

Molecular phylogeny of Asian woody bamboos: Review for the Flora of China

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ABSTRACT

Molecular data was reviewed for the woody bamboo account in the English language Flora of China. The implications for recognition of suprageneric taxa and genera, for macro-morphological characters used in classification systems, and for the inferred biogeographical history of Asian bamboos are discussed. Support was not found for large supertribes based on inflorescence structure. Instead a restricted number of suprageneric taxa was suggested, with only 3 subtribes for Asian woody bamboos. The presence of both iterant and semelant inflorescences within subtribes shows that bamboos with these contrasting forms can be closely related, suggesting that simpler evolutionary pathways are required to explain them. Differences in sequence divergence between tropical and temperate subtribes suggests different biogeographical histories. It is hypothesised that temperate bamboos diversified later in Asia, only after the collision of the Indian and African tectonic plates with the Eurasian plate, and that the poor resolution of temperate taxa from sequence data is largely the result of rapid diversification after this biotic interchange. Sequence data provided somewhat equivocal evidence for recognition of genera. It was useful in demonstrating the polyphyly of broad interpretations of genera *Sinarundinaria*, *Thamnocalamus*, *Schizostachyum*, *Racemobambos*, *Drepanostachyum*, *Arundinaria* and *Bashania*. However, in the temperate *Arundinariinae*, sequence data was not capable of refining boundaries between closely related genera, for which different molecular markers may prove more useful.

1. Introduction

Preparation of the English language bamboo account for the Flora of China (Li *et al.* 2006) required a consideration of the molecular data available, in order to discuss which suprageneric and generic names to recognize in the treatment, and to balance molecular evidence with other considerations governing the recognition of genera. Morphological characters associated with major divisions within the bamboos were considered in the light of the molecular data. The evolutionary history of the Asian woody bamboos was also important, in order to assess whether they may have evolved first within China. This paper discusses the evidence available at the time of preparation of the account.

Several revisions of Asian woody bamboos have been undertaken over the past three decades in Europe and Asia. These have differed substantially in the recognition of particular subtribes and genera, partially because they give emphasis to different suites of characters, and classifications based on vegetative and floral characters are not always in agreement. In woody bamboos vegetative characters are both more numerous than in other grasses, and also more useful for identification in these infrequently flowering plants. A consensus on appropriate generic breadth and the characters of major importance at different ranks is still emerging, but a global nomenclatural account (Ohrnberger 1999) has been published, reflecting the names currently in more widespread international use.

Against this background molecular data has appeared over the last 15 years, providing some valuable insights into phylogeny. The molecular data can now start to be used effectively to examine the grouping or separation of many taxa, allowing a more natural classification to develop. It also suggests an interesting historical biogeographic hypothesis for the evolution of temperate Asian bamboos, and raises questions about the implications of molecular topologies for their systematics.

2. Recognition of suprageneric taxa

The woody bamboos had usually been considered (Clayton & Renvoize 1986; Watson & Dallwitz 1992; Soderstrom & Ellis 1988a, Stapleton 1994a; Zhang & Clark 2000; Li 1997; Ohrnberger 1999) to constitute a tribe, *Bambuseae* Kunth ex Nees within subfamily *Bambusoideae* and the grass family *Poaceae*. Molecular support for the monophyly of the tribe varied, with different relationships with a potentially sister group of herbaceous bamboos, the Olyreae, being suggested in different analyses. More recently *Bambuseae* has received less support. Bouchenak-Khelladi *et al.* (2008) and Sungkaew *et al.* (2008) inferred non-monophyly of woody bamboos, with Olyreae placed sister to the 2 tropical *Bambuseae* clades and the temperate clade (now known as *Arundinarieae*) as the most outlying group of *Bambusoideae*.

Suprageneric classification within the woody bamboos has been very complex. A variety of characters were utilised at different times to define more than 50 suprageneric taxa at different ranks (Ohrnberger 1999). The largest taxa proposed, which divided the woody bamboos into two groups on the basis of gross inflorescence structure, were described at the level of supertribe as *Bambusodae* Liou and *Arundinarodae* Liou, (synonymous with the invalid but widely used *Bambusatae* Keng & Keng f. and *Arundinariatae* Keng & Keng f.). Below these were a wealth of different tribes and subtribes applied in conflicting ways in different treatments. The Chinese language Flora of China bamboo account (Keng & Wang 1996) used 13 taxa at three suprageneric ranks: 2 supertribes and 6 tribes, some of which were subdivided into subtribes (table 1). Other morphological classifications have simplified this to a system using only subtribes (Soderstrom & Ellis 1988a; Stapleton 1994a; Dransfield & Widjaja 1995; Li 1997; Judziewicz *et al.* 1998).

From the very first phylogenies to be inferred from molecular data (Watanabe 1994; Xia 1994; Zhang 1996; Kobayashi 1997) there has been no support for the two large supertribes. From a biogeographical perspective this is not surprising as the supertribes included different elements from different continents. The limited dispersal capabilities of bamboos and the effects of isolation lead us to expect to find parallel

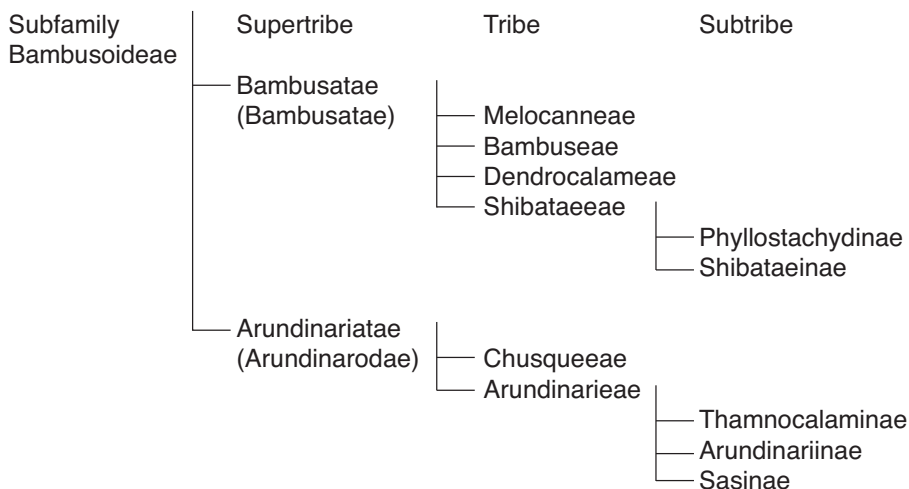


Table 1. Suprageneric taxa used in Flora of China (Chinese version), Keng & Wang (1996).

evolution in geographically distant bamboos, and the molecular evidence has clearly demonstrated its existence. Examples are the S American genera *Guadua* and *Otatea*, morphologically similar to the Asian genera *Bambusa* and *Yushania* respectively, but shown to be unrelated in molecular phylogenies (Kobayashi 1997; Zhang 1996; Ni Chonghaile 2002). Supertribes *Bambusodae* and *Arundinarodae* Liou were based on homoplasious characters (morphologically similar but not homologous) and hence grouped genera from Asia, Africa, and S America.

The two supertribes were distinguished by the morphological character of inflorescence form, either iterant (indeterminate) or semelant (determinate), defined respectively by presence and absence of buds, prophylls, and other bracts. This distinction had long been considered fundamental to bamboo morphology and classification (Holttum 1958; McClure 1966; Keng 1982; Clayton & Renvoize 1986; Zhang 1992), with implications for how bamboos are related to the rest of the grass family (Holttum 1958; Clayton & Renvoize 1986). The absence of any support for these groups in the molecular data has justified a rethinking of bamboo classification and morphology (Soderstrom & Ellis 1988a; Stapleton 1994a; Dransfield & Widjaja 1995). It was noted (Li 1997) that it is not always easy to distinguish between the two inflorescence types, and that intermediate forms exist, making it difficult to apply the distinction. It has also been suggested (Stapleton 1997) that the classic distinction merely represents 2 poorly defined syndromes, applied in different ways by different authors, and that a critical analysis of the several individual component characters and their states is more appropriate and useful.

Instead of the occurrence of a major dichotomy in the woody bamboos at supertribe level reflecting inflorescence form, molecular evidence (Xia 1994; Zhang 1996; Ni Chonghaile 2002; Bouchenak-Khelladi *et al.* 2008; Sungkaew *et al.* 2009) has suggested the divergence of at least three major lineages. These three clades all include taxa with more or less ebracteate as well as bracteate inflorescences. They represent bamboos from tropical

latitudes of the Old World (paleotropical), those from tropical latitudes of S & C America (neotropical), and those from temperate latitudes. Evidence from DNA content has supported the distinction between temperate and tropical bamboos (Gielis *et al.* 1997). The temperate clade has the strongest and most consistent molecular support as a monophyletic group. Although it has often been suggested that Asian tropical bamboos retain the largest number of primitive characters within the woody bamboos, a variety of relationships between the paleotropical, neotropical, and temperate bamboos have been inferred from molecular topologies. Plastid data (Ni Chonghaile 2002) show one possible topology, with the two tropical groups more closely related than the temperate clade, when herbaceous bamboos are used as an outgroup (Fig. 1).

As all 3 clades include both bracteate and ebracteate taxa, and particularly as the Asian temperate clade includes both bracteate and ebracteate taxa in a complex pattern, it is clear that the two morphological forms can be closely related. Holttum (1958) and Clayton & Renvoize (1986) postulated two conflicting mechanisms for evolution of the different forms, respectively assuming primitive and derived status for the bracteate condition. Soreng & Davis (1998) felt that the derived condition suggested by Clayton & Renvoize (1986) did not conform with the latest molecular results, given the apparent age of the tropical woody bamboos. For these, bracteate inflorescences would appear more likely to be primitive. It is possible, however, that Holttum (1958) and Clayton & Renvoize (1986) were both partially correct, if bracteate inflorescences in the different clades are not homologous. Holttum (1958) considered bracteate inflorescences primitive, which is likely to be correct in tropical bamboos, but envisaged a complex loss of bracts for ebracteate types. Clayton & Renvoize (1986) suggested that bracteate synflorescences evolved by reduction from a derived ebracteate inflorescence through condensation of system of spikelets, incorporating reduced vegetative bracts. This could be correct for temperate bamboos but seems less likely for tropical taxa.

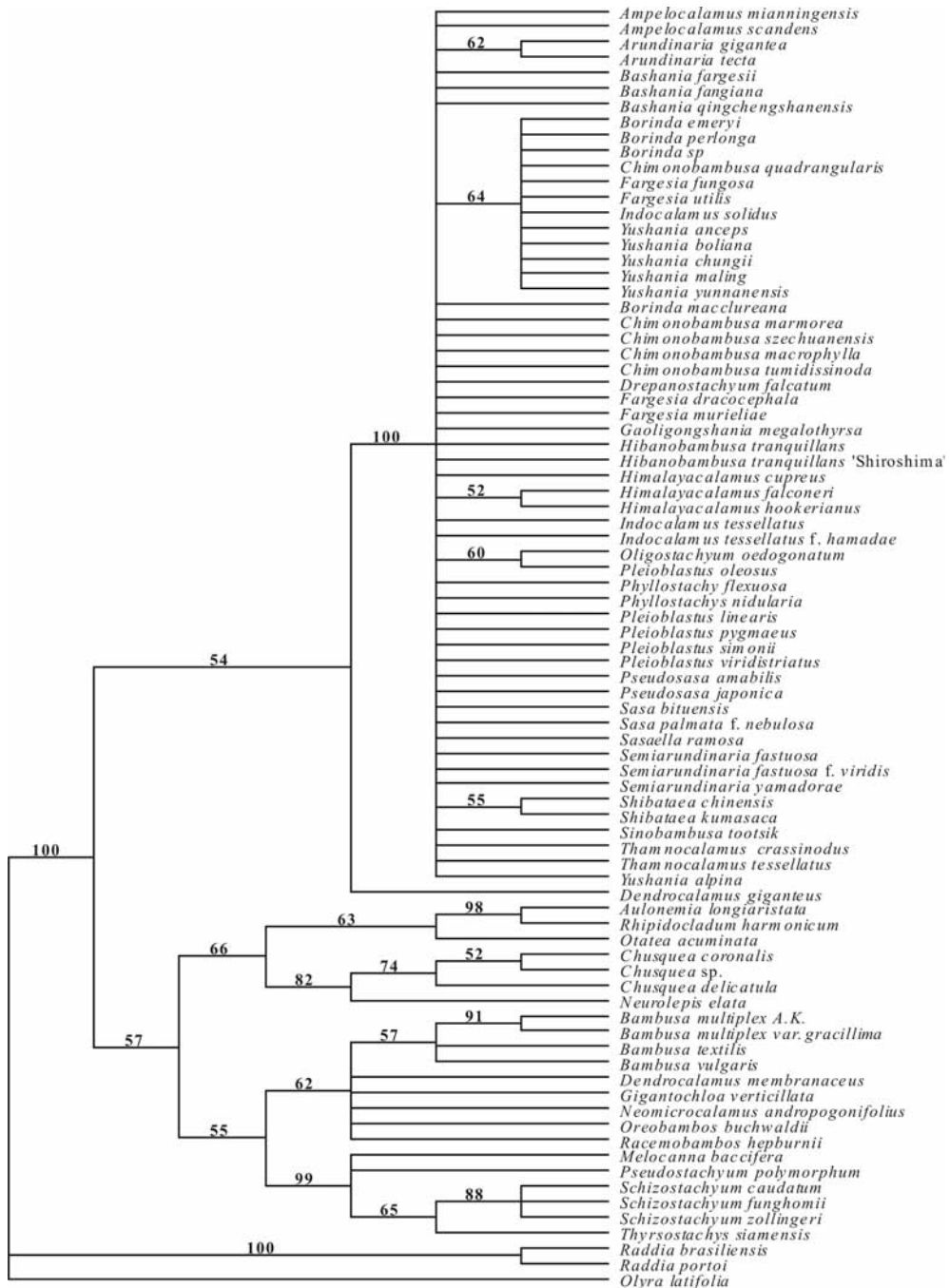


Figure 1. Bootstrap consensus tree from *trnL-F* sequence data (Ní Chonghaile 2002).

Numbers represent the bootstrap support values obtained for the respective branches.

Bootstrap support values of 90-100% are considered strong, 70-89% moderate, and less than 70% weak.

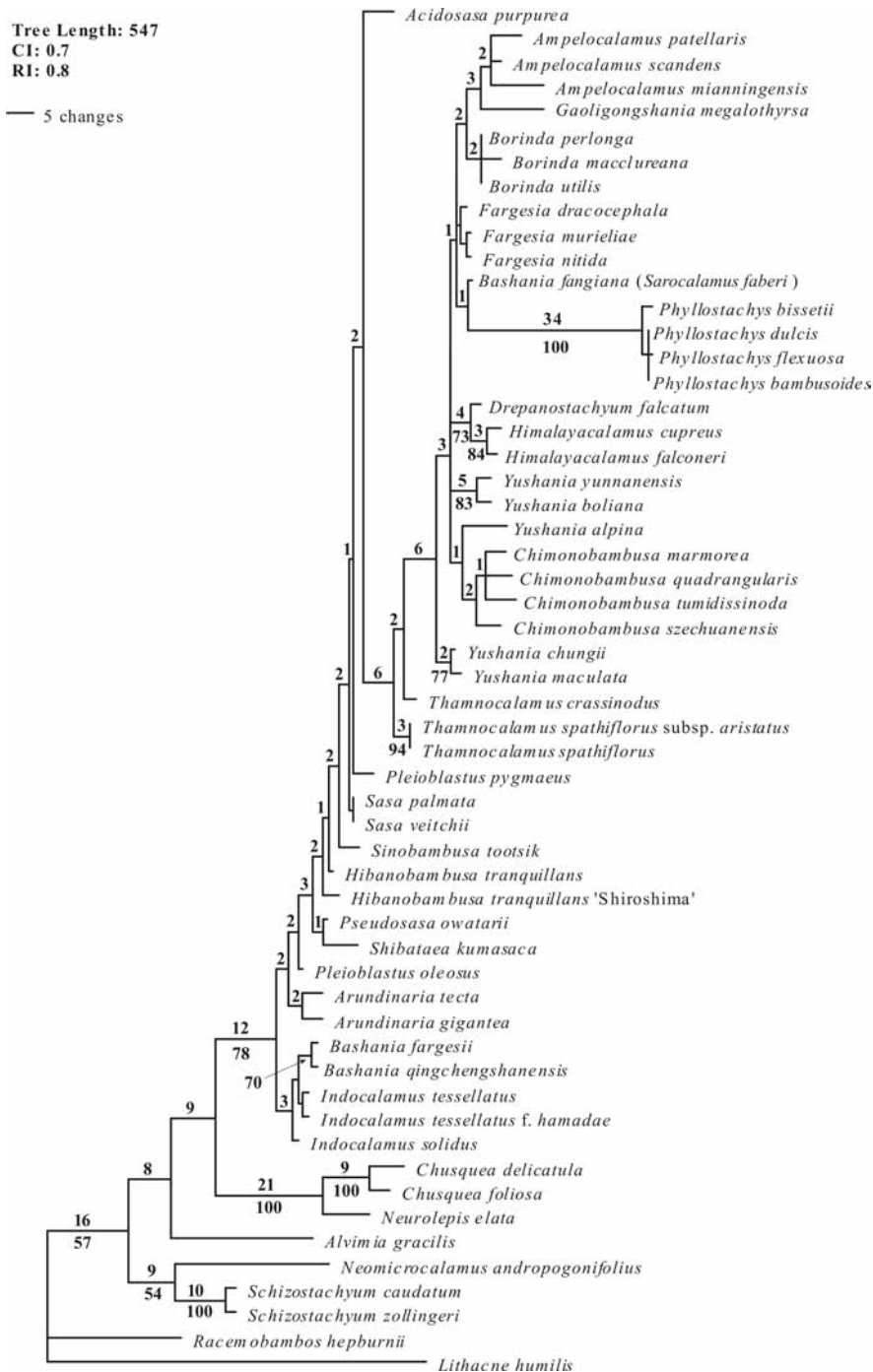


Figure 2. One of 200 equally parsimonious trees obtained following sequence analysis of the ITS data (Ni Chonghaile 2002). Bold numbers represent the number of steps supporting each branch. Numbers above branches are branch lengths, numbers below are bootstrap support.

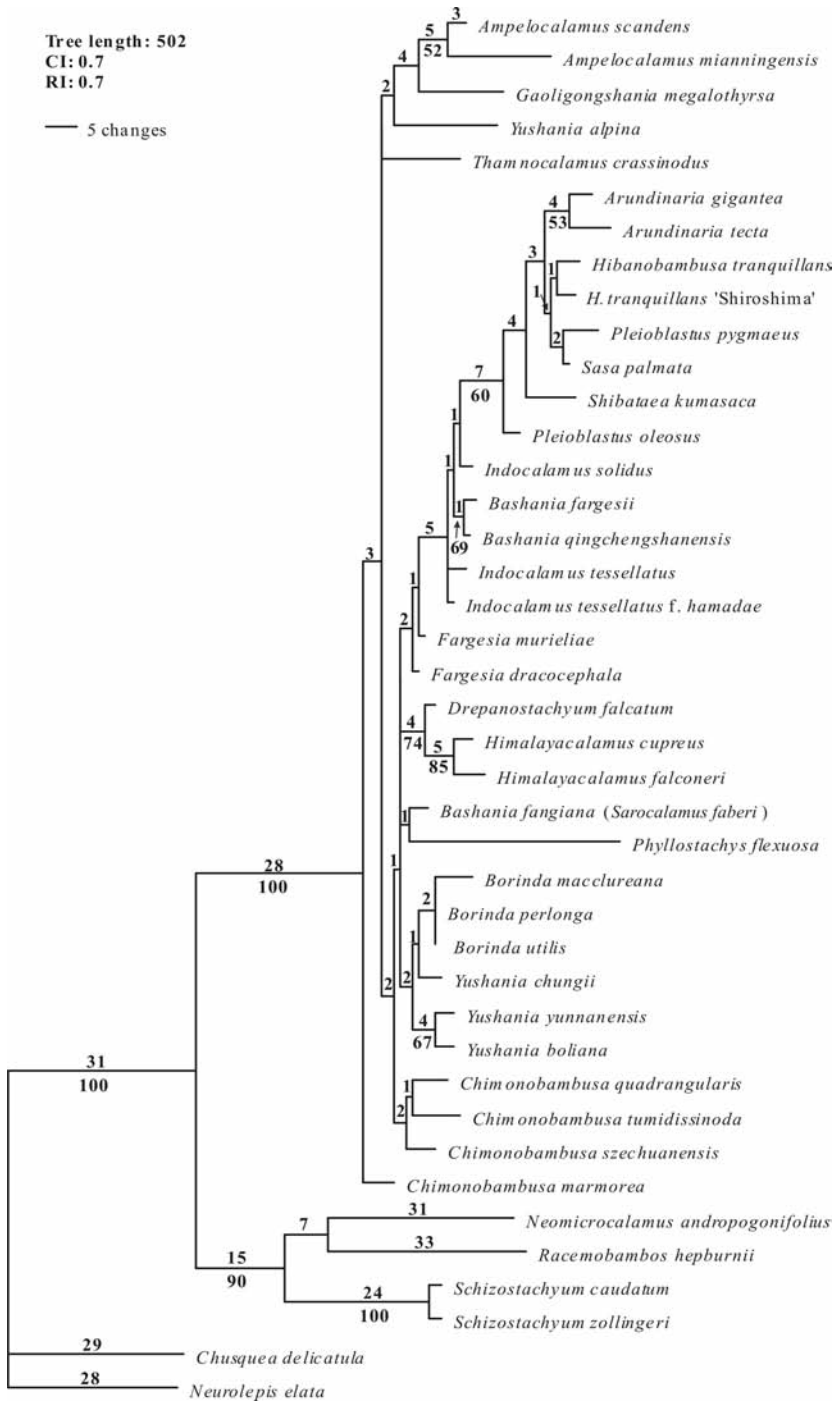


Figure 3. One of 100 equally parsimonious trees obtained following comparative sequence analysis of the combined *trnL-trnF*-ITS datasets (Ní Chonghaile, 1st draft thesis, 2002).

Numbers above branches are branch lengths, numbers below are bootstrap support values.

The mixture of bracteate and ebracteate inflorescences seen in the temperate clade would remain problematic, but there are possible homologies (Stapleton 1997) that would allow a much closer relationship than the two complex evolutionary processes previously envisaged by either Holttum (1958) or Clayton & Renvoize (1986). Direct homology between prophylls in the bracteate inflorescence and lower glumes in the supposedly ebracteate inflorescence would be a much simpler explanation, and this would conform more closely with the molecular data. Apparent loss of bracts would then be explained instead by elongation of the axes on which they are borne, as has been described and illustrated elsewhere (Stapleton 1997).

Thus the two supertribes and the broad syndromes of semelauctant and iterauctant inflorescences, applied in the Chinese language Flora of China bamboo account (Keng & Wang 1996), are difficult to justify in the light of recent molecular evidence, as are the evolutionary mechanisms (Holttum 1958; Clayton & Renvoize 1986) proposed to explain them.

3. Recognition of subtribes

As well as supertribes, some of the more inclusive interpretations of subtribes have also now been shown to be too broadly circumscribed to represent natural lineages. *Bambusinae* J. Presl, as interpreted by Clayton & Renvoize (1986) included the S American genus *Guadua* as well as Asian tropical genera, and it is clearly paraphyletic (Zhang 1996). So is *Arundinariinae* Benth., as interpreted by Clayton & Renvoize (1986), as it included in addition to part of the temperate Asian & N American clade, several S American genera, now placed in separate subtribes, as well as some Old World tropical genera, none of which are closely related (Zhang 1996; Kobayashi 1997). Similarly, Keng & Wang (1996) placed *Chimonocalamus* and *Drepanostachyum* in the group *Chusqueae*, a group recognized at tribal level although probably more appropriate as a subtribe. This group included the S American genus *Chusquea*, making it paraphyletic according to molecular evidence. Thus any superficial similarity in ramification of a multitude of

small branches would seem from the molecular data to be entirely homoplasious.

The phylogeny inferred from one fairly comprehensive molecular data set (Ni Chonghaile 2002) would support the recognition of 3 Asian subtribes (Fig. 1). Only one temperate subtribe, *Arundinariinae* Benth. is supported. Within that subtribe sequence data provides little information on further divisions or the primitive versus derived nature of character states. The three genera with 6 stamens, *Sasa*, *Acidosasa* and *Hibanobambusa*, are well nested within the temperate clade but not strongly associated. The same can be said for those with bracteate inflorescences: *Phyllostachys*, *Chimonobambusa*, *Hibanobambusa*, and *Shibataea*. Nevertheless, this suggests that they have retained or regained these character states independently and should not be combined on the basis of these characters alone. Thus there is no molecular evidence for the existence of separate lineages represented by subtribes *Sasinae* and *Shibataeinae*.

In addition, there is only evidence for two paleotropical subtribes, *Bambusinae* Benth. and *Melocanninae* Benth. Molecular evidence does not support the existence of a single, separate lineage for the 3 genera of tropical 6-stamened Asian bamboos with more derived character states in the inflorescence, once united under the general term semelauctant. On those grounds it would appear that it was probably not necessary to describe subtribe *Racemobambosinae* (Stapleton 1994c) to accommodate such a group. Two genera placed in this subtribe, *Racemobambos* and *Neomicrocalamus*, are now suspected from ITS data (Ni Chonghaile 2002) to be only distantly related. However, the long branches on which both these genera are placed in the ITS analysis (Fig. 3) has suggested that neither of them are closely related to the core *Bambusinae*, although that was considered to be the best subtribe in which to place them for the Flora of China English version.

4. Relative diversity of the subtribes: possible implications for biogeography

Molecular investigations that have sequenced genes from tropical and temperate

bamboo subtribes have all revealed similar patterns of relative sequence divergence between the clades (Xia 1994; Zhang 1996; Ni Chonghaile 2002). Variation between sequences has been greater in the paleotropical bamboos than in the temperate clade (Fig. 1). It is noteworthy that while paleotropical bamboo species that are difficult to distinguish morphologically have often revealed significant sequence divergence, many molecular investigations have failed to separate temperate bamboos that demonstrate relatively larger differences in morphology, including different forms of rhizome and inflorescence. While cladistic analysis of morphological characters (Zhang 1996) has shown similar levels of resolution in tropical and temperate bamboos, analysis of sequences from the temperate clade has failed to resolve a clear topology, with only weak support for most of the internal branches and a polytomic structure in consensus trees.

A similar polytomic topology has been produced from analysis of sequences from the Andean representatives of *Chusquea* (Kelchner & Clark 1997; Clark 2001), with little resolution and a high number of autapomorphies. It was suggested that such a topology, along with intergradation of morphological characters, is the result of rapid and relatively recent diversification.

There is some support for the contention that the temperate clade polytomy is also the result of such recent diversification, based on the high degree of ITS sequence heterogeneity (Ni Chonghaile 2002). Failure to homogenise the sequence types could be attributable to an insufficient number of generations, arising from more recent arrival of temperate bamboos in Asia, relative to tropical species.

Distribution of woody bamboos is strongly influenced by their reproductive biology. Any consideration of time scales for diversification in bamboos has to take into account their relatively long generation times. Because temperate bamboos have especially long flowering cycles of up to 150 years, in terms of number of generations, a 'relatively recent' diversification can have occurred up to 100 times as long ago as one for annually flowering plants, or up to 10 times as long ago as one for most tropical

bamboos, which have shorter life cycles. Effects of infrequent flowering are compounded by scarcity of dispersal mechanisms in bamboos. Bamboo lemmas are usually only shortly mucronate, without a well developed awn, and usually either glabrous or shortly scabrous. This reduces the chances of animal dispersal by attachment to fur or feathers. The caryopsis is simple, relatively large and heavy, so that wind dispersal is also unlikely. Moreover, seed viability is low, requiring prompt germination, and the exacting habitat requirements of bamboos make them poor pioneer species. The clear phylogenetic separation between most bamboos on different continents demonstrates their poor ability to effect long distance dispersal. The success of introduced bamboos in Europe and N America also suggests that natural dispersal has been problematic in the past. It would seem likely that historical causes of disjunct biogeographic distributions are probably of great importance in the woody bamboos, as they are in many other groups of plants (Raven & Axelrod 1974).

If the disparity in sequence divergence is attributable to more recent diversification in the temperate clade than in the paleotropical bamboos, then an explanation for this can be sought in the biogeographical history of the woody bamboos, but this is an area that has received little study.

Soreng & Davis (1998) reported that the earliest grass macrofossils known indicate a date in the Tertiary for the evolution of the first grasses, with the earliest published record dating from the Palaeocene, according to Linder & Barker (2000). Attempts to date the divergence of clades within the Poaceae using molecular clock approaches calibrated with fossil records (Salamin 2002) have produced more recent dates. These conclusions may only indicate that the oldest fossils still do not represent the first appearance of the taxa concerned. The molecular evidence, by showing such a clear disjunction between bamboo populations in S America and those of the rest of the world (Fig 1.), would seem to suggest that if long-distance dispersal is ruled out, primitive bambusoid grasses ancestral to both

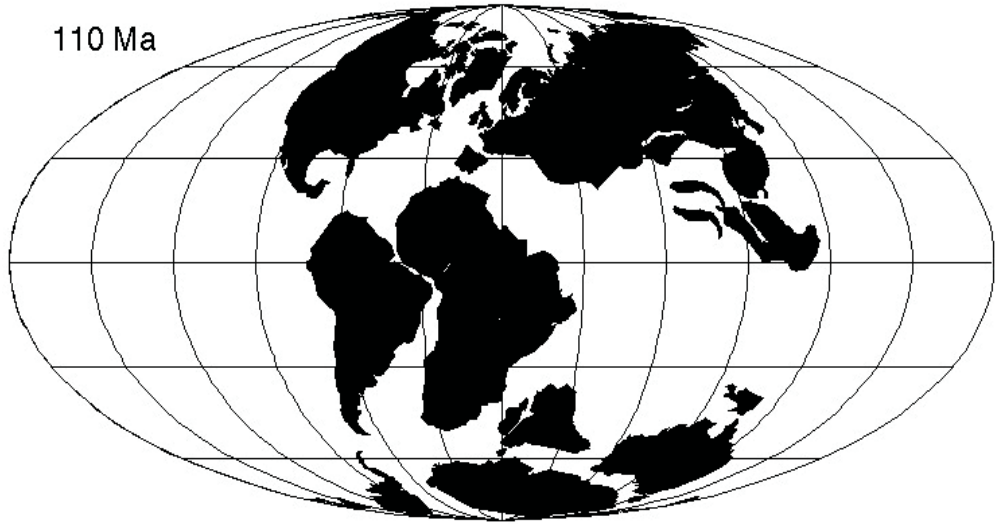


Figure 4. Positions of present-day continents at the time of break-up of Gondwanaland (precursors of present day S America, Africa, Madagascar, India, Antarctica, and Australia) in the Cretaceous Period. Bamboos of S America are very distinct from those of Africa and Asia. From the Paleogeographic Atlas Project, University of Chicago. <http://www.geo.arizona.edu/~rees/global290-0pgeogrev.mov>

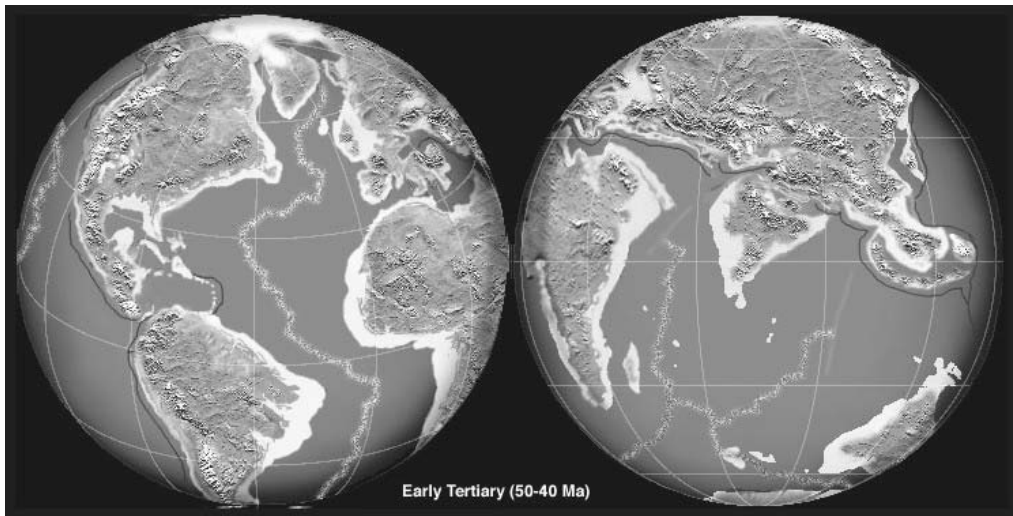


Figure 5. Positions of India and the Arabian Peninsular of the African continental block, as they approached the Eurasian plate around 40 M yrs ago. From Department of Geology, Northern Arizona University. <http://jan.ucc.nau.edu/~rcb7/globaltext.html>

Asian and S American bamboos existed prior to, or shortly after, the break-up of Gondwanaland (Fig. 4). That was substantially earlier, in the order of c.125-100 million years ago (mya). Recent investigations (Bouchenak-Khelladi *et al.*, in press) are supporting later dates, around 50 mya, for diversification in the BEP clade. Nevertheless, whether bamboos evolved in Cretaceous or Tertiary times, many tropical bamboos from Asia and S America would have enjoyed a relatively long period in which to diversify and stabilize into genetically distinguishable genera.

However, whether early bamboo ancestors originated either in Gondwanaland or later in Africa, temperate bamboos of N Asia are most likely to have only reached Asia after the arrival and collision of either Africa or India with the Eurasian plate (Fig. 5). Both those continents could theoretically have sustained populations of early temperate bamboo ancestors, both having mountain refuges in which they could feasibly have passed through the tropics. Both have extant temperate bamboos, and both collided with the Asian plate from the Eocene onwards, beginning about 45 million years ago. Thus either Africa/Arabia or India may have provided Asia with early temperate bamboos as a result of this geologically driven biotic interchange. This could only have occurred after the eventual establishment of land routes across the seas of the Tethys Ocean as Alpine and Himalayan orogenic activity strengthened, 20 mya or later, as Africa and India continued to move slowly northwards. Global cooling and consequent drying of the Mediterranean/Tethys Seas might have aided the delay or channelling of this dispersal process towards N Asia. Such a relatively recent biotic interchange and sudden rapid dispersal could explain the lack of genetic variation in the temperate clade. It would seem possible that for much of the Tertiary Period, ancestors of the N Asian temperate bamboos were isolated on African or Indian mountains travelling northwards through the tropics. This period could have provided the isolation suggested by the strong support for monophyly of the temperate clade. Following this isolation, eventual

dispersal into Eurasia from Africa or India could have suddenly provided a wealth of subtropical to temperate montane habitats and large areas of lower boreal temperate land to the north and east for colonisation and rapid diversification.

One alternative scenario is evolution and diversification of temperate bamboos in China, with dispersal west into N America and south into India and Africa. For that to be the case, temperate bamboos would have to have been present in Laurasia at a much earlier time. The presence of temperate N American bamboo species would potentially suggest that these are Laurasian remnants, as is the case in many other Angiosperms. However, that would have required an earlier evolution of temperate bamboos, and early crossing of the North Atlantic Land Bridge from Europe to N America. The polytomy in Asian temperate bamboos with poor resolution and a high degree of ITS sequence heterogeneity would suggest a much more recent diversification instead, most likely due to more recent biotic interchange. Moreover, the molecular evidence (Stapleton *et al.* 2004) suggests that the closest Asian relative of the N American bamboos is *Pseudosasa japonica* from Japan, rather than the morphologically closer species of *Sarocalamus* from the western, Himalayan, end of the range of Asian temperate bamboos. This suggests later dispersal along the NE coast of Asia and across the Bering Land Bridge into N America instead. Another problem with a Laurasian origin for temperate bamboos is the apparent presence of temperate species in Madagascar, which became isolated before the collision of India and African plates with Asia. While many plants and animals could disperse from Africa across the Mozambique Channel, this appears less likely for temperate bamboos.

Key innovations allowing temperate opportunities to be exploited to the full could have included tessellated, frost-hardy leaves, and more open inflorescences with a lower ratio of anthers to ovaries, making them more efficient on a windy mountain instead of a tropical forest environment. Long rhizomes of different form could have aided dispersal into the new

habitats. In addition development of denser, more productive branch complements in bamboos susceptible to browsing may have paralleled the evolution of mammalian herbivores, rosette plants and tillering grasses.

Thus the vicariance events associated with the break-up of Gondwanaland, and the sudden dispersal following biotic interchange after its constituent parts collided with Asia could explain the molecular topologies in the woody bamboos. Successful adaptation to temperate conditions could have been another driving force. Simultaneous cooling of global climates could have been a further, complementary factor, resulting in the great diversity of temperate Chinese bamboos seen today. Based on these observations and hypotheses, it seemed that the Flora of China should not claim that bamboos evolved within China. Further analysis of Gondwanan elements of the temperate clade, assessing relationships between those of Africa, Madagascar and S India/Sri Lanka with those of E Asia, may reveal more evidence to clarify where temperate bamboo ancestors first evolved.

5. Diversity and recognition of genera within the subtribes

5.1 BAMBUSINAE

Within the Bambusinae there was inadequate sampling for any detailed assessment of genera for the Flora of China. Surprising molecular results came from plastid data (Ní Chonghaile 2002), with isolated inferred positions for *Bambusa oldhamii* from analysis of *rpl16* sequences, and *Dendrocalamus giganteus* from *trnL-trnF* sequences. Both species have been placed in the infrequently recognised genus *Sinocalamus*, which has morphological characteristics intermediate between those of *Bambusa* and *Dendrocalamus*. *Sinocalamus* is not generally recognized, as it cannot be distinguished readily on morphological grounds. The distinction between *Bambusa* and *Dendrocalamus* is itself problematic, although there is early indication from molecular data (Fig.1) that *Bambusa* species can be separated. Loh *et al.* (2000) also found *D. giganteus* to resolve away from *D. brandisii* in their AFLP study.

Caution should be taken in drawing conclusions about relationships within this group, however, until a broader range of species has been studied, including representatives of the four genera *Sinocalamus*, *Neosinocalamus*, *Dendrocalamopsis* and *Sellulocalamus*. Keng & Wang (1996) in FRPS recognized three of these four morphologically intermediate genera, while Li (1997) recognized none, and there was insufficient molecular data to influence decisions for the Flora of China (Li *et al.* 2006).

The semi-scandent bamboos within this subtribe have caused considerable taxonomic difficulties in the past. Along with advanced branch structures and other adaptations to assist climbing and branch proliferation within a tree canopy, there has often been modification of the inflorescence and the interpretation of floral morphology has been problematic.

Within *Bambusinae* two such genera with relatively derived partially ebracteate, budless inflorescences are *Racemobambos* from SE Asia, and *Neomicrocalamus* from the E Himalayas and SW China.

Gamble (1890) described *Microcalamus prainii* as a monotypic genus with bracteate panicles of 6-stamened, distant spikelets, initially described as having peduncles (l.c.), later corrected to pedicels (Gamble 1896). Oliver (1891) pointed out the illegitimacy of the name, meanwhile misidentifying it completely as *Sasa kurilensis*. Keng (1983) re-described Gamble's invalid genus as *Neomicrocalamus*, considering it to be related to *Ampelocalamus*, another semi-scandent genus, but with 3 stamens. Holttum (1958) had earlier described *Racemobambos* with bracteate racemes of spikelets borne on short stalks, which to him suggested some similarity to *Arundinaria*. Thus in both these genera the presence of pedicellate spikelets drew attention to a similarity to genera such as *Arundinaria*, *Ampelocalamus* and *Sasa*, unusual in a bracteate inflorescence with 6 stamens. This similarity caused the author of *Neomicrocalamus* to decide to combine both genera as *Racemobambos* (in Wen 1986), a decision followed by Chao & Renvoize (1989), although *Neomicrocalamus* was later resurrected for FRPS (Keng & Wang 1996).

Nowhere is the confusion caused by the two syndromes termed iterauctant and semelauctant more apparent than in the various interpretations of the inflorescences of these two genera. Much of the discussion about whether to recognize one or two genera centred around which, if either, were semelauctant. McClure (1966) described the inflorescence of *Neomicrocalamus prainii* as iterauctant on the basis of the alleged presence of buds in glume axils. Chao & Renvoize (1989) described it as iterauctant on the basis of small bracts subtending the spikelets. Dransfield (1992) objected to this, and decided that it was the presence of prophylls that made it iterauctant, pointing out that they were absent in *Racemobambos*. Stapleton (1994c) decided that the prophyll was present in both genera, but inserted at a different point, suggestive of an intermediate evolutionary position between other bracteate inflorescences and the ebracteate semelauctant inflorescences of the temperate bamboos, with the prophyll inserted away from the point of branching on an extended promontory, to form a 'pedicel'. Li (1997) considered once more that the presence of bracts was most critical, and lumped the genera on the grounds that they are both iterauctant.

In conclusion, from the floral morphology there are two genera, both with bracteate, budless, inflorescences with shortly stalked spikelets, with the prophyll below the 'pedicel' in *Neomicrocalamus* and above it (as the lower glume) in *Racemobambos*. Further vegetative distinctions from a detailed analysis of branch structure in these 2 genera (Stapleton 1991) support this distinction.

The topology arising from molecular data (Fig. 3) would suggest strongly that the two genera are not closely related. They probably represent independent evolution of semi-scandent habit and more derived inflorescence forms within the subtribe *Bambusinae*, and on the basis of this molecular data *Racemobambos* and *Neomicrocalamus* should clearly be treated as separate genera. As other genera of semi-scandent bamboo have also been described, and further taxa await description, it is clear that such genera should not automatically be combined on the basis of this morphological similarity.

5.2 MELOCANNINAE

Subtribe *Melocanninae* is conventionally distinguished by long tapering ovary appendages instead of the shorter ovary of *Bambusa*, as described by Holttum (1958). The position of *Thyrsostachys* in topologies inferred from some molecular data is inconsistent with this morphological character (Fig. 1). Holttum (1958) attributed it with having 'the same type of ovary as *Bambusa*', but it would be included in the subtribe *Melocanninae* on the basis of evidence from molecular phylogeny. It is not basal to the subtribe. Closer inspection of the character state in this taxon is indicated.

Cephalostachyum has only been represented by one species (*C. pergracile*) in molecular studies. Xia (1994) found that it resolved unambiguously in *Bambusinae* rather than *Melocanninae*, while Zhang (1996) and Kobayashi (1997) found that it was grouped with *Melocanna* and *Dendrocalamus asper* respectively, although *Melocanninae* was not well resolved in either study.

Analysis of floral morphology was undertaken in a very preliminary fashion by Holttum (1958), who proposed the merger of several genera. Following Holttum (1958), *Cephalostachyum*, *Pseudostachyum* and *Teinostachyum* have often been reduced to synonyms of *Schizostachyum*, despite the lack of any more detailed morphological investigations (Chao & Renvoize 1986; Majumdar 1989; Tewari 1993). However, others have maintained them as separate genera (Zhang 1992; Stapleton 1994a; Keng & Wang 1996; Stapleton et al 1997; Li 1997), on the basis of inflorescence and rhizome form.

Thus there is a degree of uncertainty about the separation and boundaries of this subtribe from molecular and morphological evidence. As a strong morphological distinction has been applied, it will continue to be used to define the subtribe, pending further study of incongruence between morphological and molecular data. Given the satisfactory separation of *Schizostachyum* from other genera using *trnL-trnF* sequence data (Fig. 1), separate genera were recognized in the Flora of China.

5.3 ARUNDINARIINAE

5.3.1 Introduction

In molecular studies to date, sequencing of plastid or nuclear DNA regions in the temperate clade has produced polytomic results from which little reliable phylogenetic resolution can be inferred (Xia 1994; Zhang 1996; Ní Chonghaile 2002). From the data available it would seem that evolution proceeded rapidly and left little evidence of the order of events. This makes it difficult to recognize synapomorphic groups or to relate these to morphological characters in a conventional manner. It also makes it difficult to determine generic boundaries, or to make comparative judgements of the appropriate sizes for genera.

One question that arises from the molecular topology (Fig. 1) is whether the temperate bamboos are simply 'over-taxonomised', and whether the polytomy is the result of intensive sampling, suggesting that the number of taxa has become too large. If this were the case then it should be possible to group the taxa into fewer, larger natural units, representing lineages supported by shared, derived characters. This does not seem to be the case, however. With so little structure resolved it is not possible to justify any lumping of genera on molecular grounds, unless the entire temperate clade were to be united in one genus, *Arundinaria*. It could be argued that even *Phyllostachys* should not be recognized, as that would render *Arundinaria* paraphyletic. Where internal branches receive weak bootstrap support, for example the clade *Arundinaria*, *Pleioblastus*, *Hibanobambusa*, *Sasa*, and *Shibataea* which has 60% support (Fig. 3), there is little correlation with morphological characters, as this group includes taxa with ebracteate and bracteate inflorescences as well as those with 3 and 6 stamens.

Attempts to recognize large genera within the temperate bamboos (Chao *et al.* 1980; Clayton & Renvoize 1986; Chao & Renvoize 1989; Li 1997) on a morphological, largely floral basis have generally fallen foul of parallel evolution, as witnessed by even this limited molecular data. Although fewer, larger genera have often been recognized in the grasses with the implicit intention of simplifying iden-

tification (Barkworth 2000), in the case of infrequently flowering bamboos this would be counterproductive. The limited molecular evidence would indicate that bamboo genera including *Arundinaria*, *Sinarundinaria*, and *Thamnocalamus* when interpreted broadly in the past formed artificial groups and did not represent natural lineages.

In non-bamboo grasses, a similar situation exists. Larger genera have often been proven polyphyletic from molecular data. Broad interpretations of genera such as *Bouteloua*, *Sporobolus*, *Sorghum*, *Eragrostis* and *Chloris* have now been shown to be paraphyletic or polyphyletic from molecular evidence (Columbus *et al.* 2000; Ortis-Diaz & Culham 2000; Spangler 2000; Hilu & Alice 2000). Similarly, poor resolution of a molecular topology is not confined to bamboos. The *Rytidosperma* clade of the temperate grass tribe *Danthonieae*, includes species from up to 8 genera that form an unresolved polytomy (Barker *et al.* 2000), explained by recent divergence (Linder & Barker 2000). Other, smaller groups of grass genera have also failed to resolve well in molecular investigations (Gómez-Martínez & Culham 2000; Columbus *et al.* 2000).

As with other grasses, many temperate bamboo genera with reasonable morphological distinctions have not been resolved by molecular data. Current opinions on the grounds for recognizing taxa differ, and the criterion of molecular monophyly is by no means the only one finding favour in plant systematics. If generation times have not been sufficient for concerted evolution to take effect, as suggested by the ITS sequence heterogeneity present in the temperate clade (Ní Chonghaile 2002), then we would also expect a large number of apparently paraphyletic groupings to persist. This would be consistent with colonisation of new habitats, in which competition is scarce and extinction levels are low. These considerations should be taken into account as extenuating circumstances before non-monophyletic temperate clade genera are relegated to the trashcan. A morphologically based classification for the temperate clade would appear to be

the only available option at the present time, with the limited information from molecular data being used primarily as an indicator of homoplasy. Any revision of the classification on the basis of a strict interpretation of the molecular phylogeny would be so out of step with the current classification as to be entirely unacceptable.

5.3.2 Evidence from plastid data

Plastid data has not resolved a topology of any consistency within the subtribe *Arundinariinae*, which is here interpreted as the entire temperate Asian, African & N American clade. Branch lengths have been short and not well supported. The only taxon to show a reasonable number of autapomorphic characters in *trnL-trnF* sequence data (Ní Chonghaile 2002) was the subtropical Central African species, *Yushania alpina*, which resolved on the longest branch, with 8 steps. This bamboo can be separated from other members of the temperate clade by a suite of morphological characters, including frequently dominant lateral rather than central branches. Morphologically, it differs very clearly from *Arundinaria*, in which it was first described, and less clearly from temperate Asian members of *Yushania*, the only other genus in which it has been placed. The other African 3-stamened species in the temperate clade, *Thamnocalamus tessellatus*, was transferred from the tropical 6-stamened genus *Nastus*, and remained in *Arundinaria* until Soderstrom & Ellis (1982) transferred it to *Thamnocalamus* on the basis of similarities in leaf anatomy to the Himalayan type species of the genus, *T. spathiflorus*. Soderstrom & Ellis later stated (1988b) that leaf anatomy alone was of no use in recognizing either species or genera of the *Arundinariinae*. While the *trnL-trnF* sequence data does not separate *T. tessellatus* as well as *Yushania alpina*, the data shows substantial difference between *T. tessellatus* and *T. spathiflorus*. Therefore from the plastid data it would appear that neither of the African species, *Yushania alpina* and *Thamnocalamus tessellatus* are closely related to the other, Asian species in the genera in which they are usually placed.

One interesting result from the *trnL-trnF* sequence data is an apparent association between *Oligostachyum oedogonatum* and *Pleioblastus oleosus*. The latter is a species that has been placed with little confidence in both *Pleioblastus* and *Arundinaria*, and which has distinctive branching close to that of *Oligostachyum oedogonatum*.

The native N American temperate species *A. gigantea*, type species of *Arundinaria*, was shown by *rpl16* data (Ní Chonghaile 2002) to be closer to *Pseudosasa japonica* than any other Asian bamboo (BS 90%), a result supported by *ndhF* data (Zhang 1996). While nearly all Asian taxonomists have recognized the genera *Pseudosasa* and *Indocalamus* on the basis of their restricted branching, many authors (Chao & Chu 1981; Clayton & Renvoize 1986; Chao & Renvoize 1989; Zhang 1992; Li 1997) have sought to unite *A. gigantea* with similar genera from Asia including *Pleioblastus* and *Bashania*. However, if such genera are less closely related to *A. gigantea* than *Pseudosasa*, as the molecular evidence appears to suggest, then either they should all be combined, or they should all be kept separate.

5.3.3 Evidence from nuclear and combined plastid/nuclear data

To date, ITS sequence data has provided better resolution of relationships within the subtribe than plastid data (Fig. 2). ITS and combined ITS & *trnL-trnF* datasets provide slightly better evidence to substantiate the distinction of several genera on morphological grounds (Fig 3).

PACHYMORPH-RHIZOMED BAMBOOS

Within *Arundinariinae* the three genera *Ampelocalamus*, *Drepanostachyum*, and *Himalayacalamus* represent the pachymorph-rhizomed bamboos that have a predominantly subtropical distribution.

Ampelocalamus was considered (Clayton & Renvoize 1986; Chao & Renvoize 1989) part of *Sinarundinaria*, along with *Drepanostachyum*, but is well distinguished from the other two genera by its vegetative branching and inflorescence characters. This distinction is

supported by the molecular topology. Within *Ampelocalamus* there would appear to be substantial genetic variation. *A. mianningensis* was transferred from *Dendrocalamus* on the basis of its similarities to *A. patellaris* and *A. scandens* (Li & Stapleton 1996). These would seem to be closer relatives than any other bamboos sampled, but still not particularly close.

Himalayacalamus was traditionally considered part of *Thamnocalamus* (Munro 1868; Clayton & Renvoize 1986; Chao & Renvoize 1989), because of its tightly tufted compressed racemose inflorescences. *Drepanostachyum* was placed in *Arundinaria* (Munro 1868; Gamble 1896) or *Sinarundinaria* (Clayton & Renvoize 1986; Chao & Renvoize 1989), because it has open panicles, often in broadly sweeping falcate form, hence its name *Drepanostachyum* (drepanon in Greek and falcis in Latin mean sickle). Keng (1982) realised a similarity between *Drepanostachyum* and *Himalayacalamus* in their multitude of branches. Stapleton (1994c) pointed out other similarities in fasciculation of inflorescence branches and delicate glumes. *Himalayacalamus* has even been considered synonymous with *Drepanostachyum* (Demoly 1996; Li 1997), but differs in a range of floral and vegetative characters, and their species have remained in separate genera in floral accounts (Stapleton 1994c, Seethalakshmi 1998; Stapleton 2000). The latter approach is supported by the molecular evidence, especially ITS data (Ní Chonghaile 2002), in which *Himalayacalamus* received 84% BS in the parsimony analysis and 90% in the neighbor joining analysis.

A more temperate distribution is generally the case for the four genera *Thamnocalamus*, *Fargesia*, *Yushania* and *Borinda*.

The strong distinction in vegetative prophylls and branching between *Thamnocalamus* and the other three genera (Stapleton 1994b) is reflected in the well-supported separation of *Thamnocalamus* in both plastid and nuclear data (Guo *et al.* 2001; Guo *et al.* 2002; Ní Chonghaile 2002). Thus there is relatively strong molecular evidence for recognizing *Fargesia*, instead of the common practice of

including it in *Thamnocalamus* (Clayton & Renvoize 1986; Chao & Renvoize 1989; Demoly 1996; Li 1997).

There is also some weak molecular evidence to distinguish between the core *Fargesia* species, which share compressed inflorescences, and species of *Yushania* and *Borinda*, with open inflorescences. However, as is often the case with bamboos, the strength of the bootstrap support is reduced as the core group is expanded, and these three genera, all with very similar branching, tend to merge into a clade with less distinguishable groupings. They were not well distinguished in ITS or combined ITS & GBSSI analyses (Guo *et al.* 2001; Guo *et al.* 2002; Guo & Li 2004).

The genus *Borinda* is included in *Fargesia* by Yi (1997), in *Yushania* (as *Sinarundinaria*) by Li (1997), or maintained as a separate genus by Wang (1997). Most species were originally described in *Fargesia*, but molecular evidence (Ní Chonghaile 2002) gives support for their separation from the core species of that genus. When *Borinda* was published (Stapleton 1994b) it was pointed out that the inflorescences were similar to those of *Yushania*. The species were not transferred to *Yushania*, as there was a possibility that the similarity in inflorescences was homoplasious (Stapleton 1998), and because *Yushania* has usually been interpreted as a genus of spreading bamboos with long, running rhizomes (Takenouchi 1931; Keng 1957; Wang & Ye 1981; Chen & Chia 1988; Song & Wang 1994) while species placed in *Borinda* are all clump-forming with short rhizomes. This distinction will have to remain the morphological criterion for generic placement of non-flowering species for the time being, along with finely grooved culms in *Borinda*. As no groups had substantial bootstrap support in any DNA sequencing analysis, any similarities in their inflorescences are presumably not homoplasious. It would appear that these species are all closely related, and that fingerprinting techniques would be appropriate to investigate their phylogeny in more detail.

Molecular data is useful in suggesting affinities of species in this group, and should

be of predictive value for clump-forming species originally described in *Fargesia* for which inflorescences remain unknown. For example, the data supports the transferral of *Fargesia utilis* into *Borinda*. It resolved closer to other species of *Borinda*, which have open inflorescences, than to the species of *Fargesia* that, like the type species *F. spathacea*, are known to have compressed inflorescences (*F. nitida*, *F. murielae*, and *F. dracocephala*). It seems very likely that there are very many more species described without flowers in *Fargesia* that belong instead in *Borinda*. To avoid placement of the species of *Borinda* in two different genera in the Flora of China, it was decided to keep *Borinda* as a synonym of *Fargesia* for the time being.

Gaoligongshania, a distinctive monotypic genus, is well distinguished by both molecular and morphological evidence. Molecular evidence (Ni Chonghaile 2002; Guo & Li 2004) has not revealed any particular affinity to either *Indocalamus* or *Yushania*, to which Li (1997) suggested it might be related, nor to any other taxon within the temperate clade.

LEPTOMORPH-RHIZOMED BAMBOOS

The strongest support for any group in the temperate clade is given to *Phyllostachys* in the ITS data (Fig 2). The strength of support for this clearly monophyletic group is surprising, as it was not resolved at all from plastid data, and it would suggest that *Phyllostachys* has been separated from the rest of the subtribe for a more substantial period of time. *Phyllostachys* would appear to be similarly distant from all other temperate genera sampled. Only one species, *Bashania fangiana* (*Sarocalamus faberi*), has been suggested as a close living relative of *Phyllostachys*, based on moderate bootstrap support from a neighbour joining analysis of combined plastid and nuclear sequence data (Ni Chonghaile 2002). One character that is shared between *Phyllostachys* and *Bashania fangiana* (*Sarocalamus faberi*) is reduced compression of basal branch internodes. As this compression is almost universal in woody bamboos, its loss would be a synapomorphy for a clade uniting *Phyllostachys* and *Sarocalamus*.

Among the other temperate bamboos with leptomorph rhizomes, it is not possible to resolve a detailed topology from the molecular data. Nevertheless, as with the pachymorph-rhizomed bamboos it is possible to hypothesise some relationships. On morphological grounds it might be considered justifiable to include some or all of the genera *Pleioblastus*, *Oligostachyum*, *Bashania* or *Pseudosasa* within *Arundinaria*. However, the molecular evidence suggests that this would constitute a paraphyletic group and would not be appropriate unless all these genera were included together, in addition to several other genera such as *Indocalamus*, *Hibanobambusa*, *Sasa*, and *Shibataea*, which differ much more substantially in their morphology, and are almost universally recognized.

One genus that is often still synonymised within *Arundinaria* is *Pleioblastus*. Stapleton (1997) pointed out that *Pleioblastus* differs in prophyll structure, with the prophyll forming a fused budscale, as seen in *Sasa*, *Pseudosasa* and *Indocalamus*. The molecular evidence would not suggest that *Pleioblastus* is more strongly related to *Arundinaria* than is other Asian genus. Within *Pleioblastus* there is considerable difference in stature, and different genera have been described, although they are no longer recognized. The species of smaller stature were included in the 6-stamened genus *Sasa* in FRPS (Keng & Wang 1996), while *Pleioblastus* was recognized for the larger species.

Among Asian species, the two species that are considered to be morphologically closest to the N American type species of *Arundinaria* are *Arundinaria racemosa* from the E Himalayas, and its close relative from SW China widely known as *Bashania fangiana*. Molecular data would not suggest that they are more closely related to *Arundinaria* than any other Asian bamboos. *Bashania fangiana* has been placed in *Bashania* or *Gelidocalamus*, from which it differs appreciably. While the molecular data (Fig. 2) suggests a close relationship for *Bashania fargesii* and *B. qingchengshanensis*, there is no evidence that *Bashania fangiana*, which has simpler branching, is closely related

to these two species. If all other Asian genera are to be maintained separate from *Arundinaria*, then it would appear that on the basis of molecular data there is no justification for continuing to place species such as these in *Arundinaria* for the Flora of China. There is supporting evidence for this from the geographic disjunction, as among leptomorph bamboos, these species are geographically furthest from the N American species of *Arundinaria*. Although *Bashania fangiana* and *Arundinaria racemosa* are morphologically very close to *Arundinaria* it seemed more appropriate to maintain *Arundinaria* as an endemic N American genus, and a new genus, *Sarocalamus* was described (Stapleton *et al.* 2004) for *Bashania fangiana* (as *Sarocalamus faberi*), *Arundinaria racemosa*, and another Chinese species, although this genus was not actually recognized in the Flora of China (Li *et al.* 2006).

Chimonobambusa is a genus that has been separated into three Sections, sometimes elevated to generic rank by some authors to give three genera *Chimonobambusa*, *Oreocalamus* and *Qiongzhueta*. The type species *C. marmorea* differs markedly from the other species in loss of vegetative branch prophylls, and this was reflected in the molecular data to a certain extent (Ni Chonghaile 2002), but the other species are difficult to separate into consistent groups. Molecular analysis (Ni Chonghaile 2002) did not distinguish the two species with quadrangular culms and thorns (*Oreocalamus*) from the species with most markedly swollen nodes (*Qiongzhueta*). It would appear that as with genera such as *Yushania* and *Borinda*; *Drepanostachyum* and *Himalayacalamus*; and *Sasa* and *Sasamorphia*, the three genera *Chimonobambusa*, *Oreocalamus* and *Qiongzhueta* are closely related. Deciding whether such genera should be recognized would require better molecular data, possibly using a technique more appropriate for closely related species, such as AFLPs (Hodkinson *et al.* 2000), a broader range of species, and a thorough morphological analysis. However, based on the phylogeny inferred from molecular results, there is currently no evidence to

suggest that either grouping these genera together or separating them would better reflect natural lineages.

To summarize, DNA sequence data allowed the basic outline of woody bamboo phylogeny to be inferred as the basis of the Flora of China account (Li *et al.* 2006). Conflicting morpho-geographical classifications had previously been applied, giving different emphasis to vegetative or floral characters, and making assumptions about the homology and development paths of certain structures. Molecular data has revealed the unreliability of many such assumptions, and shown that inflorescence form should not be given priority over vegetative structures. DNA sequence data was not capable of revealing precise phylogenetic relationships between morphologically similar genera in the temperate clade. Explanations for this, linked to a potential bio-geographical history for this group, can be hypothesised and they may also help to explain the great diversity of Chinese bamboos. For tropical bamboos, insufficient taxa had been sampled for a comprehensive analysis, but enough indicators of likely relationships could still be inferred for the basic framework of a classification. Further molecular investigations have been undertaken since the publication of the Flora of China (Li *et al.* 2006), and yet more are currently underway. These will be reviewed at a later date.

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