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Livistona palms in Australia: Ancient relics or opportunistic immigrants?

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ABSTRACT

Eighteen of the 34 species of the fan palm genus *Livistona* (Arecaceae) are restricted to Australia and southern New Guinea, east of Wallace's Line, an ancient biogeographic boundary between the former supercontinents Laurasia and Gondwana. The remaining species extend from SE Asia to Africa, west of Wallace's Line. Competing hypotheses contend that *Livistona* is (a) ancient, its current distribution a relict of the supercontinents, or (b) a Miocene immigrant from the north into Australia as it drifted towards Asia. We have tested these hypotheses using Bayesian and penalized likelihood molecular dating based on 4 Kb of nuclear and chloroplast DNA sequences with multiple fossil calibration points. Ancestral areas and biomes were reconstructed using parsimony and maximum likelihood. We found strong support for the second hypothesis, that a single *Livistona* ancestor colonized Australia from the north about 10–17 Ma. Spread and diversification of the genus within Australia was likely favoured by a transition from the aseasonal wet to monsoonal biome, to which it could have been preadapted by fire-tolerance.

1. Introduction

Wallace's Line is one of the longest recognized biogeographical boundaries on Earth (Whitmore, 1982). It is thought to represent an ancient divide between the biotas of Laurasia and Gondwana, which were separated by continental drift (vicariance) 180–160 Ma, then came into proximity again only recently (<25 Ma) as the Australian plate drifted north to collide with southeast (SE) Asia (Hall, 2002; McLoughlin, 2001; Scotese, 2004). Despite the marine barrier—there has been deep water between the continental shelves of Sundaland and Australia-New Guinea for >150 Ma (Hall, 2002; McLoughlin, 2001; Scotese, 2004)—some organisms are thought to have crossed Wallace's Line and established sister taxa on either side of the barrier by allopatric speciation (Barlow and Hyland, 1988; Metcalfe et al., 2001; Whitmore, 1987). However, it remains unclear how much mixing there has been between the two continental biotas (Bowman et al., 2009a,b; Truswell et al., 1987). Vicariance and long-distance colonization hypotheses make contrasting predictions about the timing of divergences between sister taxa on either side of oceanic gaps (Crisp et al., 2009; Poux et al., 2005), such as Wallace's Line. Vicariant taxa on either side of Wallace's Line should have diverged more than 150 Ma, whereas divergences resulting from dispersal should be younger and increasing in frequency as the two continental plates came into proximity.

The fan palm genus *Livistona* makes an excellent case study for testing these alternative hypotheses because it has 36 species distributed on both sides of Wallace's Line—mainly in SE Asia, Australia, New Guinea and Melanesia, with a single outlying species (*L. carinensis*) in Somalia, Yemen and Djibouti (Dowe, 2009; Rodd, 1998). Two Australian species (*L. benthamii* and *L. muelleri*) are shared with southern New Guinea but neither crosses Wallace's Line; nor does any other species occurring in Papuasia, except *L. rotundifolia* (Baker and Dransfield, 2006; Dowe, 2009). Both vicariance (Rodd, 1998) and long-distance colonization (Dransfield, 1987) have been suggested to explain the disjunction of *Livistona* across Wallace's Line. Dransfield (1987) argued that palms originated in Pangea and have both Laurasian and Gondwanan descendant lineages but that *Livistona* migrated from Sundaland (in Malesia, on the Laurasian side of

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Wallace's Line) and is not a Gondwanan relic. Rodd (1998) speculated that "proto-*Livistona* had already emerged by the time Laurasia and Gondwana began to separate, and its progeny evolved independently but extremely slowly (by flowering-plant standards) in both landmasses and their daughter lands". The Australian fossil record does not show when *Livistona* reached Australia, lacking *Livistona* or even unequivocal representatives of its subfamily (Coryphoideae), except possibly *Palmoxylon queenslandicum* (Conran and Rozefelds, 2003), whose affinity is unclear. The first aim of this study was to use phylogenetic molecular dating to determine whether the distribution of *Livistona* is the result of vicariance or more recent dispersal across Wallace's Line.

The geographic pattern and timing of diversification of *Livistona* within Australia is the second major focus of this study. Whereas *Livistona* in Asia occurs mostly in aseasonal wet communities, Australian taxa are found primarily in the monsoonal tropics, ranging east from the Kimberley to Cape York Peninsula and south along the coast and adjacent ranges of Queensland (Table 1; Fig. 1). Did the monsoonal tropics provide an ecological opportunity for an immigrant ancestor to radiate? Additionally, two Australian *Livistona* species occur as outliers in the arid zone (Fig. 1): *L. alfredii* in the Pilbara, Western Australia, and *L. mariae*, in Central Australia, often described as 'relictual' (Greenwood and Conran, 2000; Latz, 1975; Rodd, 1998; White, 1988). Are the species in the arid zone remnants of once widespread species whose ranges have subsequently contracted with the aridification of Australia (from 15 Ma, Macphail, 1997; Martin, 2006), such that they are now restricted to small refugia (Dowe, 1995; Dransfield, 1987)?

To summarize, the aims of this study were to use phylogenetic molecular dating to (1) test the Gondwanan relic hypothesis versus that of recent immigration from Asia, and (2) reconstruct the timing and direction of habitat transitions in relation to likely driving events in geological and climatic history.

2. Material and methods

2.1. Sampling

All 18 Australian *Livistona* species (after Dowe, 2009; Rodd, 1998) were sampled, as well as six of their 18 congeners from elsewhere, representing the geographic and ecological range of the genus (Table 1). Outgroup sampling (Appendix 1) was based on Asmussen et al. (2006), included all five subfamilies of Arecaceae and aimed to also include (1) genera closely related to *Livistona*, especially within the tribe Trachycarpeae and subfamily Coryphoideae, and (2) groups across the Arecaceae with known macrofossil calibration points. One individual was sampled per species.

One nDNA (malate synthase, MS) and six cpDNA loci, totalling about 4 Kb of sequence, were sampled across the tribe Trachycarpeae. To reconstruct broader relationships including nodes suitable for calibration of molecular dating, MS, *trnL* intron, *trnL-trnF* and

Table 1
Distribution and habitats of *Livistona* and *Licuala* species sampled.[a]

Species	Distribution[b]	Habitat (biome)[c]
Australia-New Guinea clade		
Livistona alfredii	Pilbara and Cape Range, WA (8)	Riparian with eucalypts and melaleucas in deep gorges with permanent water (arid region) (2)
L. australis	Coastal eastern Australia, 19-38°S (Qld, NSW, Vic) (6)	Swamp forest, rainforest and gallery forest, and adjacent wet eucalypt forest (0)
L. benthamii	Top End (NT), northern Cape York Peninsula (Qld) and Papua New Guinea (2,4,5)	Moist coastal monsoonal rainforest, swamp forest and gallery forest (0)
L. concinna	Wet tropics of NE Qld (5)	Seasonally dry open forest, swamps and stream banks (1)
L. decora	East-coastal Qld from 19.5 to 26°S (6)	Riparian in eucalypt forest on margins of gallery- or dry-rainforest; damp dune hollows (1)
L. drudei	Coastal north Qld: Townsville to Kennedy River (6)	Mainly riparian, swamp forest and margins of gallery forest (1)
L. eastonii	North Kimberley, WA (3)	Co-dominant with eucalypts in monsoonal open forest on lateritic plateaux (1)
L. fulva	Blackdown Tableland, central Qld (6)	Sandstone cliff lines and gorges in seasonally dry eucalypt forest (1)
L. humilis	Top End, NT (4)	Monsoonal open eucalypt forest, on oligotrophic soils (1)
L. inermis	Top End (NT) to far NW Qld (4)	Monsoonal eucalypt woodland; sandstone crevices, cliffs and gullies (1)
L. lanuginosa	Burdekin River basin, north Qld (6)	Riparian in seasonally dry tropics (1)
L. lorophylla	Kimberley, WA and Victoria River, NT (3)	In sparse monsoonal sclerophyll communities on sandstone cliffs and gullies (1)
L. mariae	Palm Valley and the Finke River in central Australia, NT (7)	Riparian with open sclerophyll vegetation in an arid region (2)
L. muelleri	Cape York Peninsula (Qld) and southern New Guinea (2,5)	Monsoonal woodland, rainforest margins and seasonal swamps (1)
L. nasmophila	East Kimberley (WA) (3)	Monsoonal open sclerophyll vegetation; sandstone ravines and cliffs, associated with permanent groundwater (1)
L. nitida	Inland SE-central Qld: Dawson and Comet River basins (6)	Riparian and in gorges in seasonally dry open eucalypt forest. (1)
L. rigida	Roper (Arnhem Land, NT) and Gregory-Nicholson catchments (NW Qld) (4)	Riparian in monsoonal tropics (1)
L. victoriae	Victoria River region, far northern border of WA-NT (3)	Monsoonal open sclerophyll vegetation; seepage lines in sandstone gorges and cliffs (1)
Asia-Africa		
L. carinensis	Djibouti, Somalia and Yemen (1)	Sheltered gullies, valleys and soaks in semi-arid regions (2).
L. chinensis	Islands of east Asia, from Hainan (China) NE to Shikoku (Japan) (0)	Coastal wet or dry open forest (0–1)
L. jenkinsiana	Himalayan India to southern China and Malay peninsula (0)	Rainforest (0)
L. rotundifolia	Indonesia (Java, Sulawesi, Maluku) and Philippines (0,2)	Rainforest, swamp forest and along rivers (0)
L. saribus	Widespread through SE Asia and Malesia (west of Wallace's Line) (0)	Rainforest and swamp forest and along rivers (0)
L. woodfordii Ridl.	Solomon Islands and far eastern New Guinea (2)	Rainforest and swamp forest (0)
Licuala grandis H.Wendl.	Vanuatu, Solomon Islands (2)	Rainforest (0)

[a] *Sources:* (Baker and Dransfield, 2006; Dowe, 2009; Ohtani et al., 2008; Price, 1999; Riffle and Craft, 2003; Rodd, 1998; Whitmore, 1973). Web site: http://www.pacsoa.org.au/palms/index.html.

[b] Scoring of geographic regions: SE Asia (0), Africa (1), Papuasia (2), Kimberley–Victoria River (3), Top End and western Gulf (4), Cape York Peninsula (5), east coast (6), central Australia (7), Pilbara (8). Abbreviation of Australian states: NSW, New South Wales; NT, Northern Territory; Qld, Queensland; WA, Western Australia.

[c] Scoring of biomes: aseasonal wet (0), seasonally dry (1), arid (3).