna* Trin.

Schizostachyidinae Soderstr. & R. P. Ellis in Soderstr. et al., Grass Syst. Evol.: 238. 1987. Type: *Schizostachyum* Nees.

Rhizomes (leptomorph) lacking. Culm bases sympodial, pachymorph, necks short or elongated; internodes of the aerial culms moderately long or very long, hollow, with thin walls; nodes of the aerial culms lacking a patella. Aerial branching well developed and derived from a single bud per node; thorns absent. Culm leaves well developed; margins of the sheath and blade distinct; sheaths bearing fimbriae or fimbriate auricles at the summit or neither; oral setae usually absent; blades often reflexed. Foliage leaf sheaths bearing fimbriae or small fimbriate auricles or neither; oral setae present or absent; blades with a complex, abaxially projecting midrib; intercostal sclerenchyma absent; adaxial epidermis lacking stomates or these infrequent and poorly developed, papillae often present; abaxial epidermis with (usually) or without a green stripe along the narrow-side margin, with stomates common and papillae usually well developed on at least some long cells; stomatal apparatus with

papillae absent from the subsidiary cells but usually overarched by papillae from adjacent long cells. Synflorescences indeterminate (pseudospikelets), spicate or capitate, prophylls present. Spikelets proper consisting of (0) 2 (or 4) glumes, one female-fertile floret (3 in *Schizostachyum grande*), with or without rachilla extension, if present bearing a rudimentary floret; palea keels wingless or winged. Stamens 6 (15-120 in *Ochlandra*), filaments free or fused. Ovary glabrous, with a long, slender, hollow style; stigmas (2-) 3. Caryopsis basic or baccate (*Melocanna*, *Ochlandra*, *Stapletonia*) or nucoid (*Pseudostachyum*). Base chromosome number $x = 12$; $2n = 72$.

Included genera: *Cephalostachyum* Munro (14), *Davidsea* Soderstr. & Ellis (1), *Dendrochloa* C. E. Parkinson (1), *Melocanna* Trin. (2), *Neohouzeaua* A. Camus (7), *Ochlandra* Thwaites (9), *Pseudostachyum* Munro (1), *Schizostachyum* Nees (50) (including *Leptocanna* L. C. Chia & H. L. Fung), *Stapletonia* Singh, Dash & Kumari (1), *Teinostachyum* Munro (2).

Racemobambosinae Stapleton, Edinburgh J. Bot. 51: 323-324. 1994. Type: *Racemobambos* Holttum. Rhizomes (leptomorph) lacking. Culm bases sympodial, pachymorph, necks short or elongated; internodes of the aerial culms hollow, all subequal; nodes of the aerial culms without a patella. Aerial branching well developed and derived from a single bud per node; thorns absent. Culm leaves well developed; margins of the sheath and blade more or less continuous or distinct; sheaths usually bearing small fimbriate auricles at the summit or rarely efimbriate and exauriculate; oral setae absent; blades erect or reflexed. Foliage leaf sheaths usually bearing small fimbriate auricles at the summit or rarely efimbriate and eauriculate; oral setae absent; blades with an abaxially projecting midrib; blade anatomy and micromorphology unknown. Synflorescences bracteate, determinate (spikelets), racemose; prophylls absent. Spikelets consisting of 2-3 glumes, 3-8 female-fertile florets and a rachilla extension bearing 1 rudimentary floret; palea keels wingless. Stamens 6, filaments free. Ovary usually hairy toward the apex, usually with a short style; stigmas 3. Caryopsis basic. Base chromosome number unknown.

Included genus: *Racemobambos* Holttum (16).

Olyreae Kunth ex Spenn., Fl. Friburg. 1: 172. 1825. Type: *Olyra* L.

Rhizomes (leptomorph) weakly or sometimes strongly developed (*Olyra*, *Pariana*). Culms herbaceous to subwoody, vegetative branching restricted and only one phase of culm development observed. Culm leaves usually absent, sometimes differentiated in taxa with larger culms. Foliage leaves with the outer ligule absent; sheaths sometimes bearing fimbriae (*Eremitis*, *Pariana*) and/or blister-like swellings at or near the summit (*Pariana*), more often fimbriae, swellings, and auriculate appendages absent; blades pseudopetiolate, not articulated, persistent or sometimes deciduous, exhibiting nocturnal folding (nyctinasty) in some genera (e.g., *Eremitis*, *Lithachne*, *Raddia*, *Raddiella*); epidermal silica cells usually with cross-shaped silica bodies in the costal zone and crenate (olyroid) silica bodies in the intercostal zone (these absent in *Buergersiochloa*). Flowering usually annual or seasonal for extended periods, very rarely gregarious and monocarpic. Synflorescences ebracteate or rarely enclosed by a spathaceous leaf sheath (*Eremitis*), apparently determinate. Spikelets unisexual, dimorphic and 1-flowered with no rachilla extension, the plants monoecious; pistillodes or staminodes sometimes present in male or female spikelets respectively. Female spikelets with 2 glumes; lemma chartaceous to more commonly coriaceous, several-nerved, usually non-aristate except in *Agnesia*, *Buergersiochloa* and *Ekmanochloa*; palea with few to several nerves. Male spikelets usually smaller than the females, glumes usually absent or rarely 2 and well developed;

lemmas membranous, 3-nerved. Caryopsis basic; hilum usually linear, sometimes punctate. Base chromosome number $x = 7, 9, 10, 11,$ and (12).

Buergersiochloinae (S. T. Blake) L. G. Clark & Judz., *Aliso* 23: 311. 2007.

Foliage leaf sheaths bearing fimbriae at the apex; blades lacking cross-shaped and crenate (olyroid) silica bodies in both epidermises. Synflorescences paniculate. Female lemmas awned. Stamens 2-3.

Included genus: *Buergersiochloa* Pilg. (1).

Parianinae Hack. in Engler & Prantl, *Naturl. Pflanzenfam.* 2, 2: 88. 1887. Type: *Pariana* Aubl.

Foliage leaf sheaths bearing fimbriae at the apex; blades with cross-shaped and crenate (olyroid) silica bodies in the epidermises. Synflorescences spicate. Female lemmas unawned. Stamens 2 or 6 (to 36-40).

Included genera: *Eremitis* Döll (1), *Pariana* Aubl. (35) (Generic and species delimitations in this subtribe are uncertain, so these numbers represent estimates; de Oliveira and Moreira, pers. comm.)

Olyrinae Kromb., *Fl. Luxembourg* 496. 1875. Type: *Olyra* L.

Foliage leaf sheaths lacking fimbriae at the apex; blade with cross-shaped and crenate (olyroid) silica bodies in the epidermises. Synflorescences paniculate or racemose. Female lemmas usually unawned (awned only in *Agnesia*, *Ekmanochloa*). Stamens 2-3.

Included genera: *Agnesia* Zuloaga & Judz. (1), *Arberella* Soderstr. & C. E. Calderón (7), *Cryptochloa* Swallen (8), *Diandrolyra* Stapf (3), *Ekmanochloa* Swallen (2), *Froesiochloa* G. A. Black (1), *Lithachne* P. Beauv. (4), *Maclurolyra* C. E. Calderón & Soderstr. (1), *Mniochloa* Chase (1), *Olyra* L. (24), *Parodiolyra* Soderstr. & Zuloaga (5), *Piresia* Swallen (5), *Piresiella* Judz., Zuloaga & Morrone (1), *Raddia* Bertol. (9), *Raddiella* Swallen (8), *Rehia* Fijten (1), *Reitzia* Swallen (1), *Sucrea* Soderstr. (3).

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Footnote

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