Chapter 1
Bamboo Taxonomy and Habitat

L.G. Clark, X. Londoño, and E. Ruiz-Sanchez

Abstract Bamboos (subfamily Bambusoideae) comprise one of 12 subfamilies within the grass family (Poaceae) and represent the only major grass lineage to diversify in forests. Bamboos are distinguished by the presence of well-developed, asymmetrically strongly invaginated arm cells in the leaf mesophyll as seen in cross section and also generally exhibit relatively broad, pseudopetiolate leaf blades usually with fusoid cells flanking the vascular bundles. The nearly 1,500 described species of bamboos are classified into three tribes: Arundinarieae (temperate woody bamboos, 546 species), Bambuseae (tropical woody bamboos, 812 species), and Olyreae (herbaceous bamboos, 124 species). Relationships between the three tribes remain uncertain, but a much better understanding of evolutionary relationships within the tribes has been achieved based on analyses of DNA sequence data, which we summarize. We present synoptic descriptions for the three tribes and, for the Bambuseae and Olyreae, their currently accepted subtribes, as well as lists of included genera and comments. The history of bamboo classification goes back over 200 years; we provide an overview of the most important advances leading to the current phylogenetic classification of bamboos based on their inferred evolutionary relationships. Bamboos are native to all continents except Antarctica and Europe and have a latitudinal distribution from 47° S to 50° 30′ N and an altitudinal distribution from sea level to 4,300 m. Bamboos therefore grow in association with a wide variety of mostly mesic to wet forest types in both temperate and tropical regions, but some bamboos have adapted to more open grasslands or occur in more specialized habitats.

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1.1 Introduction

Woody bamboos, or the "tree grasses," are a cultural and ecological feature of many countries of Asia, America, and Africa, where bamboos can provide environmental, social, and economic benefits. Bamboo is a multipurpose plant—it can substitute for timber in many respects due to its lignified culms, and because of its fast growth, intricate rhizome system, and sustainability, it has become a plant with conservation value, able to mitigate phenomena that result from global climate change. Bamboo is also an essential resource for many other organisms, not just pandas. Bamboo, like rice, maize, wheat, and sugar cane, is another important grass inextricably linked to human livelihood, fulfilling needs for shelter, food, paper, and more; the range of its use is hardly rivaled in the plant kingdom—not for nothing is bamboo known as "the plant of a thousand uses." Bamboos are complex plants that can be difficult to identify or classify, but given their ecological and economic importance, correct identification is critical to their conservation and development and a robust phylogenetic classification system underpins identification. In this chapter, we present a history of bamboo classification, discuss bamboo habitats, and present an up-to-date classification of bamboos based on synthesis of the most recent systematic work in this fascinating and charismatic group of grasses.

1.2 Definition of Bamboo

Bamboos comprise the subfamily Bambusoideae, one of 12 subfamilies currently recognized within the grass family (Poaceae). Unlike the other grasses, bamboos are the only major lineage within the family to adapt to and diversify within the forest habitat (Judziewicz et al. 1999; Grass Phylogeny Working Group [GPWG] 2001; Bamboo Phylogeny Group [BPG] 2012). Molecular sequence data strongly support the bamboos as a distinct lineage, as does the presence of well-developed, asymmetrically strongly invaginated arm cells in the leaf mesophyll as seen in cross section (GPWG 2001; Kelchner et al. 2013). Bamboos also generally exhibit relatively broad, pseudopetiolate leaf blades, with fusoid cells flanking the vascular bundles [but fusoid cells are often lacking in sun plants, March and Clark (2011)]. Bamboos include ca. 1,482 described species classified in approximately 119 genera, which in turn are grouped into three tribes: Arundinarieae (known as the temperate woody bamboos, even though some occur in the tropics at high elevations; ca. 546 species), Bambuseae (known as the tropical woody bamboos, even though some occur outside of the tropics; 812 species), and Olyreae (herbaceous bamboos, 124 species) (BPG 2012).

Within the Bambusoideae, the herbaceous bamboos (Olyreae) are easily distinguished by their lack of both well-differentiated culm leaves and outer ligules (contraligules) combined with relatively weakly lignified culms, restricted vegetative branching, and unisexual spikelets. Additionally, all Olyreae except for *Buergersiochloa* possess cross-shaped and crenate (olyroid) silica bodies and virtually all Olyreae exhibit seasonal flowering (BPG 2012). In contrast, woody bamboos (Arundinarieae and Bambuseae) commonly have complex rhizome systems, a tree-like habit with highly lignified, usually hollow culms, well-differentiated culm leaves, well-developed aerial branching, and foliage leaf blades with outer ligules. Culm development occurs in two phases: first, new, unbranched shoots bearing culm leaves elongate to their full height; second, culm lignification and branch development with production of foliage leaves take place. Woody bamboos also have bisexual spikelets and typically exhibit gregarious flowering cycles followed by death of the parent plants (monocarpy) (Dransfield and Widjaja 1995; Judziewicz et al. 1999; BPG 2012).

Woody bamboos have particular characteristics that make them unique grasses and an important non-timber resource. In Table 1.1 we compare bamboos with trees (wood, defined as 2° xylem) to highlight some of the unique features of bamboo.

Table 1.1 Comparison between bamboo and trees (wood)

Bamboo	Trees (wood)
Underground parts consisting of rhizomes and roots	Underground parts consisting of roots
Culms (stems) usually hollow and segmented	Stems solid and not segmented
The hardest part of the culm is the periphery	The hardest part of the stem is in the center
There is no vascular cambium so the culm does not increase in diameter with age	A vascular cambium is present so the stem increases in diameter with age
The conducting tissues, phloem and xylem, are together inside each vascular bundle	The conducting tissues, phloem and xylem, are separated by the vascular cambium
Culms lack bark	Stems have bark (cork + 2° phloem)
No radial (lateral) communication in the culms except at the nodes	Radial (lateral) communication throughout the stem
Culms grow extremely fast (to as much as 36 m tall at 6 months), reaching full height in one growing season	Stems grow slowly in height and diameter over many seasons
Culms grow in an association from a network of rhizomes, such that each culm depends on the others and the harvest of a culm directly affects the rest of the community	Each stem usually grows as an independent individual, and the harvest of a stem does not directly affect the rest of the community

1.3 History of Bamboo Taxonomy

While the first uses of bamboo in arts and technology were documented by early Chinese scholars, early taxonomic studies of bamboos were dominated by the Western world [see Soderstrom (1985) for a detailed review]. Within the last century, however, much work by botanists in the regions where bamboo is most diverse (Asia, India, and Central and South America) has contributed greatly to a vastly improved understanding of bamboo diversity and evolution. DNA sequence data in combination with morphological and anatomical studies form the basis of the most recent comprehensive and phylogenetically based classification system for bamboos (BPG 2012). We have used Soderstrom (1985) and Bedell (1997) as primary sources and recommend them especially to those readers interested in the earliest phases of bamboo classification. We here summarize recent advances, but begin our overview with the more global perspective on bamboos that emerged starting in the mid-nineteenth century.

Munro (1868) published a world monograph on the representatives of the Bambuseae known at the time, which remains a useful reference to this day even though the divisions are clearly not natural. In this work, he described 170 species grouped into 21 genera divided into three divisions: (a) Triglossae or Arundinarieae (*Arthrostylidium*, *Arundinaria*, *Chusquea*, among others), (b) Bambuseae verae (e.g., *Bambusa*, *Gigantochloa*), and (c) Bacciferae (*Dinochloa*, *Melocanna*, and others with fleshy fruits). Munro included only woody bamboos in his treatment, a taxonomic concept of bamboos that persisted for nearly a century.

A few botanists in the early twentieth century (e.g., Arber 1927) examined the flowering structure of bamboos (mainly Asiatic ones) in more detail and suggested modifications in bamboo classification, but none conducted a comprehensive study. In Japan, Nakai (1925, 1933) described a number of new genera and species, while Takenouchi (1931a, b) examined morphology and development of bamboos, with a particular focus on vegetative structures. In one of his earlier papers, McClure (1934) analyzed the inflorescence structure of *Schizostachyum* and coined the term "pseudospikelet" to refer to the peculiar rebranching spikelet found in this and a number of other bamboo genera. The next influential work on bamboo classification from a global perspective was that of Holttum (1956), who critically examined inflorescence, spikelet, ovary, and fruit structure and proposed a classification scheme for bamboos based on perceived evolutionary trends. This, to our knowledge, represents the first attempt to produce a natural classification for bamboos.

The 1960s was a period of active bamboo research in many parts of the world. McClure (1966), in his exhaustive work on the bamboo plant, pointed out that all parts of the vegetative and the flowering structures should be used for bamboo classification. This was revolutionary in grass taxonomy, where floral characters often continue to be given undue weighting to this day. He offered a significant step forward in the taxonomic conquest of the bamboos of the Americas (McClure 1973) based on this philosophy of synthesizing all available knowledge. Meanwhile, the Argentinian agrostologist Parodi (1961) offered a broader concept of the

Bambusoideae, including the herbaceous grass tribes Olyreae, Phareae, and Streptochaeteae in addition to the woody bamboos (as the tribe Bambuseae).

The next phase in the history of bamboo systematics was led by T. R. Soderstrom, who made significant contributions to the systematics and evolution of grasses with particularly enlightening studies of bamboos. A hallmark of Soderstrom's approach was to study and collect bamboos in the field, and he strongly supported such efforts by others. In collaboration especially with C. E. Calderón, L. G. Clark, R. Ellis, E. J. Judziewicz, and X. Londoño, Soderstrom investigated bamboo diversity and evolution with a special focus on American and Sri Lankan woody bamboos (e.g., Calderón and Soderstrom 1973, 1980; Soderstrom and Ellis 1988; Soderstrom and Londoño 1988) as well as detailed studies of herbaceous grass groups including Olyreae (e.g., Soderstrom and Zuloaga 1989). Soderstrom (1981) placed much cytological and morphological data on bamboos in an evolutionary context. One of Soderstrom's most important contributions to bamboo systematics was his revised classification of bamboos based on leaf anatomical features analyzed in an evolutionary context (Soderstrom and Ellis 1987). This classification and that of Keng (1982–1984) and Clayton and Renvoize (1986) were the last global bamboo treatments published prior to the advent of molecular sequence data in plant systematics. Although they differ in many generic concepts and hypotheses of relationships, both classifications include the woody bamboos (as the Bambuseae) and several tribes of herbaceous grasses, building on the broader Bambusoideae of both Nees (1835) and Parodi (1961).

During the 1980s and 1990s, bamboo research in China began in earnest. Landmarks included the global generic revision of Keng (1982–1984) and the publication of an account of all the Chinese bamboos for the *Flora Republicae Popularis Sinicae* (Keng and Wang 1996), with contributions by a number of Chinese bamboo botanists. The history of bamboo classification in China was reviewed in detail by Zhang (1992), who especially highlighted the contributions of Keng Y.-L., considered to be the father of Chinese bamboo taxonomy, and his son Keng P.-C. (Geng B.J.), as well as Wen T.-H., Yi T.-P., and Hsueh C.-J. These masters trained the next generation of bamboo systematists in China, including Li D.-Z. and Xia N.-H., who have now trained a fourth generation. Two contrasting schools of thought on bamboo taxonomy in China clashed over generic recognition for 25 years (Stapleton, pers. comm.). The innovative classification system established by Keng and colleagues used vegetative characters extensively, while others continued to follow a more traditional system, which emphasized floral characters in a classic grass taxonomy approach. Phylogenetic information (see below) was incorporated to achieve a more modern treatment in the English-language version of the *Flora of China* (Li et al. 2006).

This period also saw the production of several compilations of knowledge about bamboos. Ohrnberger (1999) compiled the published names of bamboos of the world, reporting the occurrence of 110 genera and 1,110–1,140 species. A compendium of bamboos from India (Seethalakshmi and Kumar 1998), a compendium of Chinese bamboos (Zhu et al. 1994), and a compendium of American bamboos (Judziewicz et al. 1999) were published. Dransfield (1992, 1998), Dransfield and

Widjaja (1995), Stapleton (1994a, b, c), Widjaja (1987), and Wong (1993, 1995, 2005), among others, advanced knowledge of the diversity of Madagascan and Asiatic bamboos, including the description of many new genera. Yi et al. (2008) recently produced an updated and beautifully illustrated compendium of Chinese bamboos.

Even into the early 1990s, the Bambusoideae were defined as all perennial, forest-inhabiting grass groups with broad, pseudopetiolate leaf blades, usually with fusoid cells in the mesophyll (Clayton and Renvoize 1986; Soderstrom and Ellis 1987). The first comprehensive DNA sequence analysis of the grass family that included good representation of the various tribes of the subfamily clearly showed that this broader Bambusoideae, however, was not a natural group (Clark et al. 1995). These results were confirmed and extended by the GPWG (2001), and the concept of the Bambusoideae was restricted to the woody bamboos (as Bambuseae) and the herbaceous bamboos (as the Olyreae, including Buergersiochloeae and Parianeae). Herbaceous grass tribes formerly regarded as bamboos were transferred to the Anomochlooideae (Anomochloeae and Streptochaeteae), Ehrhartoideae (Ehrharteae, Phyllorachideae, Oryzeae), Pharoideae (Phareae), Pooideae (Brachyelytreae, Diarrheneae, Phaenospermateae), and Puelioideae (Guaduelleae and Puelieae), and Streptogyneae was placed without a fixed position in the Bambusoideae–Ehrhartoideae–Pooideae (BEP) clade (Clark and Judziewicz 1996; GPWG 2001). Additionally, the Anomochlooideae, Pharoideae, and Puelioideae were strongly supported as the three early-diverging lineages within the family, unequivocally indicating that grasses originated in the forest habitat.

The Bamboo Phylogeny Group, consisting of an international team of 21 bamboo taxonomists coordinated by L. G. Clark, was formed in 2005 primarily to generate a global evolutionary tree (phylogeny) for bamboos based on extensive chloroplast sequence data and to produce a revised tribal and generic classification based on the phylogeny. A number of papers addressed phylogenetic relationships within bamboo lineages (e.g., Fisher et al. 2009; Triplett and Clark 2010; Zhang et al. 2012), but both Sungkaew et al. (2009) and Kelchner et al. (2013) explicitly addressed broader relationships across the subfamily. All studies with sufficient sampling resolved three strongly supported lineages which are now recognized as tribes (BPG 2012): temperate woody bamboos (Arundinarieae), tropical woody bamboos (Bambuseae), and the herbaceous bamboos (Olyreae). A review of phylogenetic work in the bamboos and the revised tribal, subtribal, and generic classification, which we follow here with a few updates, can be found in BPG (2012).

1.4 Bamboo Habitat

Bamboos, both woody and herbaceous, are well known as forest grasses, even though some species have radiated into open, grassy, or shrubby habitats at high elevations in montane systems of the tropics (Soderstrom and Calderón 1979;

Soderstrom and Ellis 1988; Judziewicz et al. 1999; Judziewicz and Clark 2007). Native to all continents except Antarctica and Europe, bamboos have a latitudinal distribution from 47° S to 50°30′ N and an altitudinal distribution from sea level to 4,300 m (Soderstrom and Calderón 1979; Judziewicz et al. 1999; Ohrnberger 1999). Bamboos therefore occupy a broad range of habitat types, especially forests, from temperate to tropical climatic zones and bamboos are often dominant or highly visible elements of the vegetation. We here summarize these habitats, and note that although there has been some important recent work on bamboo ecology (BPG 2012 and references cited therein), much more needs to be done.

With some exceptions, the Arundinarieae occupy temperate deciduous forests or mixed coniferous and deciduous forests or coniferous forests in the temperate to subtropical zones of the Northern hemisphere in Eastern Asia and Eastern North America (Stapleton 1994a, b, c; Li and Xue 1997; Taylor and Qin 1997; Triplett et al. 2006; Dai et al. 2011). Temperate bamboos are common in the understory and often form the dominant element on wetter sites (Taylor and Qin 1997; Noguchi and Yoshida 2005; Tsuyama et al. 2011). In Chinese montane forests, species of *Bashania*, *Chimonobambusa*, *Fargesia*, *Indosasa*, and *Yushania* are characteristic (Li and Xue 1997; Taylor and Qin 1997), while in the more seasonally dry areas of the central Himalayas clump-forming bamboos are more prevalent, especially *Thamnocalamus* and *Drepanostachyum*, with spreading bamboos of *Yushania*, *Sarocalamus*, and *Chimonobambusa* restricted to the wetter ends of the mountain range (Stapleton 1994a, b, c and pers. comm.). In wetter forests of E China, Korea, and Japan, rampant species of *Sasa* and *Sasamorpha* are especially aggressive and dominant in the understory (Noguchi and Yoshida 2005; Tsuyama et al. 2011). Some temperate bamboos in Asia, such as *Acidosasa*, *Drepanostachyum*, *Indosasa*, and *Sinobambusa*, extend into dry or evergreen subtropical forests as well (Stapleton 1994a, b, c; Li and Xue 1997). In the Eastern USA, *Arundinaria* occurs in the Southeastern Coastal Plain in woodlands and forests, and often along water courses. Switch cane (*A. tecta*) is notable for often occurring in swamps, and like other Arundinarieae known to grow in wetter sites (see below), air canals are a prominent feature of its rhizomes (Triplett et al. 2006). Although the extensive canebrakes in the Southeastern USA have virtually disappeared (Judziewicz et al. 1999), temperate bamboo-dominated habitats in China are classified as bamboo forests and may form a significant portion of the vegetation in some regions (Yang and Xue 1990; Dai et al. 2011).

Many Bambuseae, especially genera of larger stature such as *Bambusa*, *Dendrocalamus*, *Eremocaulon*, *Guadua*, *Gigantochloa*, and *Schizostachyum*, grow in lowland moist tropical forests or lower montane forests up to ca. 1,500 m in elevation in both the Old and New Worlds (Soderstrom and Calderón 1979; Seethalakshmi and Kumar 1998; Judziewicz et al. 1999). It is common to see these bamboos in valleys or along rivers or streams, especially in secondary forest, often to the exclusion of other vegetation. However, a number of lowland tropical bamboos, including species of *Alvimia*, *Chusquea*, *Dinochloa*, *Hickelia*, *Neomicrocalamus*, and *Racemobambos*, have smaller culms that twine around or scramble over trees and shrubs or form beautiful curtains of hanging foliage

(Soderstrom and Londoño 1988; Dransfield 1992, 1994); species of *Ochlandra* may form dense, reed-like thickets along stream banks (Seethalakshmi and Kumar 1998; Gopakumar and Motwani 2013). Some lowland species or genera (e.g., *Dendrocalamus strictus* in India, *Guadua paniculata* in Latin America, *Otatea* in Mexico and Colombia, *Perrierbambus* in Madagascar) are well adapted to drier forest types, and some populations of *Otatea acuminata* inhabit xerophytic scrub, often on calcareous substrates, or they may occupy early successional sites created by forest clearing (Soderstrom and Calderón 1979; Gadgil and Prasad 1984; Rao and Ramakrishnan 1988; Seethalakshmi and Kumar 1998; Ruiz-Sanchez et al. 2011b). Some lowland bamboos, such as *Actinocladum* and *Filgueirasia* in Brazil (Soderstrom and Calderón 1979; Judziewicz et al. 1999), and *Vietnamosasa* in Indochina (Stapleton 1998), are drought tolerant and fire adapted for survival in their grassland habitats. Natural tropical bamboo forests are known from some regions (Li and Xue 1997; Judziewicz et al. 1999); probably the most extensive of these are the *Guadua*-dominated forests of the Amazon Basin (Judziewicz et al. 1999).

A significant portion of tropical bamboo species diversity, however, is associated with moist subtropical montane forests above 1,500 m in elevation, especially in the Neotropics and Asia (Li and Xue 1997; Judziewicz et al. 1999; Uma Shaanker et al. 2004). Although a few montane forest species of *Chusquea* with erect to arching culms attain diameters of up to 7 cm, most montane tropical bamboos have culms not more than 2–3 cm in diameter and are often smaller, in keeping with a general decrease in size with increasing elevation. These bamboos are usually scandent or scrambling, in moist ravines arching over streams or hanging from sometimes steep slopes, but they may also occupy ridges or form part of the understory (Dransfield 1992; Wong 1993; Judziewicz et al. 1999). In the Neotropics, *Aulonemia*, *Chusquea*, and *Rhipidocladum* are characteristic of Andean montane forests, whereas *Chusquea* and *Merostachys* are the most common bamboos of the Atlantic forests of Brazil (Judziewicz et al. 1999). Some species of *Chusquea* extend northward to Mexico in cloud forest and pine–oak–fir forests, but others extend southward into *Nothofagus* or *Araucaria* forests in Chile and Argentina (Judziewicz et al. 1999). Some tropical bamboos form characteristic belts of vegetation within montane forests—*Nastus borbonicus* on Réunion Island is a good example (T. Grieb, pers. comm.) while others, including many species of *Chusquea*, commonly invade gaps formed by treefalls or landslides (Judziewicz et al. 1999). Species of genera such as *Holttumochloa* and *Racemobambos* are characteristic of montane forests in South-east Asia (Dransfield 1992; Wong 1993). And as noted for both Arundinarieae and lowland Bambuseae, some tropical bamboos can form bamboo forests in montane systems (Yang and Xue 1990).

Members of both Arundinarieae and Bambuseae occur above treeline in high elevation grasslands or shrublands, where they are characteristic or often dominant plants (Soderstrom and Calderón 1979; Soderstrom and Ellis 1988; Judziewicz et al. 1999). High elevation bamboos are usually erect and have a shrubby habit, sometimes lacking aerial branching (e.g., species of *Chusquea*) and giving the appearance of non-bambusoid grasses. In the temperate mountains of China, species of *Fargesia* (Arundinarieae) are the most common above treeline, but a few species of *Yushania* (Arundinarieae) also occur at high elevations in relatively open habitats (Li et al. 2006). Some Arundinarieae occur in tropical mountain grasslands and shrublands, notably *Bergbambos* from South Africa and species of *Kuruna* from Sri Lanka and India (Soderstrom and Ellis 1982, 1988). Both *K. densifolia* from Sri Lanka and *B. tessellata* from South Africa grow in wetter habitats and have air canals in their roots. Interestingly, all of the high elevation, open-habitat Arundinarieae possess pachymorph rhizomes. In the tropical Americas, the high montane open habitats known as *páramos*, *subpáramos*, and *campos de altitude* are populated mainly by species of *Chusquea*, which may form extensive and sometimes impenetrable stands (Judziewicz et al. 1999). Species of *Aulonemia* may also form mono-dominant stands at high elevations, as can *Cambajuva* in southern Brazil (Judziewicz et al. 1999; Viana et al. 2013). The very odd *Glaziophyton*, resembling a giant rush (*Juncus*), is endemic to rocky mountaintops near the city of Rio de Janeiro (Fernandez et al. 2012). Among Arundinarieae, *Fargesia yulongshanensis* reportedly reaches 4,200 m in elevation, and there may be other Chinese or Himalayan species with comparable elevational ranges (Li et al. 2006). Among Bambuseae, the species with the highest documented elevational ranges are (note that only the high end of the range is cited): *Chusquea acuminatissima* (to 4,000 m, Clark & Londoño pers. obs.), *Chusquea aristata* (to 4,200 m, TROPICOS), *Chusquea guirigayensis* (to 4,000 m, Clark & F. Ely, pers. obs.), *Chusquea tessellata* (to ca. 4,200 m, Judziewicz et al. 1999), and *Chusquea villosa* (4,250–4,400 m, TROPICOS).

Olyreae usually occupy the understory of humid, lowland tropical forests at elevations from sea level to ca. 1,000 m, with *Pariana* often occurring in the periodically flooded *várzea* in Amazonian Brazil. Some herbaceous bamboos, especially strongly rhizomatous ones such as *Pariana*, may even be dominant in the herbaceous layer (Judziewicz et al. 1999). Some species of *Cryptochloa*, *Lithachne*, *Pariana*, *Raddiella* (*R. esenbeckii*), and *Olyra* (*O. latifolia*) occur in lower montane forests at up to 1,500 m in elevation, although *Olyra standleyi* may extend up to 2,200 m in elevation (Judziewicz et al. 1999; Judziewicz and Clark 2007). Other Olyreae are found in more specialized habitats in savannas or wet cliff faces associated with waterfalls or in semi-deciduous seasonal forests, whereas *Ekmanochloa* is a serpentine endemic (BPG 2012 and references cited therein; Ferreira et al. 2013). A few species, especially of *Lithachne* or *Olyra*, may become weedy (Judziewicz et al. 1999; Judziewicz and Clark 2007). Olyreae exhibit their greatest species diversity from 7 to 10° N and 12 to 18° S, with minimal diversity near the equator. The monotypic *Reitzia* is the only member of the tribe with a strictly extratropical distribution in the southernmost extension of the Atlantic forests (Judziewicz et al. 1999). The highest level of endemism for Olyreae is in the Atlantic forests of Brazil; many species of Olyreae and woody bamboos are endangered due to the continuing loss of these and other types of forests (Soderstrom et al. 1988; Ferreira et al. 2013).

1.5 Phylogenetic Relationships Within the Bamboos

As noted previously, that the Bambusoideae all share a common ancestor (i.e., the subfamily is monophyletic) is well established based on molecular sequence data, primarily from the plastid genome (GPWG 2001; GPWG II 2012). The presence of strongly asymmetrically invaginated arm cells in the chlorenchyma, as seen in cross section, appears to be uniquely derived in this lineage (GPWG 2001). All recent studies with sufficient sampling also strongly support Bambusoideae as the sister lineage to the Pooideae (bluegrass or wheat subfamily) in the BEP clade (Fig. 1.1; GPWG II 2012; Wu and Ge 2012), but no unique structural feature that supports or diagnoses this relationship has been identified.

Within Bambusoideae, three major lineages are resolved in all studies to date with sufficient sampling [Fig. 1.1; Kelchner et al. (2013); see also the more detailed review in BPG (2012)]: Arundinarieae (the temperate woody bamboos); Bambuseae (the tropical woody bamboos); and Olyreae (herbaceous bamboos). However, the relationships between these three lineages are not known with certainty. Analyses of sequence data from the chloroplast genome (represented by up to five markers) consistently indicate paraphyly of the woody bamboos with strong statistical support for branches; that is, there are two distinct lineages of woody bamboos and they are not each other's closest relative (Bouchenak-Khelladi

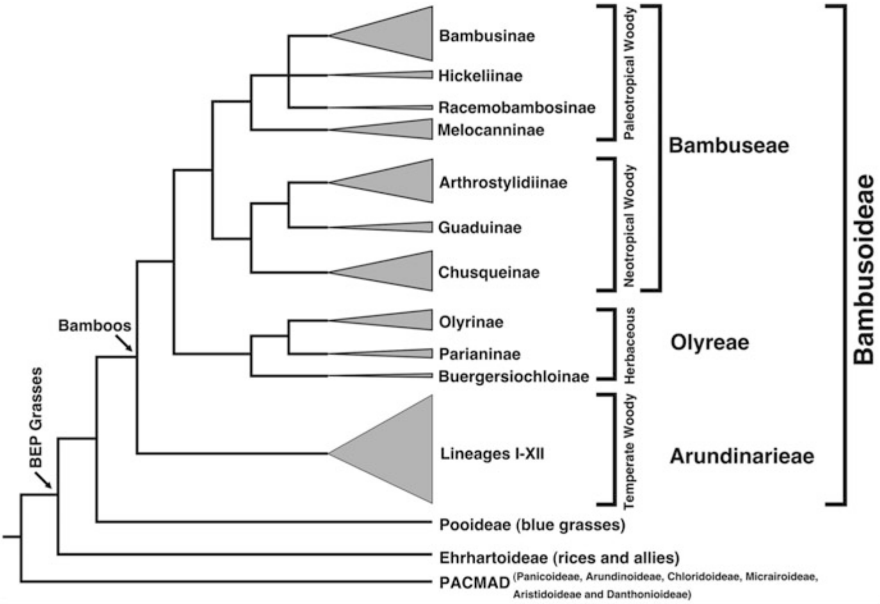

Fig. 1.1 Summary phylogeny of the relationships among Bambusoideae (bamboos), Ehrhartoideae (rices and allies) and Pooideae (wheat and allies), and among the tribes and subtribes of the Bambusoideae.

et al. 2008; Sungkaew et al. 2009; Kelchner et al. 2013). But tests of alternate relationships show that the possibility of a single lineage of woody bamboos cannot be rejected based on the chloroplast sequence data (Kelchner et al. 2013). Sequence data from the nuclear genome is only now becoming available for a reasonable sampling across the bamboos. Preliminary findings reveal that a single origin of woody bamboos may be supported, but that their evolutionary history is more complex than previously suspected and involves ancient hybridization events and allopolyploidy (Triplett et al. 2014).

Whether Olyreae is the closest lineage to the tropical woody bamboos (Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; Kelchner et al. 2013) or a distinct, basically diploid lineage (Triplett et al. 2014) within the Bambusoideae, the herbaceous bamboos are strongly supported as monophyletic in all analyses of molecular sequence data. Notably, the herbaceous bamboos also show rates of sequence evolution at many loci much higher than those of woody bamboos and more similar to other grasses (Gaut et al. 1997). *Buergersiochloa*, a monotypic endemic of New Guinea, is consistently supported as sister to the remaining Olyreae, which are all native to the New World, at least based on morphology and chloroplast sequence data (Fig. 1.1; Kellogg and Watson 1993; Zhang and Clark 2000; Kelchner et al. 2013; Oliveira et al. 2014). *Pariana*, *Eremitis*, and *Parianella* form a lineage sister to the remaining olyroid genera (Ferreira 2013; Oliveira et al. 2014), but a comprehensive phylogenetic analysis is still lacking for the tribe, so evolutionary relationships within the Olyreae remain obscure. However, close relationships between *Raddia* and *Sucrea* on the one hand and *Raddiella* and *Parodiolyra* on the other hand are evident, and it is likely that *Olyra* is not monophyletic (Judziewicz et al. 1999; Zhang and Clark 2000; Oliveira et al. 2014).

The temperate woody bamboos (Arundinarieae) were resolved as a distinct phylogenetic group from the earliest molecular investigations onwards [see BPG (2012) and references cited therein] and form a robustly supported lineage in all recent molecular analyses (e.g., Bouchenak-Khelladi et al. 2008; Peng et al. 2008; Sungkaew et al. 2009; Triplett and Clark 2010; Zeng et al. 2010; Zhang et al. 2012). Eleven lineages have been identified within the Arundinarieae, and a twelfth has now been characterized (Attigala et al. 2014), but inferred relationships within and among them are poorly supported at best (Peng et al. 2008; Triplett and Clark 2010; Zeng et al. 2010; Zhang et al. 2012; Yang et al. 2013). The often decades-long generation times in temperate woody bamboos may explain the low rate of sequence evolution in this group (Gaut et al. 1997), which in turn may be partially responsible for the lack of resolution among the recognized phylogenetic lineages. A long and presumably largely isolated evolutionary history followed by recent, rapid radiation has also been suggested as an explanation for the lack of molecular resolution (Hodkinson et al. 2010). More complete and rigorous molecular analyses may reveal relationships in more detail, and improved knowledge of the fossil record (e.g., Wang et al. 2013) should help to better understand divergence times. Both ancient and recent (and ongoing) reticulation are important in the evolutionary history of the Arundinarieae, further complicating efforts to reconstruct the phylogeny of this group (Triplett et al. 2010; Yang et al. 2013; Triplett et al. 2014).

The tropical woody bamboos (Bambuseae) form two (Paleotropical woody and Neotropical woody) lineages (Fig. 1.1; Sungkaew et al. 2009; Kelchner et al. 2013). The Paleotropical woody bamboos (PWB) consistently receive strong support, and hexaploidy appears to be the general condition (Soderstrom 1981; Li et al. 2001), but support for the monophyly of the Neotropical woody bamboos (NWB), which as far as is known are all tetraploid, is moderate at best (Kelchner et al. 2013) and no defining character for the NWB has been identified. The rate of sequence evolution in the Bambuseae is mostly comparable to that of the Arundinarieae, although sequence evolution in the Chusqueinae appears to be somewhat accelerated (Kelchner et al. 2013). Seven subtribes (three in the NWB, four in the PWB) based on morphological and anatomical differences have been recognized within the Bambuseae in the recent literature (BPG 2012 and references cited therein) and these are, to a large extent, supported by molecular sequence data.

Within the NWB, Arthrostylidiinae and Guaduinae are consistently supported as sister to each other and each is well supported as monophyletic (Ruiz-Sanchez et al. 2008, 2011a; Fisher et al. 2009; Sungkaew et al. 2009; Ruiz-Sanchez 2011; Tyrrell et al. 2012; Kelchner et al. 2013). The presence of refractive papillae on the leaf epidermises may be a diagnostic feature supporting the sister relationship of these two subtribes (Ruiz-Sanchez et al. 2008), but further investigation is needed. Within the Arthrostylidiinae, the *Glaziophyton* clade, defined by erect, tessellate leaf blades, is sister to the remainder of the subtribe, which exhibit reflexed leaf blades (Tyrrell et al. 2012). Within this group, three other subclades are also identified and well supported, but the monophyly of larger genera such as *Arthrostylidium*, *Aulonemia*, and *Rhipidocladum* is not supported (Tyrrell et al. 2012). Relationships within the Guaduinae are less well understood, but evidence to date supports a sister relationship between *Guadua* and *Eremocaulon* and *Otatea* and *Olmeca*, respectively (Ruiz-Sanchez et al. 2011a, b). Within the Chusqueinae, the two clades of the species formerly recognized as *Neurolepis* form the earliest diverging branches, with *Chusquea* subg. *Rettbergia* as the next diverging lineage sister to the highly diverse Euchusquea clade. *Chusquea* subg. *Rettbergia*, plus the Euchusquea clade, comprises *Chusquea* in the strict (and traditional) sense, but the concept of the genus is now expanded to include the two *Neurolepis* clades, which will be recognized as subgenera (Fisher et al. 2009; Fisher et al. 2014).

The PWB are more diverse than the NWB in terms of both number of genera and number of species (Table 1.2), but despite their diversity and enormous ecological and economic importance (Dransfield and Widjaja 1995), an understanding of broad relationships within the PWB lags behind that of the NWB. Sungkaew et al. (2009) resolve the Melocanninae as robustly monophyletic and sister to the remainder of the PWB, a finding confirmed by Kelchner et al. (2013) with sampling from all four subtribes. Molecular phylogenetic studies of the PWB to date have focused on the Melocanninae and Bambusinae, but resolution of relationships within each subtribe is still tentative, with a few exceptions (Yang et al. 2007, 2008, 2010; Goh et al. 2010, 2013). Within Melocanninae, *Melocanna* and *Pseudostachyum* are supported as distinct genera, but the relationship between

Table 1.2 Diversity of Bambusoideae by tribe and subtribe

Taxon	Number of genera	Number of species
Arundinarieae	**31**	**546**
Bambuseae	**66**	**812**
Neotropical	21	405
Arthrostylidiinae	15	183
Chusqueinae	1	172
Guaduinae	5	50
Paleotropical	45	407
Bambusinae	27	268
Hickeliinae	8	33
Melocanninae	9	88
Racemobambosinae	1	17
Olyreae	**22**	**124**
Buergersiochloinae	1	1
Parianinae	3	38
Olyrinae	18	85
Total for subfamily	**119**	**1,482**

Cephalostachyum and *Schizostachyum* requires further study (Yang et al. 2007, 2008). The core of the Bambusinae consists of *Bambusa*, *Dendrocalamus*, and *Gigantochloa* and a few other small genera [the BDG complex of Goh et al. (2013)], and although there is good support for the monophyly of *Bambusa* in some analyses, species of *Dendrocalamus* and *Gigantochloa* are completely interdigitated (Yang et al. 2008, 2010; Goh et al. 2013). Hybridization and introgression among species of *Dendrocalamus* and *Gigantochloa* are documented and clearly contribute to the evolutionary and taxonomic complexity of the core Bambusinae (Wong and Low 2011; Goh et al. 2013). *Dinochloa* and several other clambering Bambusinae form a lineage distinct from the BDG complex (Yang et al. 2008; Goh et al. 2010, 2013). Racemobambosinae (*Racemobambos*) and Hickeliinae are supported as monophyletic, but their relationships to other PWB remain unclear (Goh et al. 2013; Kelchner et al. 2013).

Despite recent efforts to understand phylogenetic relationships among bamboos at the tribal and subtribal levels, to date there is no phylogenetic study that clearly shows well-resolved internal relationships between genera within subtribes. Future work in bamboos will require adding more taxa from the different recognized subtribes, especially targeting genera not previously included in molecular analyses, and sampling more plastid markers to generate increased internal resolution. Sequencing of low-copy nuclear loci is also needed, but this must be undertaken with the complex reticulate history of the woody bamboos in mind. Detailed morphological analyses of many bamboos are still needed to understand their phylogenetic relationships, but also to facilitate identification and classification, all of which will ultimately guide conservation and development decisions.

1.6 Tribal and Subtribal Classification of the Bamboos

A detailed description of the Bambusoideae can be found in BPG (2012). We here present synoptic descriptions for the currently recognized tribes and subtribes of bamboos, followed by additional comments about each group. Features characteristic of all or most members of a particular group are underlined. Although we follow the treatment presented in BPG (2012), the description of new species and genera continues, so we have updated numbers and lists accordingly; bamboo diversity is summarized in Table 1.2. We also list the included genera within each tribe or subtribe, with the number of species for each in parentheses, after the tribal or subtribal descriptions. For more detailed descriptions, see BPG (2012). A key to the bamboo genera of the world will be included in the forthcoming volume on Poaceae by E. A. Kellogg, which will be published as part of the series *The Families and Genera of Vascular Plants* edited by K. Kubtizki.

1.6.1 Herbaceous Bamboos: Tribe Olyreae

Description: Plants with rhizomes, these sometimes only weakly developed, or only pachymorph rhizomes present. Culms herbaceous to weakly lignified, with limited aerial branching. Culm leaves usually absent, sometimes present in taxa with larger culms (*Olyra*). 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 these or auricular appendages absent; blades with 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 usually lacking well-developed bracts, apparently determinate. Spikelets unisexual, dimorphic, and 1-flowered with no rachilla extension, the plants monoecious. Female spikelets with 2 glumes, the floret usually leathery. Male spikelets usually smaller than the females, glumes usually absent or rarely 2 and well developed, the floret membranous. Caryopsis basic.

The Olyreae are the herbaceous bamboos. This group of 22 genera and 124 described species is native to tropical America, with two exceptions: *Buergersiochloa*, a rare monotypic bamboo endemic to New Guinea and Papua New Guinea, and *Olyra latifolia*, a widespread American species presumably introduced into Africa and Sri Lanka (Judziewicz and Clark 2007; BPG 2012). Members of Olyreae typically occur in rain forests or less commonly in lower montane forests up to 1,500 m in elevation. The four centers of diversity for Olyreae are (1) Bahia, in eastern Brazil; (2) northern Brazil (Amapá) and the Guianas; (3) the Chocó region of Colombia and Panama; and (4) Cuba (Soderstrom and Calderón 1979; Soderstrom et al. 1988). Herbaceous bamboos often develop strikingly beautiful synflorescence colorations, including bright displays of often numerous stamens, suggesting pollination by insects (Soderstrom and Calderón 1971).

Molecular data combined with traditional morphological and anatomical evidence have shown the herbaceous bamboos to be well supported as a lineage within the Bambusoideae. However, there is no single unique feature that diagnoses the Olyreae, although the presence of functionally unisexual spikelets and the lack of outer ligules distinguish Olyreae from the woody bamboos (Judziewicz and Clark 2007; BPG 2012), in addition to the limited aerial branching and less lignified stems of the Olyreae. Preliminary molecular data support three lineages (recognized as subtribes Buergersiochloinae, Parianinae, and Olyrinae, below) (Kelchner et al. 2013; Oliveira et al. 2014).

Amerindian tribes in Central and South America have reportedly used certain herbaceous bamboos as antifungal agents, an ointment for head lice, a snakebite remedy, for alleviation of general body aches, and to combat fevers, headaches, and coughs (Londoño 1990; Judziewicz et al. 1999). The herbaceous bamboos also have great potential value as ornamental plants.

1.6.1.1 Subtribe Buergersiochloinae

Description: 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. Endemic to New Guinea/Papua New Guinea.

Included genus: *Buergersiochloa* (1).

1.6.1.2 Subtribe Parianinae

Description: 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, 3, or 6 (to 36–40). Costa Rica and Trinidad, northern South America to Amazonian Bolivia and Atlantic Brazil (Bahia).

Included genera: *Eremitis* (3), *Pariana* (33), *Parianella* (2).

1.6.1.3 Subtribe Olyrinae

Description: 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. Mexico and the West Indies, Central America, northern South America to Argentina and southern Brazil.

Included genera: *Agnesia* (1), *Arberella* (7), *Cryptochloa* (8), *Diandrolyra* (3), *Ekmanochloa* (2), *Froesiochloa* (1), *Lithachne* (4), *Maclurolyra* (1), *Mniochloa* (1), *Olyra* (24), *Parodiolyra* (5), *Piresia* (5), *Piresiella* (1), *Raddia* (9), *Raddiella* (8), *Rehia* (1), *Reitzia* (1), and *Sucrea* (3).

1.6.2 Temperate Woody Bamboos: Tribe Arundinarieae

Description: Rhizomes well developed, some taxa with pachymorph rhizomes only. Culms woody, usually hollow; branch development beginning at the apex and continuing toward the base (basipetal); aerial vegetative branching complex, usually derived from a single bud per node (multiple, subequal buds per node in *Chimonobambusa*). Culm leaves usually well developed. Foliage leaves with an outer ligule; sheaths often bearing fimbriae and/or auricular appendages at the summit. Flowering usually cyclical, gregarious, and monocarpic. Synflorescences with well-developed bracts 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 and paleas similar in texture to the glumes. Caryopsis basic, uncommonly baccate (e.g., *Ferrocalamus*). Base chromosome number $x = 12$; $\underline{2n} = \underline{48}$.

Included genera: *Acidosasa* (11), *Ampelocalamus* (13), *Arundinaria* (3 + ca. 6 of uncertain placement), *Bashania* (2), *Bergbambos* (1), *Chimonobambusa* (37), *Chimonocalamus* (11), *Drepanostachyum* (10), *Fargesia* (90), *Ferrocalamus* (2), *Gaoligongshania* (1), *Gelidocalamus* (9), *Himalayacalamus* (8), *Indocalamus* (23), *Indosasa* (15), *Kuruna* (6), *Oldeania* (1), *Oligostachyum* (15), X*Phyllosasa* (=*Hibanobambusa*) (1), *Phyllostachys* (51), *Pleioblastus* (40), *Pseudosasa* (19), *Sarocalamus* (3), *Sasa* (40), *Sasaella* (13), *Sasamorpha* (5), *Semiarundinaria* (10), *Shibataea* (7), *Sinobambusa* (10), *Thamnocalamus* (3), and *Yushania* (80).

The Arundinarieae are the temperate woody bamboos, a diverse clade of 30 genera and ca. 546 species, distributed primarily in forests of the northern temperate zone, but also in some high elevation tropical regions of both northern and southern hemispheres [see Fig. 2 in Kelchner et al. (2013)] (Triplett and Clark 2010). The center of diversity is in East Asia (ca. 430 spp.), with areas of endemism in Southwestern China (ca. 180 spp.), Japan (ca. 80 spp.), Southeast Asia (ca. 60 spp.), Madagascar (ca. six spp.), Africa (two spp.), and Sri Lanka (five spp.) (Ohrnberger 1999; Triplett and Clark 2010; BPG 2012). The diversity of Arundinarieae in East Asia and the three species of *Arundinaria* native to North America represent a classic, if asymmetrical, disjunction pattern between East Asia and eastern North America, potentially indicating a past migration across the Bering Land Bridge (Stapleton et al. 2004; Triplett and Clark 2010).

The recognition of Arundinarieae as a distinct lineage within the Bambusoideae is well supported by molecular phylogenetic studies (Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; Kelchner et al. 2013). Although a formal morphological analysis has not been done, basipetal branch development and a chromosome number of $2n = 48$ have been identified as putative defining characters and thus support recognition of this lineage at the tribal level (BPG 2012).

Species of what is now recognized as the Arundinarieae were traditionally classified in up to three subtribes, the Arundinariinae, Shibataeinae, and Thamnocalaminae, based on the presence or absence of pseudospikelets and rhizome structure (Zhang 1992; BPG 2012). Recent studies have provided strong evidence that none of these three subtribes is a natural group, so this subtribal classification has been abandoned. Eleven numbered lineages have been resolved, some at the generic level, some possibly subtribal, but several cutting across phenetically based genera or groups of genera (Triplett and Clark 2010; Zeng et al. 2010; BPG 2012). Relationships between and within these lineages have not been clearly revealed by molecular studies, although genomics tools are now being used in an attempt to obtain resolution. Intergeneric hybridization certainly plays a role in generating some of the taxonomic confusion, but other evolutionary processes (e.g., incomplete lineage sorting) also are factors (Triplett et al. 2010; Yang et al. 2013). The 12 lineages currently recognized are (Triplett and Clark 2010; Zeng et al. 2010; Yang et al. 2013; Attigala et al. 2014): (I) Bergbamboes, (II) African Alpine bamboos, (III) *Chimonocalamus*, (IV) *Shibataea* clade, (V) *Phyllostachys* clade, (VI) *Arundinaria* clade, (VII) *Thamnocalamus*, (VIII) *Indocalamus wilsonii*, (IX) *Gaoligongshania*, (X) *Indocalamus sinicus*, (XI) *Ampelocalamus calcareus*, and (XII) *Kuruna*. Five of these clades (I, VIII, IX, X, and XI) consist of a single species each. The *Arundinaria* and *Phyllostachys* clades, as defined based on data primarily from the chloroplast genome and discussed below, are by far the most diverse, including about 85 % of total species in the Arundinarieae. We note that ongoing studies, especially those including data from the nuclear genome (e.g., Yang et al. 2013), will undoubtedly reveal additional complexity and suggest additional phylogenetic lineages.

Arundinaria clade (VI)

With at least ten genera and more than 130 species, this is the second most speciose lineage in Arundinarieae. The morphology-based taxonomy of *Arundinaria* and its relatives has been especially problematic, but the phylogenetic study of Triplett and Clark (2010) revealed that some of the taxonomy of this group was inconsistent with its evolutionary history. The *Arundinaria* clade is united by rhizome type (leptomorph) but exhibits significant morphological diversification (e.g., spikelets, pseudospikelets, various numbers of branches, and three or six stamens). The concept of *Arundinaria* itself is limited to the three species native to North America, and work continues to place the other species still classified in *Arundinaria* in the broad sense (Stapleton 2013). Other genera minimally included in the *Arundinaria* clade are *Acidosasa*, *Oligostachyum*, X*Phyllosasa* (=*Hibanobambusa*), *Pleioblastus* (in part), *Pseudosasa*, *Sasa* (in part), *Sasaella*, *Sasamorpha*, and *Semiarundinaria*. At least four of these (X*Phyllosasa*, *Pseudosasa*, *Sasamorpha*, and *Seminarundinaria*) are wholly or partly derived through intergeneric hybridization (Triplett and Clark 2010).

***Phyllostachys* clade (V)**

This is the largest clade in Arundinarieae with ca. 16 genera and more than 330 species. The clade containing *Phyllostachys* and allies comprises about 50 % of the temperate genera and more than 70 % of the temperate bamboo species. The clade unites members from all three of the earlier morphology-based subtribes, combining plants with true spikelets or pseudospikelets, bracteate or ebracteate synflorescences, and pachymorph or leptomorph rhizomes. Clade V includes at least four genera from the traditional Shibataeinae (*Brachystachyum, Chimonobambusa, Phyllostachys*, and *Sinobambusa*, with ebracteate, indeterminate synflorescences), six from the traditional Thamnocalaminae (*Ampelocalamus, Drepanostachyum, Fargesia, Himalayacalamus, Thamnocalamus*, and *Yushania*, with ebracteate to bracteate determinate synflorescences and pachymorph rhizomes), and five from the traditional Arundinariinae (*Bashania, Gelidocalamus, Indocalamus, Pleioblastus* in part and *Sarocalamus*, with semelauctant inflorescences) (Triplett and Clark 2010). Chinese *Sasa* also fall within this clade. The *Phyllostachys* clade is remarkable for contrasting high morphological diversity with low chloroplast DNA variation. Sequences in this group are nearly identical, differing by only a few point mutations or indels, most of which are found in only one taxon (Triplett and Clark 2010; Zeng et al. 2010).

1.6.3 Tropical Woody Bamboos: Tribe Bambuseae

Description: Rhizomes well developed, usually pachymorph but some taxa amphimorph. Culms woody, usually hollow (solid in most *Chusquea* and a few species of other genera); branch development from the base to the apex (acropetal) or bidirectional; aerial vegetative branching complex (but absent in a few taxa), 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, sometimes poorly differentiated from foliage leaves or absent. Foliage leaves with an outer ligule; sheaths often bearing fimbriae and/or auricular appendages at the summit; blades usually pseudopetiolate, deciduous. Flowering usually cyclical, gregarious, and monocarpic. Synflorescences with well-developed bracts or not, determinate (spikelets) or indeterminate (pseudospikelets). Spikelets (or spikelets proper of the pseudospikelets) bisexual with 1 to many bisexual florets; glumes (0–) 1 to 4 (–6), sometimes very reduced; lemmas and similar in texture to the glumes. Caryopsis usually basic, sometimes baccate (e.g., *Alvimia*, *Dinochloa*, *Melocanna*, *Ochlandra*, *Olmeca*, at least one species of *Guadua*) or nucoid (e.g., *Actinocladum*, *Merostachys*, *Pseudostachyum*). Base chromosome numbers $x = 10$, (11), and 12; $2n = (20)$ 40, (44), 46, 48, 70, 72.

The tribe Bambuseae comprises the Paleotropical and Neotropical woody bamboos, widespread in both the Old World and New World. It includes seven subtribes, 66 genera, and 812 species (BPG 2012). The recognition of Bambuseae as a distinct lineage within the Bambusoideae is well supported by molecular phylogenetic studies (Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; Kelchner et al. 2013). Although a formal morphological analysis has not been done, acropetal or bidirectional branch development has been suggested as a possible defining character for Bambuseae, including both the Paleotropical and Neotropical lineages (BPG 2012). Recent analyses suggest that sympodial, pachymorph rhizomes and determinate spikelets are likely ancestral within the tribe (Clark et al. 2007; Kelchner et al. 2013), but it is clear that patterns of morphological evolution within the Bambuseae are complex and much work remains to be done to characterize this tribe. The two major groups within the Bambuseae are the Neotropical and Paleotropical woody bamboos. We here discuss the Neotropical and Paleotropical groups and their respective subtribes separately.

1.6.3.1 Neotropical Woody Bamboos

Neotropical woody bamboos are a moderately well-supported subclade within the Bambuseae, with three well-supported subtribes: Arthrostylidiinae, Chusqueinae, and Guaduinae. The NWB comprise 21 genera and at least 405 species (BPG 2012), and new genera and new species continue to be discovered and described. The NWB have a geographical distribution from Mexico along Central America to South America and also in the Caribbean Islands, with an altitudinal range from sea level to 4,300 m (Judziewicz et al. 1999; BPG 2012).

1.6.3.1.1 Subtribe Arthrostylidiinae

Description: Rhizomes necks short to somewhat elongated; internodes of the aerial culms usually hollow, all subequal or sometimes very short internodes alternating in various combinations with elongated internodes. Aerial branching derived from a single bud per node; thorns absent. Culm leaves with sheaths usually bearing fimbriae or fimbriate auricles; oral setae absent. 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 without bracts, indeterminate (pseudospikelets) or determinate (spikelets), paniculate or racemose. 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). Ovary glabrous, with a short style; stigmas 2 (3). Caryopsis basic, uncommonly baccate (*Alvimia*) or nucoid (*Actinocladum*, *Merostachys*).

Included genera: *Actinocladum* (1), *Alvimia* (3), *Arthrostylidium* (32), *Athroostachys* (1), *Atractantha* (6), *Aulonemia* (47), *Cambajuva* (1), *Colanthelia* (7), *Didymogonyx* (2), *Elytrostachys* (2), *Filgueirasia* (2), *Glaziophyton* (1), *Merostachys* (48), *Myriocladus* (12), and *Rhipidocladum* (18).

The Arthrostylidiinae can be distinguished from other woody bamboo subtribes using branch leaf micromorphology and anatomy (Soderstrom and Ellis 1987). The leaf blades possess a unique combination of intercostal sclerenchyma fibers in the mesophyll of the blades and simple vasculature in the midrib, and the leaf blades are basically hypostomatic with papillae usually developed on the abaxial epidermis (Tyrrell et al. 2012). With 15 genera and 183 species, Arthrostylidiinae comprises 70 % of the genera and 45 % of the total diversity in NWB (BPG 2012). Arthrostylidiinae is arguably the most morphologically diverse subtribe of the NWB.

1.6.3.1.2 Subtribe Chusqueinae

Description: Rhizomes with short necks, sometimes leptomorph rhizomes present; internodes of the aerial culms usually solid, all subequal. Aerial branching when present derived from a multiple, dimorphic bud complement, absent in two clades (=*Neurolepis*) but a single bud per node usually present in these; thorns absent. Culm leaf sheaths usually lacking fimbriae or fimbriate auricles; oral setae absent. 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 papillae per subsidiary cell and also often overarched by papillae from adjacent long cells. Synflorescences usually without bracts, determinate (spikelets), paniculate, or rarely racemose. Spikelets consisting of 4 glumes and 1 female-fertile floret, rachilla extension absent; palea keels lacking wings. Stamens (2) 3. Ovary glabrous, with a short style; stigmas 2. Caryopsis basic.

Included genus: *Chusquea* Kunth (172).

Chusqueinae, which includes the single, well-supported yet very diverse genus *Chusquea*, can be distinguished from other woody bamboo subtribes by the presence of two papillae on each subsidiary cell of the foliar stomatal apparatus and spikelets consisting of four glumes, one fertile floret, and no rachilla extension (Fisher et al. 2009). Species of Chusqueinae are characteristic of montane forests throughout Mexico, Central and South America, and the Caribbean, but a number of species inhabit high altitude grasslands and a few species occur in lowland tropical forest or in temperate forests at higher latitudes (both north and south) (Fisher et al. 2009). Species of *Chusquea* range from sea level to 4,300 m in elevation, giving this genus the broadest altitudinal range of any bamboo. *Chusquea* species tend to form a visible and sometimes dominant component of the vegetation

(Judziewicz et al. 1999). Although including only one genus, with 172 described species the Chusqueinae has 42 % of the total species diversity in NWB (BPG 2012).

1.6.3.1.3 Subtribe Guaduinae

Description: Rhizomes with necks short to elongated; internodes of the aerial culms hollow to solid, all subequal. Aerial branching usually derived from a single bud per node (1–4 subequal buds per node in *Apoclada*); thorns absent or present (*Guadua*). Culm leaves with sheaths often bearing fimbriae or fimbriate auricles at the sheath summit; oral setae usually present (absent in *Apoclada* and *Guadua*). 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 with bracts or not, indeterminate (pseudospikelets) or determinate (spikelets), paniculate. 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. Ovary glabrous or hairy, with a short style; stigmas 2 or 3. Caryopsis basic, uncommonly baccate (some species of *Olmeca* and *Guadua sarcocarpa*).

Included genera: *Apoclada* (1), *Eremocaulon* (4), *Guadua* (32), *Olmeca* (5), *Otatea* (8).

Guaduinae can be distinguished from other woody bamboo subtribes by the presence of abundant stomates on both adaxial and abaxial foliage leaf blade surfaces, often combined with the presence of papillae on the adaxial surface whether or not papillae are present on the abaxial surface (Judziewicz et al. 1999; Ruiz-Sanchez et al. 2008). Species of Guaduinae inhabit low to mid-elevation wet or dry tropical forests and form extensive mono-dominant *Guadua* forests in part of the Amazon basin (Judziewicz et al. 1999). With 5 genera and 50 species, this subtribe represents slightly less than 25 % of the generic diversity and only 12 % of the total species diversity in NWB (BPG 2012). Despite the relatively low diversity of this subtribe, it occupies an estimated area of 11 million ha. from Mexico to Argentina and it has great economic importance due to the utility of *G. angustifolia* and a few other species of the genus (Judziewicz et al. 1999).

1.6.3.2 Paleotropical Woody Bamboos

The PWB or Old World bamboos include 45 genera and 407 species and are grouped into four subtribes: Bambusinae, Hickeliinae, Melocanninae, and Racemobambosinae (Table 1.2). They are distributed throughout South-East Asia, northern Australia, India, Sri Lanka, Africa, and Madagascar (Soderstrom and Ellis 1987; Dransfield and Widjaja 1995; Ohrnberger 1999; BPG 2012).

The areas with greatest diversity of Old World bamboos are (1) the region including southern China, northern Burma (Myanmar), Thailand, and Vietnam, and (2) Madagascar, where almost all known native species and genera are endemic (Dransfield and Widjaja 1995). The largest numbers of species occur in the largest countries, China and India. *Bambusa* is the most widespread genus of bamboo in tropical and subtropical Asia, and several species of it and the related genera *Dendrocalamus* and *Gigantochloa* have been introduced to Central and South America where they can play an important role in local economies.

1.6.3.2.1 Subtribe Bambusinae

Description: Rhizomes with 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 derived from a single bud per node (multiple buds in *Holttumochloa*); thorns usually absent, sometimes present (*Bambusa*). Culm leaves with sheaths bearing fimbriae or fimbriate auricles at the summit or neither; oral setae present or absent. 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. 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; stigma 1, 2, or 3. Caryopsis basic or baccate (*Cyrtochloa*, *Dinochloa*, *Melocalamus*, *Sphaerobambos*).

Included genera: *Bambusa* (100), *Bonia* (5), *Cyrtochloa* (5), *Dendrocalamus* (41), *Dinochloa* (31), *Fimbribambusa* (2), *Gigantochloa* (30), *Greslania* (4), *Holttumochloa* (3), *Kinabaluchloa* (2), *Maclurochloa* (2), *Melocalamus* (5), *Mullerochloa* (1), *Neololeba* (5), *Neomicrocalamus* (5), *Oreobambos* (1), *Oxytenanthera* (1), *Parabambusa* (1), *Pinga* (1), *Pseudobambusa* (1), *Pseudoxytenanthera* (12), *Soejatmia* (1), *Sphaerobambos* (3), *Temochloa* (1), *Temburongia* (1), *Thyrsostachys* (2), and *Vietnamosasa* (3).

No single feature has been identified to define this subtribe, but a core Bambusinae [also known as the BDG complex, Goh et al. (2013)] defined primarily by molecular evidence clearly includes *Bambusa*, *Dendrocalamus*, *Gigantochloa*, *Maclurochloa*, *Melocalamus*, *Oreobambos*, *Oxytenanthera*, *Phuphanochloa* (if recognized as distinct from *Bambusa*), *Soejatmia*, *Thyrsostachys,* and *Vietnamosasa* (Yang et al. 2008; Sungkaew et al. 2009; Goh et al. 2013), although these have not all been included in a comprehensive molecular analysis and some genera remain unsampled. A distinct clade of primarily climbing bamboos includes at least *Dinochloa*, *Mullerochloa*, *Neololeba*, and *Sphaerobambos*, and may merit recognition at the subtribal level once additional studies are completed (Goh et al. 2010, 2013; Chokthaweepanich 2014). This subtribe is notable for its paramount economic importance in tropical Asia, due to the cultivation and use of many species of *Bambusa*, *Dendrocalamus*, and *Gigantochloa* (e.g., Dransfield and Widjaja 1995; Lucas 2013). Many species of all three genera are also cultivated widely in tropical and subtropical regions around the globe (Dransfield and Widjaja 1995; Ohrnberger 1999).

1.6.3.2.2 Subtribe Hickeliinae

Description: Rhizomes with necks short to elongated; internodes of the aerial culms usually hollow or rarely solid, all subequal. Aerial branching derived from a single bud per node (multiple buds in *Nastus productus*), central branch dominant; thorns absent. Culm leaves with sheaths bearing fimbriae or fimbriate auricles or neither; oral setae absent. Foliage leaf sheaths with fimbriae or fimbriate auricles present or absent; oral setae absent; blades with a complex, sometimes 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. Synflorescences determinate (spikelets), bracteate or ebracteate, paniculate, racemose, or capitate. 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.

Included genera: *Cathariostachys* (2), *Decaryochloa* (1), *Hickelia* (4), *Hitchcockella* (1), *Nastus* (20), *Perrierbambus* (2), *Sirochloa* (1), and *Valiha* (2).

The Madagascan and Réunion Island Hickeliinae are strongly supported as a distinct lineage within the PWB, although relatively few species have been sampled in molecular analyses to date (Clark et al. 2007; Kelchner et al. 2013). Adaxially projecting midribs have been proposed as a diagnostic character for this subtribe (Soderstrom and Ellis 1987), but further analyses do not support this (Stapleton 1994c; Chokthaweepanich 2014). All of the diversity in this subtribe, except for one species of *Hickelia* and several Asiatic species of *Nastus*, are endemic to Madagascar and Réunion Island (Ohrnberger 1999; Clark et al. 2007), indicating a remarkable level of generic diversity in Madagascar. Dransfield (1994, 1998) has provided detailed morphological descriptions for many of these taxa and continues to study this unique bamboo radiation.

1.6.3.2.3 Subtribe Melocanninae

Description: Rhizomes with 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 derived from a single bud per node; thorns absent. Culm leaves with sheaths bearing fimbriae or fimbriate auricles at the summit or neither; oral setae usually absent. 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. 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*).

Included genera: *Cephalostachyum* (14), *Davidsea* (1), *Melocanna* (2), *Neohouzeaua* (7), *Ochlandra* (9), *Pseudostachyum* (1), *Schizostachyum* (51), *Stapletonia* (1), and *Teinostachyum* (2).

With nine genera and 88 species, Melocanninae is the second most diverse subtribe of PWB. *Melocanna* is perhaps the best known representative of this subtribe, primarily due to its large, fleshy, pear-shaped fruits that are implicated in rat population explosions when the bamboo flowers gregariously approximately every 48 years (Singleton et al. 2010). Holttum (1956) hypothesized that *Cephalostachyum*, *Pseudostachyum*, *Schizostachyum*, and *Teinostachyum* should be combined into one genus, but molecular data support maintaining at least *Pseudostachyum* as a distinct genus (Yang et al. 2007, 2008; Sungkaew et al. 2009) and Yang et al. (2008) present evidence in support of maintaining *Cephalostachyum* and *Schizostachyum* as separate genera. Given the well-supported position of this subtribe as sister to the remaining PWB, a more detailed morphological and molecular analysis of this subtribe, including all of the recognized genera, is needed.

1.6.3.2.4 Subtribe Racemobambosinae

Description: Rhizomes with necks short or elongated; internodes of the aerial culms hollow, all subequal; nodes of the aerial culms without a patella. Aerial branching derived from a single bud per node; thorns absent. Culm leaves with sheaths usually bearing small fimbriate auricles at the summit or rarely efimbriate and exauriculate; oral setae absent. 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. Spikelets consisting of 2–3 glumes, 3–8 female-fertile florets and a rachilla extension bearing one rudimentary floret; palea keels wingless. Stamens 6, filaments free. Ovary usually hairy toward the apex, usually with a short style; stigmas 3. Caryopsis basic.

Included genus: *Racemobambos* (17).

Two genera initially included within this subtribe, *Neomicrocalamus* and *Vietnamosasa*, are clearly allied with the Bambusinae based on chloroplast sequence data (Yang et al. 2008; Goh et al. 2013) and have been transferred to that subtribe (BPG 2012). *Racemobambos* is resolved as a distinct lineage among the PWB, but its affinities are uncertain and no unique structural character has yet been found to diagnose this genus (or subtribe) (Goh et al. 2013).

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