



Multi-locus plastid phylogenetic biogeography supports the Asian hypothesis of the temperate woody bamboos (Poaceae: Bambusoideae) [☆]



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ARTICLE INFO

Article history:

Received 19 June 2015

Revised 22 November 2015

Accepted 26 November 2015

Available online 23 December 2015

Keywords:

Arundinarieae

Biogeography

Multi-locus plastid phylogeny

Divergence time

Rapid radiation

Bambusoideae

ABSTRACT

In this paper we investigate the biogeography of the temperate woody bamboos (Arundinarieae) using a densely-sampled phylogenetic tree of Bambusoideae based on six plastid DNA loci, which corroborates the previously discovered 12 lineages (I–XII) and places *Kuruna* as sister to the *Chimonocalamus* clade. Biogeographic analyses revealed that the Arundinarieae diversified from an estimated 12 to 14 Mya, and this was followed by rapid radiation within the lineages, particularly lineages IV, V and VI, starting from c. 7–8 Mya. It is suggested that the late Miocene intensification of East Asian monsoon may have contributed to this burst of diversification. The possibilities of the extant Sri Lankan and African temperate bamboo lineages representing 'basal elements' could be excluded, indicating that there is no evidence to support the Indian or African route for migration of temperate bamboo ancestors to Asia. Radiations from eastern Asia to Africa, Sri Lanka, and to North America all are likely to have occurred during the Pliocene, to form the disjunct distribution of Arundinarieae we observe today. The two African lineages are inferred as being derived independently from Asian ancestors, either by overland migrations or long-distance dispersals. Beringian migration may explain the eastern Asian–eastern North American disjunction.

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1. Introduction

The bamboos (Poaceae: Bambusoideae) are popularly known for their universal uses in human life, their adaptation to shady forests, as well as being the exclusive staple food for the giant pandas (Judziewicz et al., 1999; Li, 1999) and for some Madagascan lemur species (Bystrakova et al., 2004). The most recent studies based on plastid genomes and nuclear genes strongly support Bambusoideae as sister to Pooideae in the Poaceae 'BEP clade' (Zhang et al., 2011; Wu and Ge, 2012; Zhao et al., 2013). The Arundinarieae, i.e., temperate woody bamboos, is one of three well-supported Bambusoideae tribes, with the other two namely the Bambuseae (tropical woody bamboos) and the Olyreae (herbaceous bamboos)

(BPG, 2012). Tribe Arundinarieae, containing about 28 genera and 530 species, is highly heterogeneous in terms of morphology with 12 major lineages (Triplett and Clark, 2010; Zeng et al., 2010; Yang et al., 2013; Attigala et al., 2014). Tribe Bambuseae is divided into two lineages, namely the paleotropical and the neotropical woody bamboos, with the former group possessing four subtribes, c. 47 genera, 400 species and the latter three subtribes, c. 19 genera, and 370 species (Sungkaew et al., 2009; Kelchner and BPG, 2013), while the Olyreae consists of three subtribes with c. 21 genera and 120 species (BPG, 2012).

Extant bamboos display a markedly disjunct distribution particularly at the generic levels, occurring in every continent except Europe and Antarctica (Fig. 1, modified from Ohrnberger, 1999). The biogeographic patterns exhibited by the Arundinarieae is of particular interest: more than 510 species are distributed in eastern and southeastern Asia (Li et al., 2006; BPG, 2012), around 20 in the Afro-Indian area (Sri Lanka, southern India, Africa and Madagascar) (Ohrnberger, 1999), and only three species in eastern North America (Triplett and Clark, 2010). Bambuseae displays a

[☆] This paper was edited by the Associate Editor Wang Xiao-Quan.

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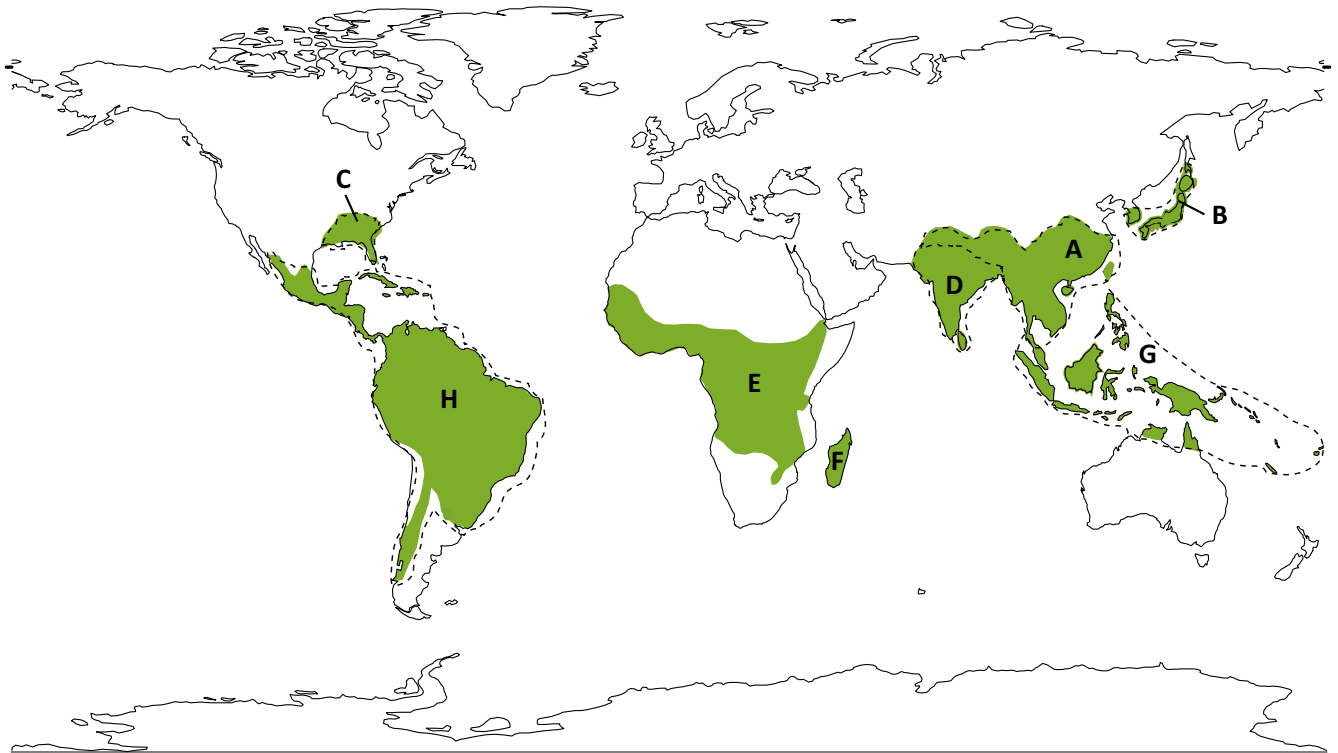


Fig. 1. Present geographic distribution of bamboos. Labels A–H show the eight area units used in biogeographic analyses.

pan-tropical disjunction: the neotropical lineage being distributed from northern Mexico, Central America to Chile in South America, and the paleotropical one in southern China, Indo-Malaya, northern Australia, New Guinea, New Caledonia, Madagascar and Africa (Judziewicz et al., 1999; Wong, 2004). Olyreae mainly diversified in the Neotropics, with one species (*Buergersiochloa bambusoides* Pilg.) being restricted to New Guinea, and another variable species (*Olyra latifolia* L.) found throughout tropical America, Africa and Madagascar (Judziewicz et al., 1999; Ohrmberger, 1999). To date there are very few bamboo macrofossils i.e. culms and leaves that have been studied comprehensively. Well preserved *Guadua* culm fossils were described from the Neotropics (Brea and Zucol, 2007; Olivier et al., 2009; Brea et al., 2013). Other well-preserved Miocene bamboo fossils (leaves and culm segments) were unearthed recently from China (Wang et al., 2013b, 2014), however, it is not possible to ascertain their membership in a tribe. Based on phytoliths surveys, Strömberg (2005) documented late Eocene *Chusquea*-like fossils from North America. A few putative bambusoid fossils were also reported from Europe (Worobiec and Worobiec, 2005), but much better evidence for their assignment to Bambusoideae is necessary.

Clark's (1997) hypothesis of a Gondwanan origin for the Bambusoideae was widely accepted with evidence from available grasses (including bamboos) systematics (GPWG, 2001; Bremer, 2002; GPWG II, 2012). Two theories have been presented to explain the disjunct distribution of the temperate woody bamboos (Hodkinson et al., 2010). An 'Asian hypothesis' suggested that ancestors of the Arundinarieae dispersed to Asia at an early date but failed to diversify until recent times; while the 'outside Asia hypothesis' suggested that ancestors of the Arundinarieae evolved outside Asia (for example in Africa or India) and arrived in Asia recently, concurrently with their radiation. Collision of the African or the Indian plate with the Eurasian plate was suggested as providing an opportunity for a recent arrival of the Arundinarieae in Asia (Stapleton et al., 2009; Hodkinson et al., 2010; Stapleton,

2013), in an attempt to understand the sudden diversification of the Arundinarieae. However, although 7 representatives of the Arundinarieae endemic to Sri Lanka and one from Madagascar were included in a recent molecular phylogeny study (Attigala et al., 2014), the phylogenetic position of the former and the identity of the latter were not conclusive to shed light on whether India or Madagascar hold taxa basal to the tribe, or to investigate where northern temperate bamboos first evolved.

Hodkinson et al. (2010) using two markers, *trnL-F* and ITS (without cloning), based on 34 Arundinarieae species mostly from the *Phyllostachys* clade (Clade V, Zeng et al., 2010) plus 8 species of Bambuseae and Olyreae, suggested that temperate woody bamboos underwent a rapid late Miocene radiation. Based on phylogenomic analyses of 7 Arundinarieae species, 3 Bambuseae species and 1 species of Olyreae, Burke et al. (2012) suggested that North American *Arundinaria gigantea* (Walter) Muhl. diverged from within Arundinarieae between 1.9 and 3.9 Mya (million years ago). However, it has been shown that appropriate and extensive taxon sampling is particularly significant for accurate phylogenetic estimation and ancestral distribution inference that are derived from phylogenetic trees (Heath et al., 2008; Lamm and Redelings, 2009). An inadequacy of taxon sampling probably impaired the results of previous studies (e.g., Hodkinson et al., 2010; Burke et al., 2012), as increasing taxon sampling to include proper fossil calibration nodes is a better option than relying on secondary calibration in molecular dating analyses (Ho and Phillips, 2009; Sauquet et al., 2012). Including all the extant 12 Arundinarieae lineages sampled throughout their known geographic ranges, within the context of a broad phylogenetic framework for the Bambusoideae, is of great importance to analyze the biogeography of this group.

The present paper provides, to the best of our knowledge, the first molecular biogeographic analyses for the Arundinarieae with a deep tribal and subtribal sampling for the Bambusoideae based on multi-locus plastid DNA fragments. The main goals of this study

were: (1) to recover the phylogenetic positions of the Sri Lankan and the African Arundinarieae lineages, (2) to estimate the divergence times for the Arundinarieae and its subordinate major lineages, and (3) to infer the likely biogeographic scenarios for the Arundinarieae.

2. Materials and methods

2.1. Taxon sampling and sequencing

We sampled 130 accessions representing 125 species from 57 genera of Bambusoideae, in all 12 known lineages of Arundinarieae, 6 subtribes of Bambuseae and 2 subtribes of Olyreae (Triplett and Clark, 2010; Zeng et al., 2010; BPG, 2012; Yang et al., 2013; Attigala et al., 2014). Seven species of Ehrhartoideae, 12 species of Pooideae and 6 species of Panicoideae were selected as outgroups according to previous studies (Zhang et al., 2011; Wu and Ge, 2012; Zhao et al., 2013) (Appendix A: Table S1, in supplementary material).

Six plastid intergenic spacers i.e. *rbcl-psal*, *rpl32-trnL*, *rps15-ndhF*, *trnG-trnT*, *trnT-trnL* and *ycf4-cemA* were amplified and sequenced (Appendix A: Table S2). Most of the sequences were newly generated for this study (Appendix A: Table S1). The final length of the aligned matrix of the six plastid DNA loci was 7301 nucleotides: *rbcl-psal* = 1079 bp, *rpl32-trnL* = 1258 bp, *rps15-ndhF* = 613 bp, *trnG-trnT* = 1960 bp, *trnT-trnL* = 1174 bp and *ycf4-cemA* = 1217 bp.

2.2. Phylogenetic analyses

Six plastid DNA regions were combined to reconstruct the phylogeny after assessing the congruence of the trees recovered for each individual marker using the incongruence length difference (ILD) test (Farris et al., 1994), for 1000 replicates performed in PAUP*v4.0b10 (Swofford, 2003). The ILD value for the entire dataset was 0.16, suggesting congruence among the datasets.

Phylogenetic analyses of the combined dataset were carried out by maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). MP analyses were implemented in PAUP*v4.0b10 (Swofford, 2003). Parsimony heuristic tree searches were performed with 1000 random addition sequence replicates, TBR branch swapping, MulTrees option not in effect. The most parsimonious trees were summarized into a strict consensus tree. Branch support (MPBS) was evaluated by 1000 bootstrap replicates (Felsenstein, 1985). ML analyses were conducted using RAxML v7.2.6 (Stamatakis et al., 2008). Under ML optimization, the GTR + *I* model was selected for RAxML searches. The bootstrap values (MLBS) were calculated based upon 1000 replicates. BI was performed in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). The best-fit models were determined using the Akaike Information Criterion (AIC) (Posada and Buckley, 2004) computed with jModeltest v0.1 (Posada, 2008). Mixed-models analyses were used to assign the appropriate evolutionary model for each data partition. The models used for *rbcl-psal*, *rpl32-trnL*, *rps15-ndhF*, *trnG-trnT*, *trnT-trnL* and *ycf4-cemA* data sets were 012010+G+F, 012010+G+F, 010213+I+G+F, 012310+G+F, 012013+G+F, 012010+G+F, respectively. All parameters were set accordingly to the best-fit models. Two parallel Markov chain Monte Carlo (MCMC) analyses were run simultaneously for 3 million generations with a sampling every 1000 generations till convergence (the average standard deviation of split frequencies was less than 0.01). The first 25% of trees were discarded as a burn-in (Yang et al., 2013), and the remaining trees were used to construct majority-rule consensus tree and estimate posterior probabilities (PP).

The approximately unbiased (AU) test was conducted in CONSEL (Shimodaira and Hasegawa, 2001) to evaluate competing phylogenetic hypotheses (e.g., monophyly of woody bamboos, monophyly of *Kuruna* + *Bergbambos*). The trees site-wise log-likelihoods were calculated with PAUP*v4.0b10 (Swofford, 2003). We also imported our combined data into SplitsTree4 (Huson and Bryant, 2006) to conduct a neighbor-net analysis based on uncorrected *p*-distances to visualize possible contradictions between characters.

2.3. Molecular dating

The combined dataset (including the entire sampling) was analyzed with two sets of calibration points (see below) using BEAST v1.7.5 (Drummond and Rambaut, 2007). A likelihood ratio test (LRT) to the χ^2 distribution of $-2(\ln L_{\text{clock}} - \ln L_{\text{non-clock}})$ rejected the strict molecular clock model overwhelmingly ($\Delta \ln L = 1102$; $P \ll 0.01$). Due to uncorrelated evolutionary rates of plastid fragments documented in grasses (Christin et al., 2014), we used an uncorrelated lognormal distributed (UCLD) relaxed clock mode which allows evolutionary rates to vary along branches in terms of lognormal distribution (Drummond and Rambaut, 2007). The six DNA regions (*rbcl-psal*, *rpl32-trnL*, *rps15-ndhF*, *trnG-trnT*, *trnT-trnL* and *ycf4-cemA*) were partitioned using BEAUTi v1.7.5 (within BEAST) with the appropriate substitution model estimated by jModeltest (see above). The ML tree was specified as the starting tree and a birth–death tree prior was used. Two independent MCMC runs were performed, each for 60 million generations with a sampling every 1000 generations. Tracer v1.5 (Rambaut and Drummond, 2007) was used to check for convergence between the runs; the effective sampling size (ESS) for all parameters exceeded 200 indicating that the results were reliable, as suggested by the program manual. The sampled posterior trees were combined using LogCombiner (within BEAST). TreeAnnotator (within BEAST) was used to generate a maximum clade credibility tree with mean node heights and 95% highest posterior density (HPD) intervals.

2.4. Fossil calibration

Selection of fossils as calibration points for divergence time estimations in Bambusoideae, even in Poaceae, is challenging to say the least, largely due to the ambiguous or fragmentary nature of several putative bambusoid fossils (Strömberg, 2011) and the intractable taxonomy of extant bamboos (BPG, 2012). Two sets of calibration points were analyzed independently. Firstly, we conservatively selected three reliable fossils with accurate dating (Table 1, C1–C3). The Brea and Zucol (2007) *Guadua zuloagae* fossil from the Pliocene (in the Ituzaingó Formation) dated at about 3.6 Mya is well preserved with distinctive anatomical characteristics and morphological features of the nodes and internodes. Its clear affinities with the extant species *G. angustifolia* Kunth convinced us to use it to calibrate the *Guadua* crown node. The Bambusoideae cf. *Chusquea* fossil of Strömberg (2005) is correctly dated to c. 35 Mya, and based on phytoliths surveys to date, may well represent the oldest member of the ‘neotropical bamboos’, we thus conservatively used this phytolith fossil to calibrate the crown Bambusoideae. The stipoid Pooideae fossil of Strömberg (2005) is a well described phytolith with bilobate shape, showing affinities with the genus *Stipa*; we thus used it (c. 34 Mya, in the late Eocene) as a minimum constraint for Pooideae crown node.

Secondly, besides the three calibration points described above, the fossilized phytoliths and their associated cuticles from Indian late Cretaceous deposits (c. 67–65 Mya) were included as another calibration point (Table 1, C4). Based on phylogenetic analyses of Poaceae combining morphological characters and molecular data, Prasad et al. (2011) assigned these fossils to the Oryzae tribe in

Table 1
Fossils used for calibration and uniform distribution prior settings in BEAST.

Symbols	Epoch (Mya) (Lower bound, upper bound)	Systematic affinity	Fossil type	Location	Citations
C1	Pliocene (3.6, 90)	<i>Guadua–Guadua angustifolia</i>	Macrofossil	Argentina, South America	Brea and Zucol (2007)
C2	Late Eocene (35, 90)	Bambusoideae cf. <i>Chusquea</i>	Phytolith	USA, North America	Strömberg (2005)
C3	Middle Eocene (34, 90)	Pooideae– <i>Stipa</i>	Phytolith	USA, North America	Strömberg (2005)
C4 ^a	Late Cretaceous (67, 90)	Ehrhartoideae–Oryzeae	Phytolith, cuticle	India, Asia	Prasad et al. (2011)

^a Used as an additional calibration point in the second strategy.

the BEP clade. The 67 Mya phytolith fossils were consequently included as a minimal age on the stem of Oryzeae. In our combined data set, Oryzeae is the only representative of Ehrhartoideae and the minimal age of 67 Mya was consequently set to the stem of Ehrhartoideae, i.e. the crown node of BEP clade, as implemented by Christin et al. (2014).

Each calibration point was implemented as a uniform distribution between the minimal age of the constraint and the maximal age of the tree root to reduce sensitivity to parameter choice (Warnock et al., 2012; Sauquet, 2013). The tree root (crown 'BEP clade + Panicoideae') was set as 90 Mya, following Christin et al. (2014) results of including Prasad et al. (2011) fossil Oryzeae. The setting of each calibration point in BEAST was noted in Table 1.

2.5. Ancestral area reconstructions

To minimize the influence of phylogenetic uncertainty, Bayesian binary MCMC (BBM) analyses were implemented in RASP v2.0 (Nylander et al., 2008; Yu et al., 2011; Ali et al., 2012). Ancestral areas were reconstructed for the Bambusoideae group (based on the first calibration strategy). Eight operational geographic units were coded as follows: (A) Mainland East & Southeast Asia, (B) Japan & Sakhalin & Korean peninsula, (C) eastern North America, (D) Sri Lanka & (southern) India, (E) Africa, (F) Madagascar, (G) Malesia & Oceania, (H) Neotropics (Fig. 1). Each taxon was allocated to its natural geographic ranges. We randomly selected 10,000 BEAST posterior trees as a 'trees file'. The BEAST annotated tree was specified as the 'final tree' for analyses. Ten MCMC chains were run simultaneously for 10 million generations with state sampling every 1000 generations. Estimated F81+G model was used with a null root distribution (from the program manual). All possible geographic transitions were allowed and ancestral areas were reconstructed for all nodes. Given that each species is distributed across three areas at most, the maximum number of ancestral areas for each node was kept to three. The other parameters were kept with default settings.

2.6. Diversification analyses

Temporal dynamics of bamboos diversification was visualized by constructing lineages through time (LTT) plots using the APE package in the R environment (Paradis et al., 2004). The ultrametric tree of Arundinarieae pruned, in Mesquite v2.74 (<http://mesquiteproject.org/mesquite/mesquite.html>), from the BEAST annotated tree (dated with the first calibration strategy) was used to generate the semilogarithmic LTT plot. Moreover the Bambusoideae chronogram and 1000 dated phylogenetic trees randomly sampled from the BEAST (after removing the burn-in trees) were used to calculate the LTT plot of the whole Bambusoideae allowing confidence intervals.

3. Results

3.1. Phylogenetic reconstructions

Phylogenetic analyses of the combined matrix produced a congruent topology with MP, ML and BI. The strict consensus for the

359 most parsimonious trees is shown in Fig. 2, including MPBS, MLBS and PP values, with clade naming following previous studies (Triplett and Clark, 2010; Zeng et al., 2010; GPWG II, 2012; Kelchner and BPG, 2013; Yang et al., 2013; Attigala et al., 2014). Arundinarieae, Bambuseae and Olyreae are highly supported as monophyletic (99–100/100/1.00) and the sister relationship of Bambuseae and Olyreae is well supported (93/94/1.00). Three subtribes of neotropical woody bamboos are highly supported and resolved as [Arthrotyliidiinae–Guaduiniae (99/100/1.00) + Chusqueinae]. In the paleotropical woody clade, Melocanninae is recovered as monophyletic while the delimitations of Bambusinae and Hickeliinae are not clear (for *Greslania* sp., *Nastus elatus* Holttum and *Temburongia simplex* S. Dransf. et K.M. Wong).

Within Arundinarieae, 12 clades (I–XII) are supported moderately or highly. Clade XII (*Kuruna*) consists of three species from Sri Lanka i.e. *K. debilis* (Thwaites) Attigala, Kaththriarachchi et L. G. Clark, *K. densifolia* (Munro) Attigala, Kaththriarachchi et L.G. Clark and *K. walkeriana* (Munro) Attigala, Kaththriarachchi et L.G. Clark with high support values (99/100/1.00). The *Kuruna* lineage is placed as sister to the *Chimonocalamus* clade (Clade III) from eastern Asia with high supports (94/98/1.00). *Arundinaria wightiana* Nees and a Madagascan species identified as *A. ibityensis* A. Camus seem to cluster with some eastern Asian taxa (62/71/1.00) in the *Phyllostachys* clade (Clade V).

Clade XI (*Ampelocalamus calcareus* C.D. Chu et C.S. Chao) from China is confirmed to be the earliest diverging lineage within the Arundinarieae (91/91/1.00). Two African lineages, i.e. Clade I (*Bergbambos*) and Clade II (African alpine bamboos) cluster within the 'Branch A' (–/–/0.95). Clade II is somehow supported as being sister to the eastern Asian Clade IX (*Gaoligongshania*) (53/86/0.91) and Clade I as sister to eastern Asian Clade X (*Indocalamus*) (–/51/0.97). Lineages II, III, IX and XII cluster collectively with a moderate to high support (81/87/1.00). Two subclades have been recovered within the *Arundinaria* clade (Clade VI), one containing the three North American native *Arundinaria* species and some taxa restricted to Japan (mainly *Sasa* spp.) (61/93/0.99), and the other consisting of some Chinese native bamboos and other Japanese endemic taxa (such as *Semiarundinaria* spp.) (59/78/0.97). However, relationships among Clade IV (*Shibataea* clade), Clade VI and Clade VIII [*Indocalamus wilsonii* (Rendel) C.S. Chao et C.D. Chu] are equivocal.

Results of the AU test are summarized in Table 2. Based on the AU test, our data reject the monophyly of *Kuruna* (Clade XII) + *Bergbambos* (Clade I) and the monophyly of the Sri Lankan *Kuruna* + African alpine bamboos (Clade II). Data also reject the monophyly of the Sri Lankan *Kuruna* + *Phyllostachys* clade (Clade V) and the hypothesis of Sri Lankan *Kuruna* being the basal most lineage of Arundinarieae. Further, the monophyly of woody bamboos is rejected by the AU test. The network analysis recovers the three tribes of Bambusoideae, but there are characters that make the placement of some taxa (e.g., Chusqueinae in neotropical woody clade) ambiguous in the network (Appendix A: Fig. S1).

3.2. Divergence estimates

Estimation of dates associated with the divergences of Arundinarieae and its subordinate lineages were major objectives for this

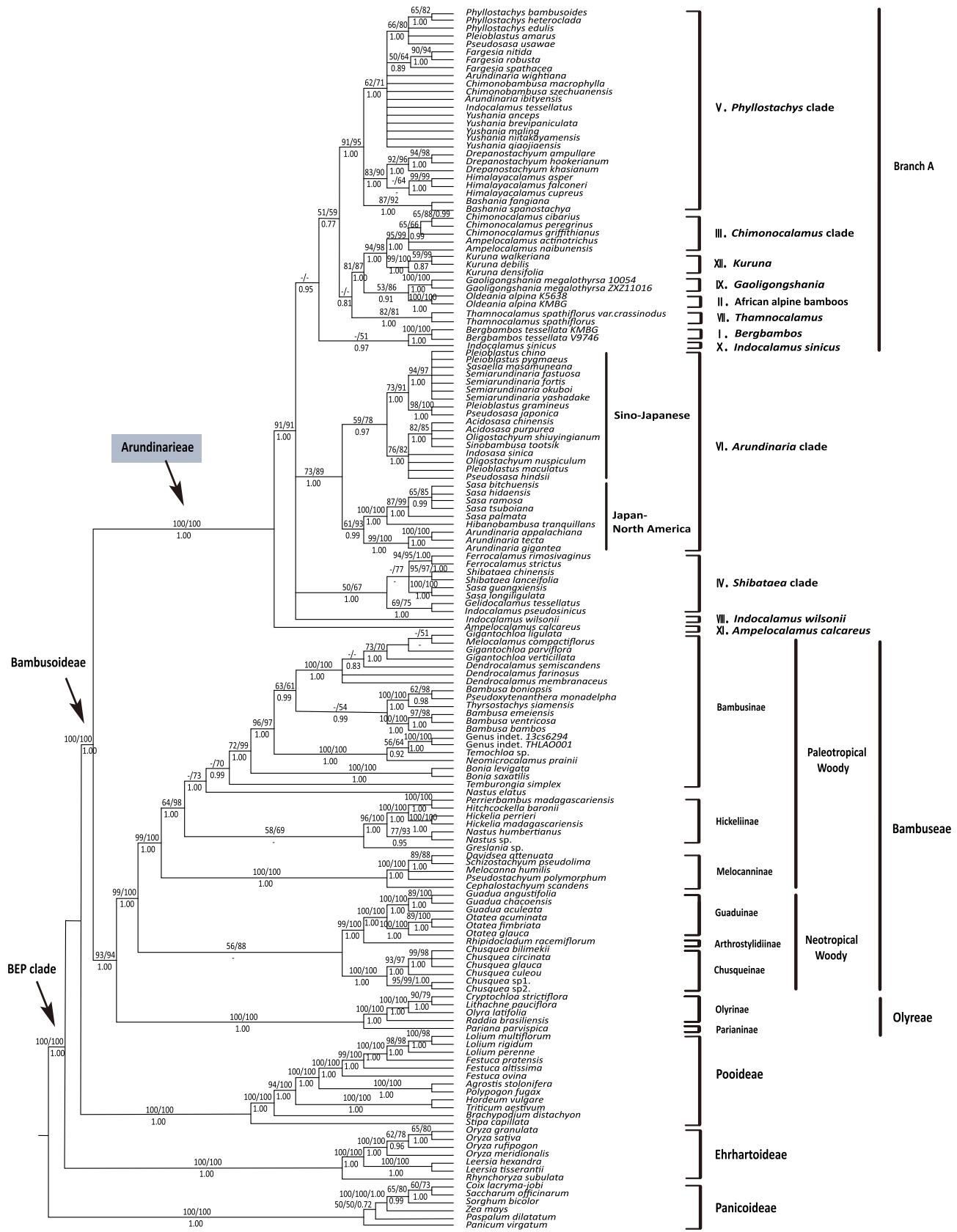


Fig. 2. Strict consensus of 359 equally most parsimonious trees based on the 6-region cpDNA dataset (*rbcL-psal*, *rpl32-trnL*, *rps15-ndhF*, *trnG-trnT*, *trnT-trnL* and *ycf4-cemA*). Values above the branches represent maximum parsimony bootstrap (MPBS)/maximum likelihood bootstrap (MLBS) greater than 50% and number below the branches indicates Bayesian inference posterior probability (PP) more than 0.70. Abbreviations of voucher numbers of *Bergbambos tessellata*, *Gaoligongshania megalothyrsa*, Genus indet. and *Oldeania alpina* indicate the alternative accessions.

Table 2

Hypotheses regarding relationships among clades. All hypotheses were tested using the approximately unbiased (AU) test in CONSEL.

Hypothesis tested	Results of AU test
<i>Kuruna</i> (Clade XII) is sister to <i>Bergbambos</i> (Clade I)	Reject ($p = 0.011^*$)
<i>Kuruna</i> (Clade XII) is sister to African alpine bamboos (Clade II)	Reject ($p = 0.003^*$)
<i>Kuruna</i> (Clade XII) is sister to the <i>Phyllostachys</i> clade (Clade V)	Reject ($p = 0.006^*$)
<i>Kuruna</i> (Clade XII) is the basal most lineage of Arundinarieae	Reject ($p = 0.000^*$)
Arundinarieae plus Bambuseae are monophyletic	Reject ($p = 0.013^*$)

* Indicates $p < 0.05$.

study. The Bayesian relaxed clock chronograms (Fig. 3a; Appendix A: Fig. S2) were similar to the congruent topology from MP, ML and BI analyses (Fig. 2), differing only in the placement of a few statistically unsupported nodes (e.g., the [VIII + (IV + VI)] clade). The different calibration points produced two sets of estimates (Table 3; Fig. 3a, Appendix A: Fig. S2). In the absence of the constraints of the 67 Myr *Oryzaea* fossil (the first calibration strategy), younger estimated divergence dates were generally produced. For example, the estimated divergence of Arundinarieae from Bambuseae–Olyreae was younger when using the first calibration strategy (43.26 Mya, 95% HPD: 34.55–56.11) than the second calibration strategy (47.35 Mya, 95% HPD: 35.83–58.34).

Divergence time estimates for the crown node of Arundinarieae ranged from 12.72 Mya (95% HPD: 6.88–20.96) to 14.34 Mya (95% HPD: 8.11–24.32). The ‘Branch A’ and ‘[VIII + (IV + VI)] clade’ split was dated to late Miocene, ranging from 7.24 Mya (95% HPD: 4.81–10.56) to 8.32 Mya (95% HPD: 5.65–12.03). Within a short time interval, roughly 4 million years after this event, 11 extant lineages (Clade I to Clade X plus Clade XII) diverged rapidly (Fig. 3a). In the diversification analyses, the slopes of Arundinarieae and Bambusoideae LTT plots both became steeper during c. 7–8 Mya (Fig. 3b).

The two African lineages (Clade I and Clade II) and the Sri Lankan *Kuruna* (Clade XII) diverged from their respective eastern Asian sisters during the Pliocene, ranging from an estimated 2.89 Mya

(95% HPD: 1.61–4.42) to 5.08 Mya (95% HPD: 2.44–7.96). The estimates for the stem node of North American *Arundinaria* lineage ranged from 3.62 Mya (95% HPD: 2.20–5.45) to 4.04 Mya (95% HPD: 2.26–6.17). The Sino-Japanese subclade in the *Arundinaria* clade (Clade VI) appeared to diversify during the Pliocene as well, with an estimated date ranging from 3.07 Mya (95% HPD: 1.62–4.54) to 3.42 Mya (95% HPD: 1.58–5.44). The Bambuseae and Olyreae both initially diversified during the Oligocene, with nodes date estimate ranging from 25.86 Mya (95% HPD: 16.89–35.78) to 30.84 Mya (95% HPD: 20.26–42.20).

3.3. Biogeographic analyses

The results of the ancestral area reconstructions (AARs) based on BBM analyses are presented in Fig. 4. The most recent common ancestor (MRCA) for extant temperate woody bamboos was most likely distributed in Mainland East & Southeast Asia. The extant Sri Lankan and African Arundinarieae lineages were estimated to have originated recently from Mainland East & Southeast Asia (probably during the Pliocene). At least two independent dispersal events in ‘Branch A’, from Mainland East & Southeast Asia to Africa, are needed to explain the present Asia–Africa disjunct distribution pattern for the (II + IX) and (I + X) clades respectively. The dispersal events from Mainland East & Southeast Asia to Sri Lanka were estimated as well for the (III + XII) clade. A species from Sri Lanka

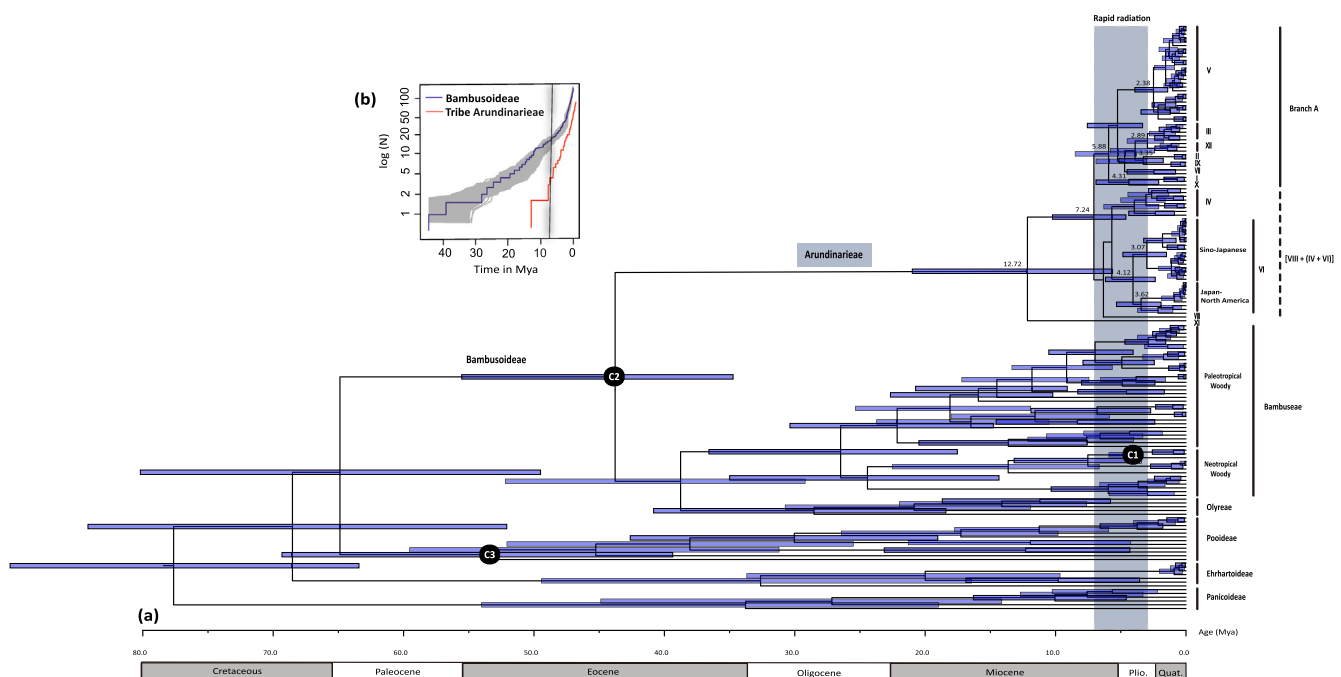


Fig. 3. Chronogram of Arundinarieae and relatives based on six plastid sequences (*rbcl-psal*, *rpl32-trnL*, *rps15-ndhF*, *trnG-trnT*, *trnT-trnL* and *ycf4-cemA*) estimated from the first calibration strategy as implemented in BEAST (a). Calibration points are indicated with C1–C3 (Table 1). Node bars represent the 95% highest posterior density intervals for node ages and mean ages of some interesting nodes in Arundinarieae are indicated. Names of lineages refer to Fig. 2 and the text. Lineages through time (LTT) plots for the tribe Arundinarieae and whole Bambusoideae inferred from R-APE package (b).

Table 3

Divergence times estimation (Mya) for selected nodes of Bambusoideae under different calibration strategies, excluding or including *Oryzae* fossil of Prasad et al. (2011) (Fig. 3a; Appendix A: Fig. S2, in supplementary material).

Node ^a	Age (95% HPD)	
	First calibration strategy	Plus <i>Oryzae</i> fossil
Bambusoideae crown	43.26 (34.55–56.11)	47.35 (35.83–58.34)
Arundinarieae crown	12.72 (6.88–20.96)	14.34 (8.11–24.32)
Branch A/Clade [VIII + (IV–VI)] split	7.24 (4.81–10.56)	8.32 (5.65–12.03)
Clade III/Clade XII split	2.89 (1.61–4.42)	3.54 (2.11–5.26)
Clade II/Clade IX split	3.35 (1.82–5.16)	3.75 (2.01–5.82)
Clade I/Clade X split	4.31 (2.02–6.78)	5.08 (2.44–7.96)
Clade [(II–IX) + (III–XII)] crown	3.82 (2.27–5.69)	4.57 (2.90–6.62)
Branch A crown	5.88 (3.65–8.24)	7.12 (5.01–10.03)
Clade III crown	1.64 (0.71–2.74)	2.00 (0.92–3.22)
Clade IV crown	4.01 (2.16–6.58)	4.62 (2.51–7.29)
Clade V crown	2.38 (1.24–3.82)	3.10 (1.98–4.95)
Clade VI crown	4.12 (2.58–6.82)	4.92 (2.96–7.34)
Sino/Japan split in Clade VI	3.07 (1.62–4.54)	3.42 (1.58–5.44)
Japan/North America split in Clade VI	3.62 (2.20–5.45)	4.04 (2.26–6.17)
Clade XII crown	1.36 (0.59–2.30)	1.65 (0.74–2.81)
Bambuseae/Olyreae split	38.02 (28.75–51.68)	40.78 (30.16–52.89)
Bambuseae crown	25.86 (16.89–35.78)	28.24 (19.82–38.95)
Paleotropical woody bamboos crown	22.40 (15.02–31.02)	25.05 (17.58–33.41)
Neotropical woody bamboos crown	23.96 (13.88–34.04)	27.02 (18.11–38.05)
Olyreae crown	28.26 (18.08–40.12)	30.84 (20.26–42.20)

^a Names of lineages refer to Fig. 2 and the text; HPD, highest posterior density.

(*Arundinaria wightiana*) and another one from Madagascar (*A. ibityensis*) might be in the *Phyllostachys* clade (Clade V), implying recent dispersals from eastern Asia.

In the *Arundinaria* clade (Clade VI), migrations from eastern Asia to eastern North America are likely responsible for the present disjunct distribution. Migrations from Mainland East & Southeast Asia to Japan & Sakhalin & Korean peninsula are also suggested to have occurred, resulting in the Sino-Japanese disjunction revealed within the Sino-Japanese subclade.

The tropical bamboos (Bambuseae and Olyreae) were not the focus here and were not sampled well enough to test biogeographic hypotheses (e.g., suggested by Ruiz-Sanchez, 2011; Burke et al., 2012; Goh et al., 2013), we thus will not describe and discuss the biogeographic reconstructions for these lineages in the present paper.

4. Discussion

4.1. Phylogenetic relationships

The present study is the first attempt, to date, at investigating molecular phylogenetics and biogeography of Arundinarieae based on a broad Bambusoideae sampling using plastid markers (Kelchner and BPG, 2013; Attigala et al., 2014; Ma et al., 2014; Wysocki et al., 2015). The sister relationship of Bambuseae and Olyreae is highly supported in the phylogenetic tree (Fig. 2) and confirmed by the AU test (Table 2), but is unclear in the network diagram (Appendix A: Fig. S1). These results may somewhat imply the incongruence of plastome phylogenomic (Wysocki et al., 2015) and nuclear data (Triplett et al., 2014) analyses of Bambusoideae. The topology of major lineages of tropical bamboos (6 subtribes of Bambuseae and 2 subtribes of Olyreae) is consistent with previous studies (Yang et al., 2008; Sungkaew et al., 2009; Ruiz-Sanchez, 2011; Goh et al., 2013; Kelchner and BPG, 2013), but because the phylogenetic positions of *Greslania* sp. (assigned to Bambusinae) and *Nastus elatus* (assigned to Hickeliinae) (BPG, 2012) are elusive, further studies on paleotropical woody bamboos are necessary.

All the known 12 major lineages of Arundinarieae (I–XII) (Triplett and Clark, 2010; Zeng et al., 2010; Yang et al., 2013;

Attigala et al., 2014) have been sampled in this study, encompassing their actual distribution areas. The twelfth lineage (Clade XII) contains three Sri Lankan *Kuruna* taxa sampled by Attigala et al. (2014). Our analyses highly support the *Kuruna* lineage as sister to the *Chimonocalamus* clade (Clade III) (Fig. 2), which is recovered for the first time in a phylogenetic analysis. The hypotheses of the monophyly of *Kuruna* (Clade XII) + *Bergbambos* (Clade I); monophyly of *Kuruna* (Clade XII) + African alpine bamboos (Clade II); monophyly of *Kuruna* + the *Phyllostachys* clade (Clade V), and *Kuruna* being the basal-most lineage in Arundinarieae were further rejected by the AU tests (Table 2). The alternative hypotheses regarding relationships among *Kuruna* species and other clades tested in Attigala et al. (2014) can be ruled out by our data. Surveying the morphological characters of the *Kuruna* and *Chimonocalamus* lineages, we find that there are some vegetative and reproductive characters that support a sister relationship between these groups. For example, the rhizomes of these groups are of the pachymorph type, culm forms are unicaespitose, synflorescence types are open racemes or panicles, and spathe bracts at the base of the synflorescence are absent.

Representatives from Sri Lanka (*Arundinaria wightiana*) and Madagascar (*A. ibityensis*) were also sampled and likely contained in the *Phyllostachys* clade (Clade V) in the analyses. Another Madagascan species (tentatively identified to be *Yushania ambositrensis* (A. Camus) Ohrnberger, not included in this study) was sampled in other molecular analyses (Triplett and Clark, 2010; Attigala et al., 2014) and resolved as sister to African *Oldeania alpina* in Clade II. Given there were missing data for *A. ibityensis* and *A. wightiana* (Appendix A: Table S1) as the only representative from Madagascar and no sample from southern India in our analyses, more work is needed to assign to an appropriate clade the Madagascan and southern Indian '*Arundinaria*' species that have not yet been sampled.

The present study allows further progress in the understanding of all these lineages (Fig. 2). The Asian (Chinese) endemic species *Ampelocalamus calcareus* (Clade XI) is confirmed to be the earliest diverging Arundinarieae and as the sister taxon to all the remaining lineages in this group, which coincides well with the results from nuclear genes (Yang et al., 2013) and plastome phylogenomic analyses (Ma et al., 2014). A publication about its taxonomic status

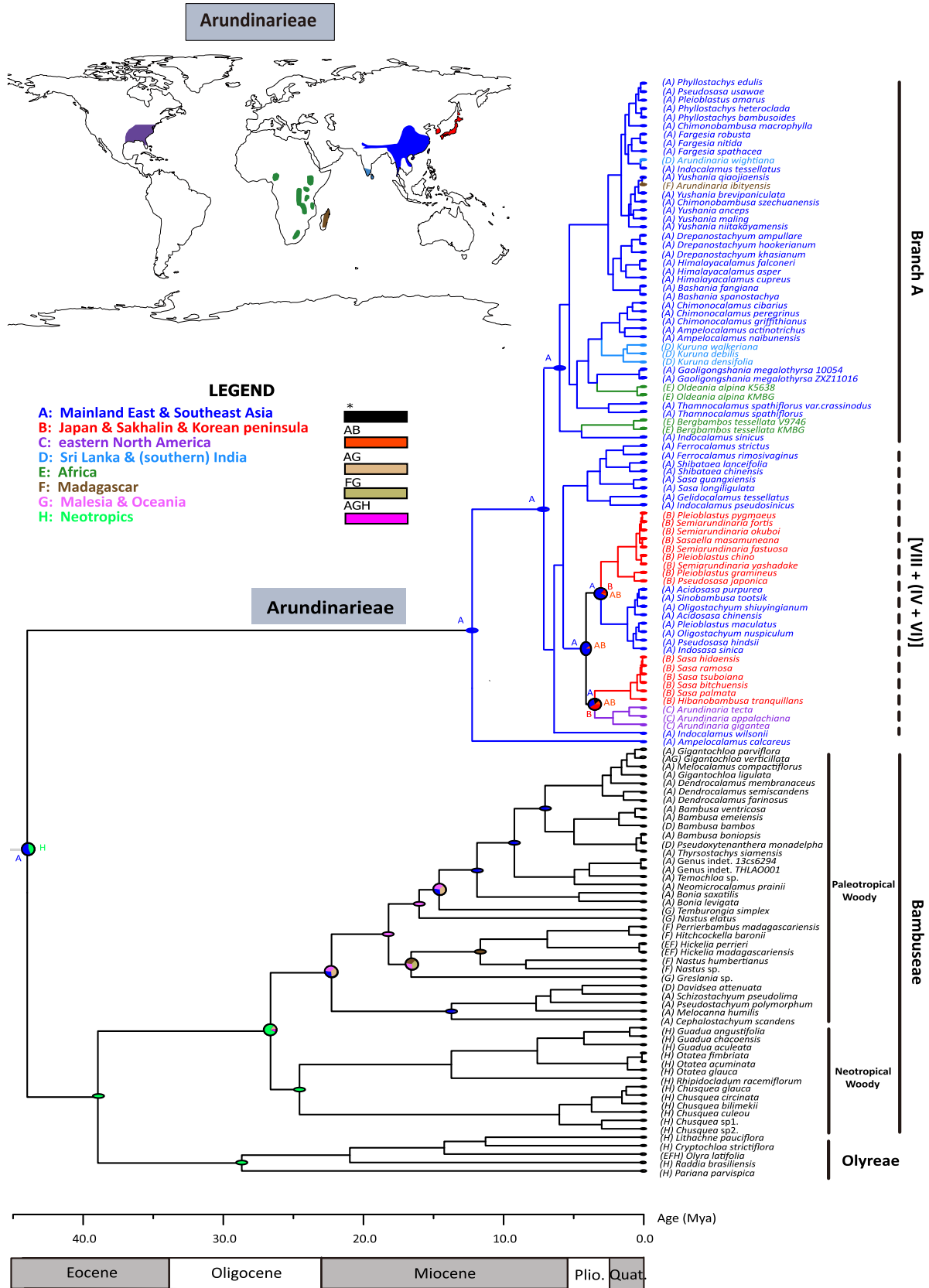


Fig. 4. Ancestral area reconstruction inferred from Bayesian binary MCMC (BBM) in RASP. The eight area units (A–H) and possible ancestral ranges at different nodes are indicated with color key; black with an asterisk represents other ancestral ranges. Optimal ancestral distributions of interesting nodes are indicated, with large pie charts showing the relative probabilities of alternative ancestral ranges. The color coding for geographic ranges of Arundinarieae is indicated on the map (left upper). Branches in Arundinarieae colored in accordance with the most probable range state of their descendant nodes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(involving its exclusion from the genus *Ampelocalamus*) is in preparation for a separate paper. The only two African lineages (I and II) do not form a clade in the phylogenetic tree, and they cluster with other six lineages i.e. III, V, VII, IX, X, and XII in the 'Branch A', in congruence with the plastid phylogenomic tree (Ma et al., 2014). The II, III, IX, and XII lineages form one monophyletic group with the following topology ((II, IX), (III, XII)). The (I + X) clade was suggested but only with a low level of confidence and is not discussed here. North American *Arundinaria* and Japanese *Sasa* species are reciprocally monophyletic, nested with other species from China and Japan in the *Arundinaria* clade (Clade VI), in agreement with the phylogeny inferred from Zhang et al. (2012). Due to the lack of enough phylogenetic signal, the relationships among clades IV, VI, VIII, V, VII, I, X were not resolved contrarily to the findings from the plastid phylogenomic analyses (Ma et al., 2014).

4.2. Rapid radiation of Arundinarieae

Aiming at the accurate estimation of divergence times for Arundinarieae and its subordinate lineages, we conducted molecular dating analyses using a broad phylogenetic framework for Bambusoideae in 'BEP clade + Panicoideae' to include proper fossil calibration nodes (Brea and Zucol, 2007; Strömberg, 2005). Two sets of calibration points (excluding or including Oryzaceae fossil of Prasad et al. (2011)) were analyzed independently. We found that the first calibration strategy (not including the Oryzaceae fossil) generally produced a little younger (within about 2 million years) estimated age for internal nodes of the Arundinarieae group (Table 3), which is consistent with the findings of Burke et al. (2012, 2014). Our estimates suggested the Arundinarieae began to diversify around 12–14 Mya, among the range of c. 9 Mya (Bouchenak-Khelladi et al., 2010), 10 Mya (Hodkinson et al., 2010) or 7–12 Mya (Peng et al., 2013) and 19 Mya (Christin et al., 2008). It may be implied that the divergence estimates here are likely to be improved because of increased taxonomic sampling (including all the extant 12 lineages) (Sauquet et al., 2012; Burke et al., 2014). Our data also shows that Arundinarieae are younger than Bambuseae and Olyreae (ranging from an estimated 25.9 to 30.8 Mya), in agreement with the results derived from other studies (Christin et al., 2008; Bouchenak-Khelladi et al., 2010; Hodkinson et al., 2010; Ruiz-Sanchez, 2011; Burke et al., 2012, 2014).

It is noteworthy that a series of short internodes connected by long branches in the chronogram of Arundinarieae (Fig. 3a), as also recovered in the phylogenomic analyses (Ma et al., 2014), imply that this tribe may have experienced rapid radiation. The 11 major lineages (I–X, and XII, at the exception of XI) were further estimated to have diverged within a short interval of about 4 million years. The LTT analyses also confirmed rapid radiation of Arundinarieae (Fig. 3b). The rapid radiation may, to some degree, account for the notorious difficulties of reconstructing the phylogeny of Arundinarieae (Hodkinson et al., 2010; Triplett and Clark, 2010; Zeng et al., 2010; Zhang et al., 2012, 2014; Wang et al., 2013; Yang et al., 2013; Attigala et al., 2014; Ma et al., 2014; Triplett et al., 2014).

Based on the geological data, sedimentary records from ocean and loess, and computer modeling, there is a general consensus for an intensification of the East Asian monsoon at about 7–8 Mya (An et al., 2001; Zheng et al., 2004; Sun and Wang, 2005; Wang et al., 2005; Harris, 2006). It has been suggested that plants diversification often correlated with significant climatic changes (Verboom et al., 2003; Janssens et al., 2009; Hampe and Jump, 2011; Zou et al., 2013). The alteration of East Asian monsoon regimes may be a trigger for the evolution of several plant groups in the area (e.g., Wang et al., 2012; Su et al., 2013). It looks as though the start of Arundinarieae rapid radiation in eastern Asia has occurred close to the late Miocene climate change, particularly

the East Asian monsoon. The increased summer rainfall (one feature of East Asian monsoon) may have facilitated the clonal growth of temperate woody bamboos, and allowed them to expand their niche breadths to colonize a variety of habitats from sea level to high elevations (Ohrnberger, 1999; Li et al., 2006; Hodkinson et al., 2010), in which divergent selections may have contributed to adaptive speciation of this group. We thus infer that the drastic intensification of East Asian monsoon (during the late Miocene) likely provided a key opportunity to trigger the rapid radiation of Arundinarieae in the area.

4.3. Biogeographic patterns in Arundinarieae

4.3.1. An 'outside Asia hypothesis' or 'Asian hypothesis'

Our molecular biogeographic analyses indicate that the Arundinarieae diversified in Mainland East & Southeast Asia from the mid-Miocene (ranging from an estimated 12.7 to 14.3 Mya) and demonstrate that *Ampelocalamus calcareus* (Clade XI) from China represents the earliest extant lineage (Fig. 4). The possibility for the extant Sri Lankan/southern Indian or African/Madagascan members of Arundinarieae to represent basal elements can now be excluded completely. Contrasting to the possible Indian route or African route for ancestors of Arundinarieae arriving in Asia (an 'outside Asia hypothesis', Stapleton et al., 2009; Hodkinson et al., 2010; Stapleton, 2013), results from our molecular data show that the extant temperate woody bamboos likely radiated in the opposite direction, from East & Southeast Asia to Africa/Madagascar, Sri Lanka/southern India and North America during the Pliocene or even more recently. The most recent phylogenetic data (Ma et al., 2014 and this study) suggest that there is no evidence to support the 'outside Asia hypothesis' (Stapleton et al., 2009; Hodkinson et al., 2010; Stapleton, 2013).

On the other hand, it seems plausible that ancestors of Arundinarieae have dispersed to Asia early but failed to diversify until recently (an 'Asia hypothesis', Hodkinson et al., 2010). However, we must keep it in mind that more and better evidence from Arundinarieae-like fossils, dated accurately, is required to test the 'outside Asia hypothesis' and 'Asian hypothesis' thoroughly, which will further help to understand the historical biogeography of woody bamboos (Li, 1999; Ohrnberger, 1999; Wu et al., 2003; Hodkinson et al., 2010).

4.3.2. Eastern Asian and Afro-Indian disjunction

At least two standalone relatively recent dispersal events from eastern Asia to Africa are detected (Fig. 4), Clade I and Clade II within the 'Branch A' (though its topology was not resolved as clearly as in Ma et al., 2014), in agreement with Stapleton (2013). These events probably both occurred during the Pliocene (ranging from an estimated 3.4 to 5.1 Mya), which can rule out hypotheses of migrations through the Eocene Boreotropical flora zone, and the Eocene–Oligocene Lemurian stepping stones (Schatz, 1996; Clayton et al., 2009). It has been suggested that a new migration route connecting southwestern Asia and northeastern Africa via the Arabian Peninsula and the Levant region was established during the early Pliocene, because of the collision of Afro-Arabian and Eurasian plates (Fernandes et al., 2006). Plant exchanges between Africa and Eurasia via this route have been proposed for *Lepidium* L. of the Brassicaceae (1.8–3.6 Mya) (Mummenhoff et al., 2001), Loliinae of the Pooideae (2.5–3.6 Mya) (Inda et al., 2008) and the Campanulaceae (c. 2.5–7.5 Mya) (Roquet et al., 2009). This overland route may be a scenario explaining migrations of temperate woody bamboos from eastern Asia to Africa during the Pliocene.

Alternatively, long-distance dispersals of viable seeds, across the Indian Ocean from Asian progenitors, have been suggested for several plant groups with Asian and African disjunct distribu-

tion, such as *Bridelia* Willd. in Phyllanthaceae (1.85–10.00 Mya) (Li et al., 2009), the Hernandiaceae (5–27 Mya) (Michalak et al., 2010) and *Paederia* L. in Rubiaceae (10.28–22.68 Mya) (Nie et al., 2013). There is strong evidence to support long-distance seed dispersals by 'seed predators' (Heleno et al., 2011; Nogales et al., 2012). Several birds foraging on bamboo seeds are known to be highly mobile, for example the African weaver finches, rose-breasted grosbeak, blue ground dove (Janzen, 1976). We thus infer that direct transoceanic dispersals of temperate woody bamboos from eastern Asia to Africa, during the Pliocene, may have occurred by granivorous birds.

We also recovered at least one dispersal event from eastern Asia to Sri Lanka during the late Pliocene (ranging from an estimated 2.9 to 3.5 Mya) for the (III + XII) clade (Fig. 4). The other Sri Lankan (*Arundinaria wightiana*) and Madagascan (*A. ibityensis*) taxa seemed to imply recent dispersals from eastern Asia. But we cannot rule out relatedness of African and Madagascan temperate bamboos (Triplett and Clark, 2010; Attigala et al., 2014). There are five additional 'Arundinaria' species endemic to Madagascar (Dransfield, 2003) not included in any molecular phylogenetic study yet. To understand geographic origins of Madagascan temperate bamboos, further phylogenetic and biogeographic work is much needed (Warren et al., 2010).

4.3.3. Eastern Asian and North American disjunction

In the *Arundinaria* clade (Clade VI), we identified two subclades corresponding to Japanese–North American and Chinese–Japanese disjunctions, respectively (Fig. 4). The eastern North American *Arundinaria* lineage has been inferred to migrate from eastern Asia during the early Pliocene (ranging from an estimated 3.6 to 4.0 Mya). The Bering Land Bridge (BLB) provided a likely route for temperate floristic exchanges between Asia and North America until c. 3.5 Mya (Hopkins, 1967; Wen, 1999). Beringian migrations have been documented for several plant groups, including *Penthorum* L. (Penthoraceae) (Xiang et al., 2000), *Circaea* L. (Onagraceae) (Xie et al., 2009) and *Saxifraga rivularis* L. (Saxifragaceae) (Westergaard et al., 2010). From our analyses, migrations through BLB seem to be the most plausible explanation for the eastern Asian and eastern North American disjunction of Arundinarieae. This is in agreement with previous studies (Stapleton et al., 2004; Burke et al., 2012, 2014) suggesting that the evolutionary divergence of New World *Arundinaria* nearly coincided with its geographic dispersal into North America. The Japanese archipelago was part of continental Asia from the early Miocene to the Pleistocene (Iijima and Tada, 1990), indicating Pliocene migrations from China to Japan likely occurred, in agreement with patterns documented for other plant groups (Mitsui et al., 2008; Wang et al., 2013a).

4.4. Summary

In this study, all the 12 extant lineages of Arundinarieae have been sampled, covering their present geographic ranges, to investigate the biogeography of this tribe in a broad phylogenetic framework of Bambusoideae, based on six plastid DNA loci. Our data highly support Sri Lankan *Kuruna* (clade XII) as sister to the Asian *Chimonocalamus* clade (III), clustered in one large group ('Branch A') with the African lineages (clades I and II) and other lineages (e.g., clade V). It has been suggested that there is no phylogenetic evidence to support the Indian or African route for migration of temperate bamboo ancestors to Asia (the 'outside Asia hypothesis'). Our data also suggests an association between the start of rapid radiation in the Arundinarieae with the late Miocene drastic strengthening of East Asian monsoon. Most important of all, this study has shed light on the recent (likely during the Pliocene) dispersals from Asia to Africa/Madagascar, Sri Lanka/southern India

and North America to form the modern disjunct pattern found for temperate woody bamboos. However, in order to understand with more details the evolutionary history of bamboos, biparental inherited nuclear markers (Zhang et al., 2012, 2014; Wang et al., 2013c; Yang et al., 2013; Triplett et al., 2014) need to be sequenced to compare the patterns recovered with the plastid loci only.

Acknowledgments

We would like to thank Lu Lu, Wen-Cai Wang, Cheng-Xin Fu, Yi-Chi Zhang, Xue-Qin Wang, Jie Cai, Ting Zhang, Hong-Mei Yang, Meng-Yuan Zhou, W.L. Goh and K.M. Wong for the help in sample collection. We are grateful to Missouri Botanical Garden and Royal Botanic Gardens, Kew for providing some bamboo DNA materials. Many thanks were also given to anonymous reviewers who provided valuable suggestions for improvement of this paper. This study was funded by the National Key Basic Research Program of China (Grant 2014CB954100) and the National Natural Science Foundation of China (Grants 31430011 and 31170204). TH sample collection in Laos was funded by a French Muséum National d'Histoire Naturelle grant (ATM "Formes possibles, formes réalisées") and was conducted during a Radeau des Cimes (Canopy Raft) expedition (<http://blog.radeau-des-cimes.org/>).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2015.11.025>.

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