Keynote Lecture

DIVERSITY AND EVOLUTION OF THE NEW WORLD BAMBOOS
(Poaceae: Bambusoideae: Bambuseae, Olyreae)

Lynn G. Clark, Ph.D.
Dept. of Ecology, Evolution, and Organismal Biology
Iowa State University
Ames, IA 50011-4009
lgclark@iastate.edu

R. Patricia de Oliveira, Ph.D.
Universidade Estadual de Feira de Santana / DCBIO
Programa de Pós-graduação em Botânica
Laboratório de Sistemática Molecular de Plantas
Av. Transnordestina, s/n
44036-900 - Feira de Santana, Bahia, Brasil
rpatricia@uefs.br

Abstract
Bambusoideae (bamboos), comprising 1,680+ species, is one of 12 subfamilies within the Poaceae representing the only one to diversify primarily in association with forests. Bamboos are classified into three tribes: Arundinarieae (temperate woody bamboos, 581 species), Bambuseae (tropical woody bamboos, 976 species) and the Olyreae (herbaceous bamboos, 123 species). The Arundinarieae is primarily of eastern Asia and has no native species in the American tropics. Bambuseae consists of two major clades, the Paleotropical (PWB, 554 species) and the Neotropical woody bamboos (NWB, 422 species), and is distributed broadly in the tropics and subtropics with a few taxa in subtemperate regions, and extensive diversity in montane systems. Except for 1 genus endemic to New Guinea, and 1 species occurring in both the Neotropics and Africa, the rest of the Olyreae is restricted to the Neotropics. Olyreae typically inhabit the understory, with some adapted to gaps and edges, but the woody bamboos mostly occupy gaps and edges or open habitats. Recent bamboo studies are based on both floristics and molecular phylogenomics using both plastid and nuclear DNA sequence data. In the usual absence of flowering material, complete vegetative collections are essential for discovery and identification. Previously reported relationships of subtribes within the NWB clade and the Olyreae continue to be supported, but molecular data suggest some generic realignments and new species continue to be described. Brazil has the greatest diversity of both NWB and Olyreae, but the Andes, Panama/Costa Rica, Mexico and the West Indies also harbor significant diversity and endemism. In the Neotropics, *Chusquea*, *Guadua*, *Merostachys* and *Pariana* still require significant taxonomic attention. Phylogenetic hypotheses require additional sampling of critical taxa before biogeographic patterns can be fully explored and classification stabilized; bamboo ecology and reproductive biology remain understudied.

Keywords: Arundinarieae, bamboo, bamboo diversity, bamboo evolution, Neotropical bamboos

Introduction

The bamboos (Bambusoideae) form one of the 12 subfamilies recognized within the grass family (Poaceae) (Kellogg 2015; Soreng et al. 2017). Although the grass family itself originated in forests, the Bambusoideae is the only major lineage within the family to diversify primarily in association with forests (Clark et al. 2015; Kellogg 2015). Molecular sequence data strongly support the Bambusoideae as a distinct lineage (Kelchner & BPG 2013; Saarela et al. 2018), and anatomically bamboos are characterized by the presence of well developed, asymmetrically strongly infolded arm cells in the leaf mesophyll as seen in cross section (Clark et al. 2015; Leandro et al. 2016, 2017). Reflecting their general adaptation to forest habitats, bamboos also usually exhibit relatively broad, pseudopetiolate leaf blades, with intercellular cavities often referred to as fusoid cells flanking the vascular bundles, although these may be lacking in sun plants or sun leaves (March & Clark 2011; Leandro et al. 2018). Bamboos include 1680+ species grouped into approximately 127 genera, and comprise three lineages recognized formally as tribes: Arundinarieae (temperate woody bamboos, 581 species in 31 genera), Bambuseae (tropical woody bamboos, 976 species in 74 genera), and Olyreae (herbaceous bamboos, 123 species in 22 genera) (Table 1) (Vorontsova et al. 2016; Soreng et al. 2017). Herbaceous bamboos are often important elements of the understory in tropical forests, and woody bamboos are conspicuous in gaps or along margins in tropical or temperate forests or they may form bamboo forests at lower elevations or bamboo-dominated grasslands above the treeline (Clark et al. 2015 and references cited therein).

Since the Proceedings of the 9th World Bamboo Congress, which had bamboo science as a major focus, were published (Gielis & Potters 2012), a number of important advances in bamboo systematics and evolution have appeared in the literature (see below). Some of these were incorporated into Chapter 1 of Liese & Köhl (2015) or in the bamboo treatments presented in Kellogg (2015) and Soreng et al. (2017), but we wanted to make this information more accessible to a broader bamboo audience. Although the temperate woody bamboos (Arundinarieae) are extremely important, our expertise lies with the tropical bamboos (Bambuseae and Olyreae), so we have chosen to focus on these two tribes in this paper. We here present a review of recent work and updates in our understanding of the diversity, evolution and classification of the tropical bamboos, with a particular focus on the Neotropical taxa.

RECENT LANDMARKS IN BAMBOO SYSTEMATICS

Molecular phylogenetic analyses continue to confirm unambiguously that the Bambusoideae as a whole is monophyletic, that is, that this lineage had a single origin, but these data also indicate that the bamboos have had a complex evolutionary history including hybridization and allopolyploidy (Goh et al. 2013; Fisher et al. 2014; Oliveira et al. 2014; Triplett et al. 2014; Wysocki et al. 2015; Wysocki et al. 2016; Zhang et al. 2016; Zhou et al. 2017; Saarela et al. 2018; Ferreira et al. in press). Analyses based on plastid DNA markers or, increasingly, whole plastid genomes (plastomes) consistently support a sister relationship between the Bambuseae and Olyreae (the tropical bamboos), with the Arundinarieae sister to that clade (Kelchner & BPG 2013; Ma et al. 2014; Wysocki et al. 2015; Attigala et al. 2016; Zhang et al. 2016; Saarela et al. 2018). In contrast, analyses based

on sequencing of nuclear markers or other genome-wide techniques support monophyly of the woody bamboos or do not recover the same groups within tribes as obtained in plastid analyses (Fisher et al. 2014; Triplett et al. 2014; Wysocki et al. 2016; Wang et al. 2017).

The availability of evolutionary trees derived from molecular data, as well as additional bamboo fossils (e.g., Brea et al. 2013; Wang et al. 2014), have enabled studies of bamboo evolution and biogeography. For example, Ruiz-Sanchez & Sosa (2015) examined the origin and evolution of fleshy fruit in woody bamboos using a plastid phylogeny and molecular dating. They showed that fleshy fruits evolved independently at least seven times within Arundinarieae and Bambuseae, but that neither current climatic conditions nor soil parameters could explain this pattern. Veller et al. (2015) focused on the well-known flowering cycles in woody bamboos, proposing a simple mathematical model to explain the evolution of these remarkable cycles as part of a two-step process. Zhang et al. (2016) used a plastid phylogeny and molecular dating to establish an origin of the Arundinarieae 12-14 mya with a rapid radiation in some of its lineages beginning 7-8 mya. The pattern of relationships within the tribe allowed them to infer that the Arundinarieae originated in Eastern Asia, with later dispersals to North America (*Arundinaria*) and tropical montane locations in Africa (e.g., *Oldeania*) or elsewhere in the Paleotropics (e.g., *Kuruna* in southern India and Sri Lanka).

Two major works (Kellogg 2015; Vorontsova et al. 2016) have contributed to identification resources for bamboos and documentation of their species diversity. Both of these books were influenced by some of the phylogenetic studies cited above, but their objectives were to provide an updated generic level treatment of the grasses, including bamboos (Kellogg 2015), and a peer-reviewed worldwide checklist of bamboo species (Vorontsova et al. 2016). The bamboo treatment by Kellogg (2015) includes a brief synopsis of each genus (whether presumed monophyletic or not), as well as a key to these taxonomic entities. Subsequently, some of the non-monophyletic genera have been formally described as new genera [e.g., not "*Nastus*" has been published as two genera by Wong & Dransfield (2016) and the remainder placed in the resurrected *Chloothamnus* by Widjaja & Wong (2016)] and the status of some generic names is still under study (e.g., *Parodiolyra* and *Raddiella* by RPO and her research group), but this still remains the only available modern key to the genera of the Bambusoideae. We also note that additional national- or regional-level treatments of bamboo diversity are beginning to appear [e.g., Ruiz-Sanchez et al. (2015) for Mexican bamboos, Wong et al. (2016) for Malesian bamboos, Rúgolo de Agrasar (2017) for Argentinian bamboos, and bamboo contributions for the Brazilian Flora 2020 project].

The global checklist of bamboos in Vorontsova et al. (2016) was prepared from the nomenclatural data base at the Royal Botanic Gardens, Kew, and subjected to review by a number of bamboo taxonomists. In addition to accepted names, synonymy, and geographic distribution, the checklist includes a list of all of the synonyms with their currently accepted names for easy reference. BPG (2012) estimated that there were 1,482 species of bamboo, but the Vorontsova et al. (2016) checklist documents 1,642 species, a significant increase. In part this is due to the continued description of new species, but it also represents a more accurate genus by genus estimate with input from specialists. Soreng et al. (2017) incorporated additional new species published since the checklist, and provided an estimate of 1,670 bamboo species; we have included species published or in press in the

last year to arrive at our estimate of 1,680 bamboo species (Table 1).

Table 1. Diversity of Bambusoideae by tribe (Arundinarieae, Bambuseae, Olyreae) and subtribe within the tropical bamboos (Bambuseae, Olyreae).

Taxon	Number of genera	Number of species
Arundinarieae	**31**	**581**
Bambuseae	**74**	**976**
Neotropical (NWB)	21	422
Arthrostylidiinae	15	186
Chusqueinae	1	181
Guaduinae	5	55
Paleotropical (PWB)	53	554
Bambusinae	18	324
Dinochloinae	7	56
Greslaniinae	1	2
Hickeliinae	9	32
Holttumochloinae	3	6
Melocanninae	9	99
Racemobambosinae	3	31
Temburongiinae	2	3
Incertae Sedis	1	1
Olyreae	**22**	**123**
Buergersiochloinae	1	1
Parianinae	3	34
Olyrinae	18	88
Total for tropical bamboos	**96**	**1,099**
Total for Bambusoideae	**127**	**1,680**

BAMBUSEAE

Recent phylogenetic analyses of the Bambuseae have been based primarily on individual plastid markers or whole plastomes (Kelchner & BPG 2013; Chokthaweepanich 2014; Ruiz-Sanchez & Sosa 2015; Wysocki et al. 2015; Zhou et al. 2017). Support values for both the Bambuseae and the Paleotropical woody bamboo (PWB) clade in these studies are consistently very strong, with more moderate support for the Neotropical woody bamboo (NWB) clade. A summary of the current estimate of phylogenetic relationships within the tropical woody bamboos (Bambuseae and Olyreae) based on plastid data is shown in Figure 1. The Bambuseae exhibit aerial branch development from the base of the culm to the apex (acropetal) or from the middle toward both ends (bidirectional) [vs. from the apex toward the base (basipetal) in Arundinarieae], but there are no morphological features that define either the PWB or NWB clades (Clark et al. 2015).

[insert Figure 1 here]

The sister relationship of Melocanninae to the rest of the PWB clade was already well established (Sungkaew et al. 2009; Kelchner & BPG 2013), but until recently, relationships among the Bambusinae, Hickeliinae and Racemobambosinae were not well understood. Although much more work remains to be done, Goh et al. (2013), Chokthaweepanich (2014) and Zhou et al. (2017) improved sampling and support within the PWB clade, with the resolution of several lineages. As shown in Figure 1, Holttumochloinae is supported as sister to the Bambusinae and the Dinochloiinae is sister to the Greslaniinae (this group was previously known as the DGMNS assemblage or clade), and these two lineages form a polytomy with the Racemobambosinae, Hickeliinae and Temburongiinae. The classification of the Paleotropical woody bamboos has been refined based on these results, including the description of two new genera (*Widjajachloa* and *Ruhooglandia*) for two Asian species of *Nastus* (Wong & Dransfield 2016), the resurrection of *Chloothamnus* for the remaining Asian species of *Nastus* (Widjaja & Wong 2016), and the emendation of Racemobambosinae along with the description of four new subtribes (Wong et al. 2016) (Table 2). In addition, *Sokinochloa* (the hedgehog bamboo, named for its dense, spiky-looking inflorescences) was described in the Hickeliinae to accommodate three species from Madagascar formerly classified in *Cephalostachyum*, and an additional four new species in this genus were also described (Dransfield 2016). The results of Zhou et al. (2017) clearly indicate that *Temochloa*, which was treated as of uncertain placement (Incertae Sedis) in Soreng et al. (2017), belongs in the Bambusinae, so we here make this change (Table 2).

Within the NWB clade, the relationship of Chusqueinae + (Arthrostylidiinae + Guaduinae) is consistently and strongly supported in molecular phylogenetic analyses (Kelchner & BPG 2013; Soreng et al. 2017) (Figure 1). The Arthrostylidiinae + Guaduinae clade may be defined by the presence of refractive papillae on the leaf epidermises, but these papillae apparently also occur in the Melocanninae (PWB) and their structure and evolutionary history within the Bambuseae are poorly understood (Soderstrom & Ellis 1987; BPG 2012; Kellogg 2015). The description of new species within all three subtribes continues, especially within *Chusquea* (Chusqueinae) and *Merostachys* (Arthrostylidiinae) (e.g., Viníciuis-Silva et al. 2016; Attigala et al. 2017; Ruiz-Sanchez et al. 2018; Pianissola Machado et al., in press;). In these two genera, the number of species has increased by 5% and 6%, respectively, in just the past three years (since the compilation of Clark et al. 2015), and a number of new species in both genera are in preparation. Molecular phylogenetic analyses combined with anatomical studies are also leading to generic realignments (e.g., Jesus-Costa et al., in press, in which a species of *Atractantha* is being transferred to *Athroostachys*), but a number of these studies are still in progress. A revision of *Chusquea* sect. *Tenellae* was published last year (Attigala et al. 2017) and a revision of *Colanthelia* is forthcoming (Santos-Gonçalves et al., in press); additional revisions or monographs are in progress. Within the Neotropics, Brazil has the greatest diversity of both NWB and Olyreae, but the Andes, Panama/Costa Rica, Mexico and the West Indies also harbor significant diversity and endemism (Clark et al. 2015).

Table 2. Summary of tropical bamboo classification by tribe (Bambuseae, Olyreae) and subtribe. Numbers in parentheses indicate the number of species currently recognized in each genus.

Bambuseae—Neotropical

Arthrostylidiinae: *Actinocladum* (1), *Alvimia* (3), *Arthrostylidium* (31), *Athroostachys* (2), *Atractantha* (5), *Aulonemia* (47), *Cambajuva* (1), *Colanthelia* (7), *Didymogonyx* (2), *Elytrostachys* (2), *Filgueirasia* (2), *Glaziophyton* (1), *Merostachys* (51), *Myriocladus* (12), *Rhipidocladum* (19).

Chusqueinae: *Chusquea* (181).

Guaduinae: *Apoclada* (1), *Eremocaulon* (4), *Guadua* (33), *Olmeca* (5), *Otatea* (12).

Bambuseae—Paleotropical

Bambusinae: *Bambusa* (153), *Bonia* (5), *Cochinchinochloa* (1), *Dendrocalamus* (66), ×*Gigantocalamus* (1), *Gigantochloa* (63), *Maclurochloa* (3), *Melocalamus* (14), *Neomicrocalamus* (3), *Oreobambos* (1), *Oxytenanthera* (1), *Phuphanochloa* (1), *Pseudoxytenanthera* (4), *Soejatmia* (1), *Temochloa* (1), *Thyrsostachys* (2), *Vietnamosasa* (3), *Yersinochloa* (1).

Dinochloinae: *Cyrtochloa* (7), *Dinochloa* (38), *Mullerochloa* (1), *Neololeba* (5), *Parabambusa* (1), *Pinga* (1), *Sphaerobambos* (3).

Greslaniinae: *Greslania* (2).

Hickeliinae: *Cathariostachys* (2), *Decaryochloa* (1), *Hickelia* (4), *Hitchcockella* (1), *Nastus* (12), *Perrierbambus* (2), *Sirochloa* (1), *Sokinochloa* (7), *Valiha* (2).

Holttumochloinae: *Holttumochloa* (3), *Kinabaluchloa* (2), *Nianhochloa* (1).

Melocanninae: *Annamocalamus* (1), *Cephalostachyum* (13), *Davidsea* (1), *Melocanna* (3), *Neohouzeaua* (6), *Ochlandra* (10), *Pseudostachyum* (1), *Schizostachyum* (62), *Stapletonia* (2).

Racemobambosinae: *Chloothamnus* (11), *Racemobambos* (19), *Widjajachloa* (1).

Temburongiinae: *Fimbribambusa* (2), *Temburongia* (1).

Incertae Sedis: *Ruhooglandia* (1).

Olyreae

Buergersiochloinae: *Buergersiochloa* (1)

Parianinae: *Eremitis* (5), *Pariana* (27), *Parianella* (2)

Olyrinae: *Agnesia* (1), *Arberella* (7), *Cryptochloa* (9), *Diandrolyra* (3), *Ekmanochloa* (2), *Froesiochloa* (1), *Lithachne* (4), *Maclurolyra* (1), *Mniochloa* (1), *Olyra* (25), *Parodiolyra* (6), *Piresia* (5), *Piresiella* (1), *Raddia* (9), *Raddiella* (8), *Rehia* (1), *Reitzia* (1), *Sucrea* (3).

OLYREAE

This tribe is easily distinguished from the two tribes of woody bamboos based on its relatively weakly lignified culms, lack of well differentiated culm leaves, restricted vegetative branching, lack of an outer ligule on the foliage leaves, and unisexual, often dimorphic spikelets (Clark et al. 2015). Virtually all Olyreae exhibit pluri-annual (seasonal) flowering, although there are a few, mostly anecdotal reports of possible gregarious flowering on longer cycles in the tribe (Judziewicz et al. 1999). All Olyreae except for *Buergersiochloa* apparently have epidermal silica cells containing cross-shaped or crenate (olyroid) silica bodies, the latter type unique to the tribe (Soderstrom & Ellis 1987; Clark et

al. 2015). Molecular phylogenetic analyses consistently support monophyly of the Olyreae, and the three subtribes are related in the following way: Buergersiochloinae + (Parianinae + Olyrinae) (Kelchner & BPG 2013; Oliveira et al. 2014) (Figure 1). Within the Parianinae, *Parianella* (from the Atlantic forest) is sister to a lineage consisting of *Eremitis* (also from the Atlantic forest) + *Pariana* (from Central America and northern South America) (Ferreira et al., in press). Within the Olyrinae, Oliveira et al. (2014) recovered at least four main lineages, including one consisting of *Sucrea* and *Raddia* but without strong support, and they also demonstrated the non-monophyly of both *Olyra* and *Parodiolyra*. More comprehensive molecular analyses of the subtribe by RPO and her research group are in progress, and generic realignments are to be expected based on these data and also supported by pollen morphology (Dórea et al. 2017). The currently accepted genera, with species numbers, in Olyreae are summarized by subtribe in Table 2.

Although it appears that the number of species in Olyreae has remained relatively stable in recent years [122 in BPG (2012), 124 in Clark et al. (2015) and 121 in Vorontsova et al. (2016)], in fact several new species and even a new genus have been described within the last five years (e.g., Ferreira et al. 2013a, b; Baldini & Ortiz 2015; Ferreira et al. 2016), and the description of several new taxa is in progress. Most of the difficulty in obtaining an accurate estimate of species diversity within the tribe is due to the problematic taxonomy of *Pariana* [Clark et al. (2015) estimated 33 species, whereas Vorontsova et al. (2016) accepted only 27].

CONCLUSIONS

The current estimate of bamboo diversity stands at 1,680 species, but at least in the Neotropics, a large number remain to be described, and we predict that the total number of species will easily exceed 1,700 in the near future. While most of the new species are recognized based on morphology and anatomy, better sampling and advances in molecular techniques have provided a much more detailed overview of bamboo relationships and the complex evolutionary history of the bamboos. Although much more work remains to be done, especially with the nuclear genome and with the inclusion of critical taxa, phylogenetic studies to date have produced an intriguing set of testable hypotheses regarding the broad picture of bamboo evolution. In turn, revised classifications at the subtribal and generic levels have emerged based on these molecular phylogenetic results. We emphasize the need for continued fieldwork for bamboos generally, to better document their distributions for ecological and biogeographic studies as well as for conservation purposes, and to provide material for ongoing molecular work. Better and more complete collections are also critical for documenting woody bamboos in the vegetative condition, which will facilitate better identification resources for bamboos. In the Neotropics, *Chusquea*, *Guadua*, *Merostachys* and *Pariana* still require significant taxonomic attention. We also strongly recommend further study of bamboo ecology and bamboo reproductive biology, as these areas lag behind the recent advances in bamboo systematics.

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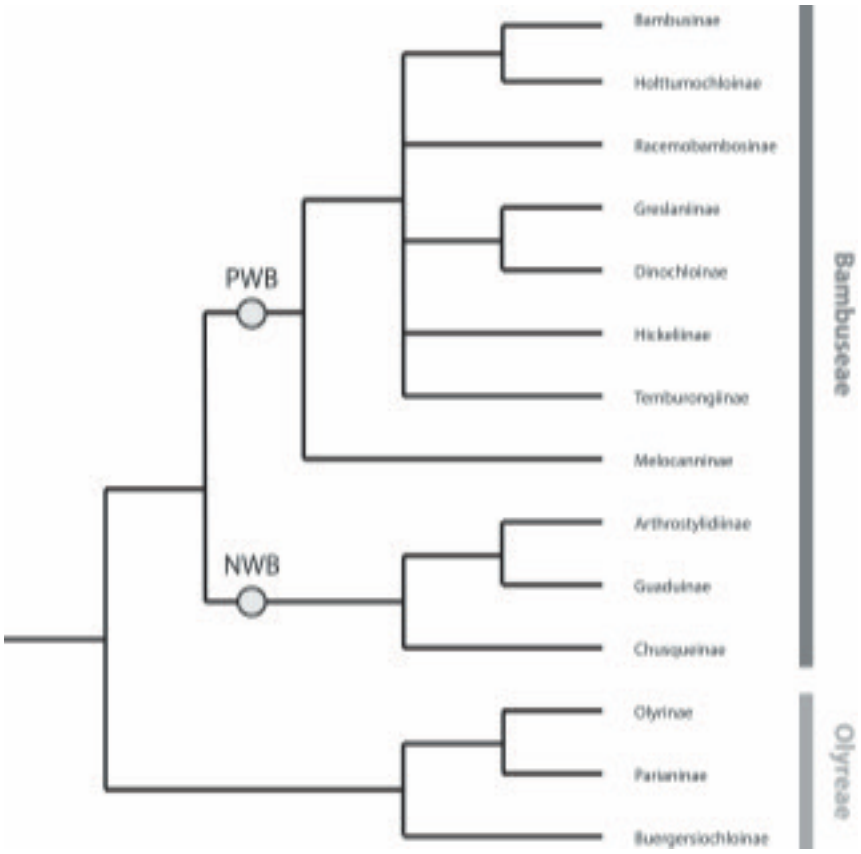
LIST OF FIGURES

Figure 1. Summary of the evolutionary relationships of subtribes within the tropical bamboo clade (Bambuseae and Olyreae). NWB = Neotropical woody bamboos; PWB = Paleotropical woody bamboos.

LIST OF CHARACTERS

mya is million years ago


Bambusinae
Holttumochloinae
Racemobambosinae
Greslaninae
Dinochloinae
Hickelinae
Temburongiinae
Melocanninae
Arthrostylidinae
Guaduinae
Chusqueinae
Olyrinae
Parianinae
Buergersiochloinae
PWB
NWB
Bambuseae
Olyreae