



Higher level phylogenetic relationships within the bamboos (Poaceae: Bambusoideae) based on five plastid markers

Scot A. Kelchner*, Bamboo Phylogeny Group¹

Department of Biological Sciences, Campus Stop 8007, Idaho State University, Pocatello, ID 83209-8007, USA

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ABSTRACT

Bamboos are large perennial grasses of temperate and tropical forests worldwide. Two general growth forms exist: the economically and ecologically important woody bamboos (tribes Arundinarieae and Bambuseae), and the understory herbaceous bamboos (tribe Olyreae). Evolutionary relationships among the 1400 + described species have been difficult to resolve with confidence. Comparative analysis of bamboo plastid (chloroplast) DNA has revealed three to five major lineages that show distinct biogeographic distributions. Taxon sampling across tribes and subtribes has been incomplete and most published data sets include a relatively small number of nucleotide characters. Branching order among lineages is often poorly supported, and in more than one study herbaceous bamboos form a clade within the woody bamboos. In this paper, the Bamboo Phylogeny Group presents the most complete phylogeny estimation to date of bamboo tribes and subtribes using 6.7 kb of coding and noncoding sequence data and 37 microstructural characters from the chloroplast genome. Quality of data is assessed, as is the possibility of long branch attraction, the degree of character conflict at key nodes in the tree, and the legitimacy of three alternative hypotheses of relationship. Four major plastid lineages are recognized: temperate woody, paleotropical woody, neotropical woody, and herbaceous bamboos. Woody bamboos are resolved as paraphyletic with respect to Olyreae but SH tests cannot reject monophyly of woody species (Arundinarieae + Bambuseae).

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1. Introduction

Bamboos are remarkably robust forest grasses that number more than 1400 described species in 115 genera (Bamboo Phylogeny Group [BPG], 2012). Most familiar and useful are those with “woody” (lignified) stems that belong to the tribes Arundinarieae (temperate woody bamboos) and Bambuseae (tropical woody bamboos). The roughly 1300 woody species often play critical roles in the ecology of their forest habitats and have long been of economic importance to humans (see McClure, 1966; Judziewicz et al., 1999). Less popularly known are the herbaceous bamboos (tribe Olyreae), a lineage of about 120 non-woody understory species found in tropical forests, predominantly in the New World. Together the three tribes constitute the grass subfamily Bambusoideae, members of which share the unique character of asymmetrically invaginated arm cells in the chlorenchyma (Zhang

and Clark, 2000). Most species also possess fusoid cells in the mesophyll, papillae on at least the abaxial leaf epidermis, and a broad leaf blade with a basal constriction called a pseudopetiole (GPWG, 2001; Judziewicz and Clark, 2007; BPG, 2012).

Members of Bambusoideae are found from sea level to over 4000 m in mainly forest and high montane grassland habitats worldwide, except for Europe and Antarctica (Fig. 1). At least 40% of species (including many awaiting formal description) are endemic to the Americas. In both the Americas and Asia, several taxa can reach gigantic proportions: plant height can be to 40 m and clonal individuals can occupy many hectares (Judziewicz et al., 1999). Famously, woody bamboos can take between 7 and 120 years to flower, often in gregarious events that lead to mass seed production and an accompanying dieback of parent plants. Because of this rarity of flowering, woody bamboos are usually encountered in their vegetative stage and identification of species can be difficult for a non-specialist.

Bambusoideae is one of three subfamilies in the BEP clade of grass family Poaceae (GPWG, 2001; GPWG II, 2012). Although each is monophyletic in molecular analyses, branching order of the BEP subfamilies has been difficult to resolve. Several recent analyses (e.g., Bouchenak-Khelladi et al., 2008; Davis and Soreng, 2010; GPWG II, 2012; Wu and Ge, 2012) support a sister relationship between Bambusoideae (B) and Pooideae (P; the bluegrasses), with

* Fax: +1 208 282 4570.

E-mail address: kelchner@isu.edu

¹ Bamboo Phylogeny Group members: Lynn Clark, Gilberto Cortés, Reyjane P. Oliveira, Soejatmi Dransfield, Tarciso Filgueiras, Amanda E. Fisher, Gerald F. Guala, Trevor Hodgkinson, Emmet Judziewicz, M. Kumar, De-Zhu Li, Ximena Londoño, M. Teresa Mejía, Ana Paula Santos-Gonçalves, Chris Stapleton, Sarawood Sungkaew, Jimmy Triplett, Elizabeth Widjaja, Khoon Meng Wong, Nian-He Xia.

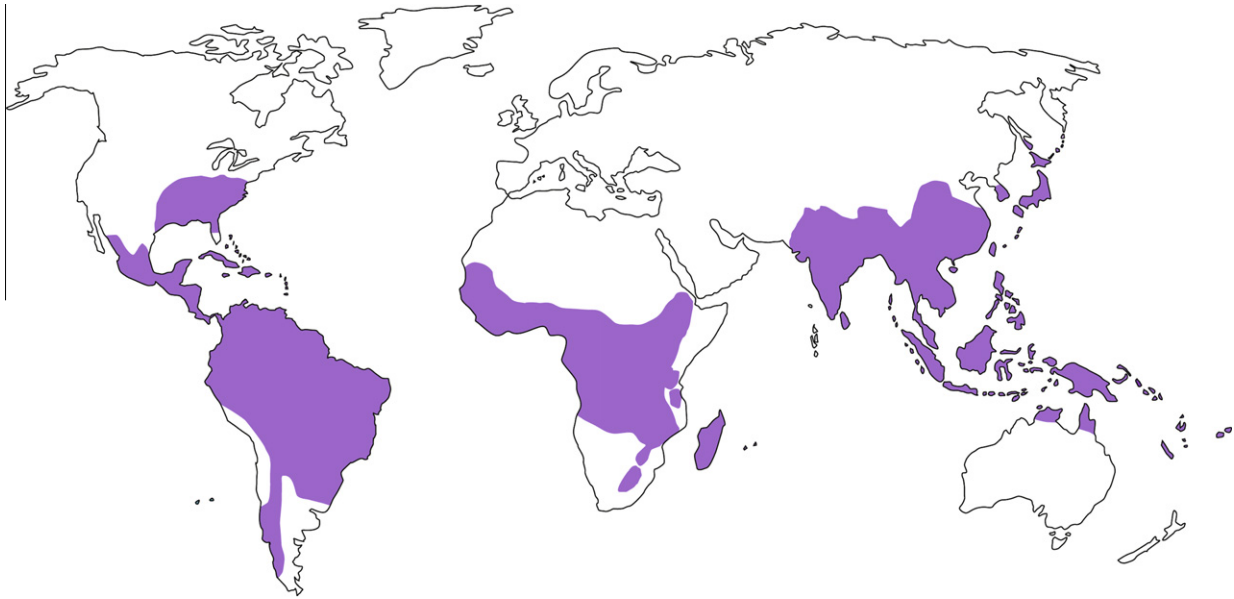


Fig. 1. World distribution of bamboos (Poaceae: Bambusoideae).

the B + P clade being sister to Ehrhartoideae (E; the rices). Branching order of the three clades varies across studies, possibly as a function of outgroup sampling.

Within Bambusoideae, three to five major lineages are recovered by comparative DNA sequence analyses (Clark et al., 1995, 2007; Kelchner and Clark, 1997; Zhang and Clark, 2000; Bouček-Khelladi et al., 2008; Sungkaew et al., 2009) despite the often marked dissimilarity of taxa and genetic loci sampled. Temperate woody bamboos form the most robust of these lineages, appearing as an uninterrupted branch in molecular phylogenies that suggests a long evolutionary history followed by recent and rapid radiation (Hodkinson et al., 2010). Herbaceous bamboos are also clearly monophyletic and at many loci show rates of sequence evolution much higher than those of other bamboos and more similar to grasses in general (Gaut et al., 1997). The tropical woody bamboos form between one and three main lineages; they are most commonly resolved as two (paleotropical woody; neotropical woody) or three (paleotropical woody; Arthrostylidiinae + Guaduinae; Chusqueinae). Rate of sequence evolution in subtribe Chusqueinae also appears to be accelerated, though to a lesser degree than the herbaceous lineage.

Since the first comparative DNA sequence analysis of bamboos by Kelchner and Clark (1997), more than 20 molecular phylogenetic analyses have been published on taxonomic subsets of Bambusoideae (reviewed by BPG (2012)). In that time, several phenomena that complicate phylogeny estimation have been observed in most bamboo nuclear and plastid (chloroplast) DNA data sets. These include strong heterogeneity of sequence evolution rates among lineages, poor support for internodes that separate major clades, long branch attraction that can affect both ingroup and outgroup topology, lack of strict congruence among trees from different studies (or data sets from different genomic compartments), and problems with attaining supported resolution in certain lineages such as the temperate woody and paleotropical woody clades.

Molecular phylogeny estimation in bamboos is thus widely considered to be a difficult problem. Maximum parsimony has been the most common optimization criterion used for tree selection in bamboo molecular systematics, yet it is well known that parsimony can mislead phylogeny estimation when the above phenomena are a feature of the data set and its analysis. Recent studies have used Bayesian inference together with parsimony (e.g., Yang et al., 2007; Peng et al., 2008; Sungkaew et al., 2009; Triplett and

Clark, 2010), which at least provides an opportunity to test robustness of a phylogeny estimation to certain changes in the model of character evolution employed. Frequently the two analytical frameworks do not produce the same topology (e.g., Yang et al., 2007; Peng et al., 2008), suggesting that the problematic issues listed here for bamboo molecular studies can indeed affect the estimate of bamboo phylogeny.

In response to the challenge of generating a well sampled, data rich, and carefully tested molecular phylogeny of Bambusoideae, the Bamboo Phylogeny Group was formed to better coordinate efforts among many of the world's bamboo systematists (BPG, 2006). Molecular studies had already suggested that a taxonomic reorganization of bamboos was inevitable; BPG members sought to align that reclassification to a strongly supported estimate of phylogeny. The endeavor was to begin with a phylogeny estimation of chloroplast genomes (plastomes) in bamboos because the task could be readily addressed with existing collections of silica-gel-dried leaf tissue from which sequence data of chloroplast loci are easily obtained. Taxon sampling was designed to include all subtribes of bamboos, and DNA sequences would be taken from five plastome loci. Phylogenetic analyses were to employ several available tests that determine data quality, tree stability, and whether bias and error were negatively affecting the phylogeny estimation.

In this paper, the Bamboo Phylogeny Group presents its first rigorously tested plastome phylogeny estimation. The estimate represents the breadth of taxonomic, geographic, and morphological diversity in the subfamily Bambusoideae. Aims of this study include (i) improvement of resolution and support for commonly recognized lineages, (ii) identification of previously unknown relationships, (iii) establishment of branching order among major clades, (iv) stabilization of the plastid phylogeny estimation, and (v) identification of remaining areas of concern in the topology that might hinder further progress in deciphering the biogeography, history, and evolution of bamboos.

2. Material and methods

2.1. Taxon sampling

A total of 40 species, including 33 ingroup (Bambusoideae) and seven outgroup (Ehrhartoideae, Pharoideae, Pooideae) taxa, was

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