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Taxonomic interpretations of Australian native bamboos (Poaceae: Bambuseae) and their biogeographic implications

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Abstract

Australia's three native bamboo species – *Bambusa arnhemica*, *Mullerochloa moreheadiana* and *Neololeba atra* – are restricted to northern Australia. The most parsimonious explanation for the occurrence of bamboo in Australia is that there have been at least three founder events from Asia, but other possibilities exist including an Australian radiation involving *Neololeba* and *Mullerochloa*. *Bambusa arnhemica* may be allied to the Asian *B. blumeana* which occurs as close as Timor. I summarise historical evidence and biogeographic patterns for *B. arnhemica*, and describe the flowering wave phenomenon in the species, evidence which collectively suggests that *B. arnhemica* is neither very ancient nor very recent in origin. Current studies of the population genetics of *B. arnhemica*, and of the relationship between Australian and Asian bamboos, may yield fascinating further biogeographic insights.

Introduction

The tall, gracefully-arching leafy culms of bamboo are not characteristic of the Australian environment and, at a popular level at least, there is some resistance to the notion that any bamboo could be native to the continent. A negative view of bamboos has been reinforced by the invasiveness of several leptomorph (running) temperate-zone Asian species of *Phyllostachys* Siebold & Zucc. that are weeds in parts of south-eastern Australia (Lazarides 2002). Australia has three native bamboo species (Mallett & Orchard 2002) that, being confined to remoter tropical regions of the continent (Fig. 1), are not well known and have received almost no scientific attention until recently.

The three species are *Bambusa arnhemica* F.Muell., *Neololeba atra* (Lindl.) Widjaja, and *Mullerochloa moreheadiana* (F.M.Bailey) K.M.Wong (Table 1). *Bambusa arnhemica* is a robust, erect, clumping bamboo endemic to the higher rainfall north-west of the Northern

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Territory. It grows mainly in riparian forests and occasionally on rocky hillsides and other fire-sheltered non-riparian sites, ranging from Kakadu National Park west and south-west to the Daly River and north to Melville Island, often occurring in monodominant stands (Franklin & Bowman 2004). *Neololeba atra* is a slender, clumping, large-leaved species found in scattered locations in rainforest and vine-thicket along the Queensland coast from Mackay to the Torres Strait and also in New Guinea, the Moluccas, northern Sulawesi and the Philippines (Widjaja 1997). *Mullerochloa moreheadiana* is a rampant, non-twining scrambler endemic to the wet tropics of Queensland (Wong 2005), where it is known from the Innisfail and Daintree areas.

Cusack (1999) and Leu (2001) refer to *Schizostachyum* sp. ‘Murray Island’ as a fourth native species from the Torres Strait. However, this record is apparently not supported by herbarium specimens, its generic placement is speculative, and my enquiries suggest the relevant populations are likely to be remnants of disused plantations. On current evidence, these reports cannot be accepted as evidence that the species has established in the wild, let alone that it is a native species.

How did the three species reach Australia and how long have they been here? What is their relationship to Asian bamboos? Are *B. arnhemica* and *M. moreheadiana* truly endemic? Do they represent an Australian radiation, separate colonisation events from Asia, or Gondwanan remnants? These questions are necessarily grounded in taxonomic interpretation, and it is only in the past decade that the status of these species has been evaluated with sufficient care to allow the generation of plausible historical biogeographic hypotheses. In this paper,

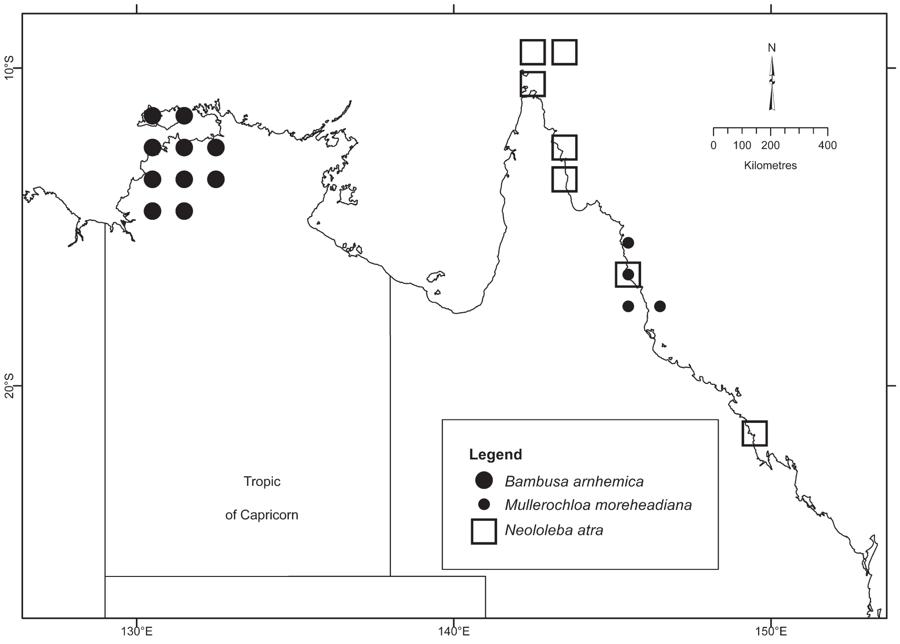

Fig. 1. Distribution of native bamboos in Australia. Data for *Bambusa arnhemica* are from the dataset underlying the distribution map in Franklin & Bowman (2004). Data for *Neololeba atra* and *Mullerochloa moreheadiana* are from CPBR (2007).

I will summarise current understandings about the taxonomic status and relationships of Australian native bamboos and briefly explore the emergent biogeographic implications.

Background: 'woody' bamboos

The 'woody' bamboos (Poaceae: Bambuseae) are a putatively monophyletic sister group to the herbaceous bamboos, tribe Olyreae, which together comprise the Bambusoideae (Zhang & Clark 2000, Grass Phylogeny Working Group 2001). The vernacular name 'bamboo' can generate confusion and reflects a chequered history of taxonomic interpretation (Clark 1997): in this paper, the term is taken to mean a member of the tribe Bambuseae.

The major centre of diversity is in Asia, especially southern China, with over 1,000 species in the Asia-Pacific region (Bystriakova et al. 2003). A second, lesser centre of diversity is in higher-rainfall tropical and temperate regions of Latin America with c. 430 species (Bystriakova et al. 2004). Five species occur naturally in continental Africa, 33 in Madagascar and three in the United States (Bystriakova et al. 2004, Triplett et al. 2006), along with three in Australia. No species occur naturally in Europe, although fossil bamboos have been found in Poland (Worobiec & Worobiec 2005).

Bamboos are obligately and fundamentally clonal. A feature of many species is a vegetative growth phase that may last decades or even centuries (Janzen 1976). Though at least a few species flower annually, many flower only at the end of this growth phase and either die, or their above-ground parts die, after flowering. Even more intriguing, many semelparous species flower and die synchronously and in spatio-temporal waves. The molecular mechanisms underlying the timing of these events remain "basic biological mysteries" (Judziewicz et al. 1999). A morphological corollary to this behaviour is the iterauctant inflorescence of some species, in which the pseudospikelets bear basal buds and are thus, theoretically, capable of indefinite proliferation. An ecological corollary of gregarious semelparity is a strong tendency for bamboos to occur in monodominant stands (Franklin & Bowman 2003, Griscom et al. 2007) or, in open forests, as monodominant understoreys (Saitoh et al. 2002, Taylor et al. 2004, Holz & Veblen 2006).

Probably no other large group of vascular plants is as poorly understood taxonomically as the Bambuseae. Natural selection appears to have favoured vegetative diversification. Key features such as rhizomes, culms, branch buds, branch complements and culm leaves do not fit well on standard herbarium specimen sheets and are not often collected. The flowers of many species are rarely available, and some species have been described without them. An Australian example is that the flowers of *M. moreheadiana* were first formally described by Clifford (1993), 104 years after the species was described. Furthermore, molecular techniques have yet to make substantial inroads into challenges at the generic and species levels.

The genus *Bambusa* Schreber, to which all three Australian bamboos were attributed until recently, appears to have been used as a repository for species of unknown affiliation. Ohrnberger (1999) recognized 139 species in *Bambusa* with a distribution centred in south Asia and extending north to Japan and south-east to the Solomon Islands and northern Australia, with an outlying species in Madagascar. The genus is demonstrably polyphyletic with at least some species of *Dendrocalamus* nested within it (Sun et al. 2005). Over recent decades, a considerable number of genera have been raised to accommodate obviously aberrant species or discrete groups (see brief reviews in Sun et al. 2005, Wong 2005). However, this process has proceeded in the absence of any clear definition of *Bambusa*, a problem at least partly addressed by Wong's (2005) "improving circumscription" of the genus. It remains unclear how many more nomenclatural changes are required to reduce *Bambusa* to coherent monophyly.

Taxonomic appraisals of Australian bamboos

After an early, chequered nomenclatural history (see Spencer 1986 for a brief summary), Queensland populations of the taxon now known as *Neololeba atra* were attributed to *Dendrocalamus forbesii*, a species described from New Guinea by Ridley (1886). Holttum (1967) transferred *D. forbesii* to *Bambusa* based on the rhachilla having distinct and equal internodes and lemmas of equal length. Whilst acknowledging its similarity to *Bambusa atra*, a species from New Guinea through to Sulawesi and the Philippines, Holttum considered them separable on the length of the lemma (8–10 mm in *B. atra*, 6–7 mm in *B. forbesii*). Widjaja (1997) argued that *B. forbesii* was indistinguishable from *B. atra*, reducing it to synonymy with the latter name taking precedence. At the same time, she described the new genus *Neololeba*, to which she transferred *B. atra* and described four new species from Indonesia. *Neololeba* can be distinguished from *Bambusa* by its simple branching system and a range of floral characteristics including pseudospikelet shape, the length of the rhachilla internodes, the absence of lodicules, and ovary shape. *Neololeba* also lacks the basal branches and robust, thick-walled culms of *Bambusa*.

Based on the original description by Mueller (1886), *B. arnhemica* has always been officially treated as an Australian endemic. Mueller's description was brief and although it does include a description of flowers – contrary to assertions by a number of subsequent authors including Ohrnberger (1999) – it was insufficient to ascertain the aptness of its placement in *Bambusa* nor to identify or exclude synonymy with Asian species. Mueller also raised the possibility that a second species occurred within the range of *B. arnhemica*. Franklin (2003a) found no evidence of a second species and concluded that, notwithstanding considerable discrepancies in the literature in the circumscription of *Bambusa*, *B. arnhemica* was a typical *Bambusa* based on pseudospikelet, floret and caryopsis features and the presence of thorns on the basal branches. The only possible discrepancy was that *Bambusa* species typically have lobed culm sheath auricles, but these are much reduced in *B. arnhemica* as they also are in *B. balcooa* Roxburgh (Stapleton 1994). Wong (2005) subsequently concurred with this judgement.

I also compared *B. arnhemica* with descriptions or illustrations of 14 other species of *Bambusa* known to have thorns (Franklin 2003a). Two of these, *B. bambos* (L.) A.Voss (syn. *B. arundinacea*) and *B. blumeana* J.H.Schultes are robust clumpers that are widely distributed (naturally and/or in cultivation) in Asia, with *B. blumeana* widespread in, and probably native to, Timor (Muller et al. 1998), 650 km north-west from the natural range of *B. arnhemica*. Most of the other species are of restricted distribution and many occur in China. *Bambusa arnhemica* appears to be closer to *B. blumeana* than *B. bambos* but can be distinguished from both on a number of vegetative and floral characteristics (Table 2). However, the smaller stature of *B. arnhemica* may be attributable to harsher growing conditions, and occasional clumps exceed 20 m in height and have culms to 13 cm in diameter (pers. obs.).

In providing the first description of the flowers of *Bambusa moreheadiana*, Clifford (1993) noted that its floral structures were consistent with the circumscription of *Bambusa* provided by Holttum (1967) with the exception of the number of anthers (Table 1). In contrast, Muller (2001) drew attention to a number of unusual vegetative traits of the species and

Table 1. Taxonomic history, distribution and key morphological features of the three Australian native bamboo species.

Morphological features selected for comparison of Australian species only.

	Bambusa arnhemica	***Neololeba atra***	***Mullerochloa moreheadiana***
Original description	Mueller (1886) as *B. arnhemica*	1. Ridley (1886) as *Dendrocalamus forbesii* 2. Lindley (1815) as *Bambusa atra* - never applied to Australian populations	F.M.Bailey (1889) as *Bambusa moreheadiana*
Source of current nomenclature	status quo confirmed by Franklin (2003a) and Wong (2005)	Widjaja (1997)	Wong (2005)
Other synonyms	-	*Bambusa forbesii* (Holttum 1967) also *Arundinaria cobonii, Gigantochloa novoguineensi*s	-
Australian distribution	the north-west of the Northern Territory	Queensland: 1. Mackay; 2. Daintree; 3. Iron Range; 4. Torres Strait	Queensland wet tropics: populations in the Daintree and Innisfail regions
Non-Australian distribution	-	north to the Philippines	-
Habit	robust clumper to 20 m	clumping, to 12 m	scandent (non-twining); loosely clumping
Culms	robust; to 10(–12) cm diameter; internodes mostly < 40 cm long	thin-walled, < 4 cm diameter; internodes 30–80 cm long	< 4.5 cm diameter; internodes < 30 cm long
Branches	often >> 3 per node	1–3 per node	1 to many per node
Foliage leaves	< 20 cm long	> 30 cm long	mostly < 30 cm long
Pseudospikelets	to 45 (–70) mm long	< 20 mm long	5–10 mm long
Lodicules	3	absent	3
Anthers	6	6	4
Features	branches often present near culm base, thorny	slender, thin-walled culms with long internodes and no basal branches; large leaves	primary branches often reiterate culms, producing”culm sequences” to 60+ m long; branch buds in contact with the ground may develop rhizome-like structures

Table 2. A comparison of traits useful to distinguish *Bambusa arnhemica* from two widespread Asian thorny *Bambusa* species.

Data on *B. bambos* and *B. blumeana* are from Dransfield & Widjaja (1995) and from observations by the author of cultivated specimens.

Character	*B. arnhemica*	*B. bambos*	*B. blumeana*
Culm dimensions (length, diameter near base)	to 20 m x 10 cm	to 30 m x 15–18 cm	to 25 m x 20 cm
Position of primary branches on culm	absent below 0.5 m and usually from c. 2–8 m	at all nodes	at most nodes
Thorns	slender, confined to lower branches, not usually giving rise to leafy shoots	robust on lower branches, often giving rise to leafy shoots; small spines may be present on upper branches	robust, on lower and upper branches and often giving rise to leafy shoots
Culm leaf shape	varying little along culm		lower leaves shorter and narrower
Culm leaf hairs	glabrous or with pale hairs	glabrous or with brown hairs	hairs on back dark brown
Culm leaf blade (culm leaf)	narrowly triangular, erect	broadly triangular, more or less reflexed	lanceolate, erect at basal and upper nodes, horizontal to deflexed on mid culm
Culm leaf auricles	rudimentary or absent	forming a prominent wrinkled margin	short, with bristles to 15 mm long
Pseudospikelets	to 4.5 (–7) cm long	c. 2 cm long	to c. 5 cm long
Other features	upper and lower branches segregated and of contrasting form	leaves slightly glaucous below	

argued that it was quite unlike typical *Bambusa* species. Wong (2005) has since provided a thorough reappraisal of the taxon in tandem with a tighter circumscription of *Bambusa*, drawing attention to a range of vegetative and floral features that render it unique amongst bamboos. Noteworthy amongst these is the capacity of primary branches to reiterate culms, thus forming “culm sequences”, and for branch buds in contact with the ground to develop rhizome-like structures. He placed it in the new, monotypic genus *Mullerochloa*, named in recognition of contribution of Len Muller, the north Queensland resident who recognised and drew attention to the uniqueness of the species. The affinities of *Mullerochloa* are unclear but may lie with *Soejatmia* K.M.Wong and *Neololeba* (Wong 2005).

Bambusa arnhemica **- an historical and biogeographic case study**

Endemicity may be interpreted as indicating that *B. arnhemica* has been in Australia for a long time. However, there are at least two plausible alternative hypotheses that could involve relatively recent arrival from Asia: *a.* that it is recently derived from *B. blumeana* in Timor or elsewhere; or *b.* that its parent population in Asia has since gone extinct. Historical and ecological perspectives provide context for considering these as yet unresolved alternatives.

The species was well-established in its current range before the arrival of Europeans, as the early European explorers found bamboo in abundance along many watercourses where *B. arnhemica* is known today (Table 3). The popular suggestion that Macassan trepangers introduced *B. arnhemica* to northern Australia from Sulawesi or nearby islands in the 18th or 19th centuries (White 1971) is not supported by the presence of live bamboo at Macassan camp sites or nearby springs (Macknight 1976, Bindon 1991, Mitchell 1995). In contrast, the introduced Tamarind tree *Tamarindus indica* L. is commonly associated with these situations. Furthermore, because trepang is most abundant in clear water, the major trepanging grounds in northern Australia were off rocky rather than mangrove-lined coasts. Thus it was that Macassan camp sites were concentrated from Cobourg Peninsula east to the Gulf of Carpentaria, and along the Kimberley coast in the west (Macknight 1973, 1976), a distribution that almost perfectly excises the coast adjacent to which *B. arnhemica* grows (Franklin & Bowman 2004).

Table 3. Some early European records of bamboo in the Northern Territory.

1839	John Lort Stokes	Darwin Harbour	Stokes (1846)
1845	Ludwig Leichhardt	South Alligator River	Leichhardt (1847)
1862	John McDouall Stuart	Mary and Adelaide Rivers	Stuart (1865)
1866	John McKinlay	Margaret, McKinlay, Mary Rivers and tributaries of the South Alligator River	McKinlay (1866)

A plausible but hypothetical case has been made that Aboriginal people could have reached Australia on bamboo rafts (Flood 1995, Bednarik et al. 1999). The Indigenous people of northern Australia made considerable use of *B. arnhemica*, principally as spear shafts but also for production of didgeridoos, long-stemmed smoking pipes, ceremonial frames, water carriers, wood-carving chisels and rafts (Tindale 1925, Bindon 1991, Marrfurra et al. 1995, Blake et al. 1998, G. Wightman pers. comm.). Bamboo was traded extensively east into Arnhem Land, and south and south-west from the Daly River area as far as the Kimberley (Thomson 1949, Berndt & Berndt 1988, G. Wightman pers. comm.). The Balamumu people from Caledon Bay on the east Arnhem coast, 420 km east of the distributional limit of *B. arnhemica*, specialised in the production of bamboo fighting spears (Tindale 1925). This evidence may be interpreted as suggesting long-standing cultural attachment to bamboo and thus a long period of co-existence. However, usage and cultural value need to be interpreted in the light of the demonstrable ability of Aboriginal people to rapidly adopt novel items into traditional diets and culture, as demonstrated by the fruit of the Tamarind *Tamarindus indica* (Mitchell 1995) and meat of Water Buffalo *Bubalis bubalis* (Bowman & Robinson 2002). Interestingly, I can find no record suggesting traditional Aboriginal use of either bamboo culm shoots or seed as food, a marked contrast with the "bamboo cultures" of Asia.

I have also been unable to identify any direct archaeological evidence from Aboriginal usage that *B. arnhemica* may have been in Australia for millennia. Remains of bamboo have been detected in archaeological deposits in Kakadu National Park, but only in deposits no more than, and possibly much less than c. 800 years of age (Clarke 1988). The lack of earlier records may reflect that bamboo does not last long in this situation (Annie Clarke pers. comm.). The persistence and detectability of bamboo residues on stone tools (Jahren et al. 1997) offers some prospect for further exploration of archaeological deposits. There is only one possible representation of bamboo in the extensive Arnhem Land Plateau rock art record (Chaloupka 1997, p189), a painting that is only a few hundred years old (P. Giuliani pers. comm.). It depicts a man playing a didgeridoo that is banded; the banding may be decorative or could represent bamboo nodes.

Thus, though the historic record provides no evidence of a human introduction of the *B. arnhemica* to Australia, it does not exclude the possibility. However, several strands of ecological evidence suggest that *B. arnhemica* has been in Australia for a considerable period of time. The first is its primarily riparian distribution, documented in detail by Franklin and Bowman (2004) and which should be interpreted in the absence of any obvious dispersal mechanism (Franklin 2003a) and a generation time of 40–50 years (Franklin 2004). The species occurs in six major and a number of minor adjacent catchments on the Australian mainland and a restricted series of minor catchments on Melville Island. Bathymetric maps indicate that these coalesced into two palaeodrainages during the last glaciation c. 20,000 years ago: the Daly River which flowed west and then north towards Timor, and the greater Adelaide River system which drained northwards between the current tip of Cobourg Peninsula and Melville Island towards Tanimbar Island (see Voris 2000 for relevant sea-level maps). Within these catchments, the species is widely dispersed and frequently abundant from minor tributaries to the edge of coastal floodplains, but missing from the upper parts of some catchments including most notably that of the Daly River. It is consistently absent from streams with shallow, poorly-drained profiles, and from rocky stream banks. Franklin and Bowman (2004) suggested these patterns reflect infrequent dispersal across catchment boundaries to random "starting points", followed by downstream dispersal.

Overlain on this distribution is a pattern of flowering patches that range from 0.002 to 3,200 km^2 (Franklin 2004). A "patch" is an area in which the majority (usually > 95%) of *B. arnhemica* clumps flowered simultaneously, i.e. typically for 4–6 months from the middle of the dry season to the early wet season, adjacent patches being distinguished by flowering in a different year, or by not flowering during the period 1996-2002 when the phenomenon was studied (Franklin 2004). The arrangement of patches bears only limited resemblance to catchments and some patches cut across catchment or sub-catchment boundaries as if superimposed arbitrarily. Both above- and below-ground parts of *B. arnhemica* die after flowering, regeneration occurring solely but often prolifically from seed with seedling densities of 1,000–2,000 m^{-2} being observed (Franklin 2004).

The patch structure of flowering in *B. arnhemica* corresponds to the flowering wave phenomenon reported in many bamboos (Janzen 1976) in which, after a long period of reproductive inactivity (about 30 years in *B. arnhemica*), a succession of patches flower in successive years. The opportunity to document the flowering wave in *B. arnhemica* across much of its range and at a variety of spatial scales, a study without parallel amongst bamboos, has facilitated the generation of an hypothesis for this perplexing phenomenon. Flowering in at least some bamboos occurs at fixed though long intervals (see Kawamura 1927 for an exceptional example). It is now generally agreed to be under the control of an endogenous mechanism (a biological clock) that operates largely independently of the physiological status of the plant and which is maintained across generations by intense selection against individuals that flower out of synchrony (Janzen 1976, Simmonds 1980, Franklin 2004). The challenge has been to relate such a mechanism to the wave phenomenon. I proposed (Franklin 2004) that a wave arises from a synchronously-flowering founder population when environmentally-triggered miscounts affect a neighbourhood of plants, causing most or all of them to flower earlier or later than others of the species but without altering the genetics underlying the biological clock. A succession of miscounts generates a temporally coherent wave. It follows that, since the wave is not generated by genetic processes, the patches remain fixed out of step and are thus reproductively isolated unless a subsequent miscount by chance brings them back into alignment. The resultant allochronic isolation may well have genetic consequences and even provide the basis for speciation. The drivers of miscounts, along with the molecular mechanisms associated with such a long-term biological clock, remain unknown, although some circumstantial evidence summarised by Franklin (2004) suggests that the clock may be sensitive to fluctuations in temperature.

Given that the flowering wave remains a temporally coherent event, it seems likely to have arisen through many small chance increments rather than a few large ones. It follows that the flowering wave in *B. arnhemica* must have taken many generations to arise. Furthermore, it appears to have been superimposed on an established distribution.

The time scales required for *B. arnhemica* to disperse across the landscape of the north-western Top End and to develop a complex flowering wave remain unclear. However, it is clear that many generations are required for this situation to have arisen, and at 40–50 years per generation, *B. arnhemica* arrived in Australia a long time before Europeans did. I suspect also that the species arrived long before the Aborigines c. 50,000 years ago, but this remains to be demonstrated. The question is under further investigation using molecular techniques.

Biogeographic hypotheses for Australian bamboos

One possible hypothesis for the origin of Australian bamboos – that they represent a local radiation following a single founder event from Asia – a naive hypothesis that might have been tempting when all three species were attributed to *Bambusa*, can be confidently ruled out. Two of the taxa are Australian representatives of Asian genera, and the third is an aberrant species of uncertain affinities.

On the current limited information, the most parsimonious biogeographic hypothesis for the occurrence of bamboos in Australia is that the three species are the products of at least three founder events from Asia (Franklin 2003b). The aptness of this perspective for *B. arnhemica* is particularly evident given its position within a prolific Asian genus. However, Wong (2005) has raised some plausible alternatives for *Mullerochloa* and *Neololeba atra* that warrant further consideration. There are two components to Wong's suggestions. The first is that *Mullerochloa* may be allied to, and derived from *Neololeba*, raising the possibility of a local radiation involving these two species. Given the aberrant nature of *Mullerochloa*, such an event may have occurred long in the past. This leads to the second component, the possibility that at least this bamboo lineage is of Gondwanan rather than Asian origin.

It is a biogeographic irony that the Bambuseae are thought to have originated in the lowland tropics of the Southern Hemisphere (Clark 1997) and yet are most prolific in Asia. Many elements of this story remain fragmentary and uncertain. Current efforts to shed light on the higher level taxonomy of the Bambuseae by the Bamboo Phylogeny Project (Iowa State University 2007), in which it is planned to include the Australian and related Asian species (K.M. Wong pers. comm.), are likely to have substantial and intriguing biogeographic implications. It is not implausible that Australia will prove to be at the centre of yet another biogeographic story to which it has long been regarded as peripheral.

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