



A long distance dispersal hypothesis for the Pandanaceae and the origins of the *Pandanus tectorius* complex



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ABSTRACT

Pandanaceae (screw-pines) is a monocot family composed of c. 750 species widely distributed in the Paleotropics. It has been proposed that the family may have a Gondwanan origin with an extant Paleotropical distribution resulting from the breakup of that supercontinent. However, fossils supporting that hypothesis have been recently reassigned to other families while new fossil discoveries suggest an alternate hypothesis. In the present study, nuclear and chloroplast sequences were used to resolve relationships among Pandanaceae genera. Two well-supported fossils were used to produce a chronogram to infer whether the age of major intra-familial lineages corresponds with the breakup of Gondwana. The Pandanaceae has a Late Cretaceous origin, and genera on former Gondwanan landmasses began to diverge in the Late Eocene, well after many of the southern hemisphere continents became isolated. The results suggest an extant distribution influenced by long-distance-dispersal. The most widespread group within the family, the *Pandanus tectorius* species complex, originated in Eastern Queensland within the past six million years and has spread to encompass nearly the entire geographic extent of the family from Africa through Polynesia. The spread of that group is likely due to dispersal via hydrochory as well as a combination of traits such as agamospermy, anemophily, and multi-seeded propagules which can facilitate the establishment of new populations in remote locations.

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1. Introduction

1.1. Pandanaceae lineages: distribution, dispersal modes, and key-character innovations

Pandanaceae is a family of c. 750 dioecious species in the order Pandanales composed of trees, shrubs, epiphytes, and lianas. The family consists of five genera: *Benstonea* Callm. & Buerki (c. 60 spp.), *Freycinetia* Gaudich. (c. 250 spp.), *Martellidendron* (Pic. Serm.) Callm. & Chassot (6 spp.), *Pandanus* Parkinson (c. 450 spp.), and *Sararanga* Hemsl. (2 spp.) (Callmander et al., 2003, 2012). Molecular phylogenetic work supports the monophyly of each of the recognized genera, (Buerki et al., 2012; Callmander et al., 2003). In the most recent study based on chloroplast sequences,

Abbreviations: BPP, Bayesian posterior probability; HPD, highest probability distribution; LDD, long distance dispersal; Ma, mega-annum; s.s., sensu stricto.

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Sararanga was found to have a sister relationship to the remaining genera with *Freycinetia* as sister to a clade consisting of *Martellidendron*, *Benstonea*, and *Pandanus* (hereafter the MBP clade = AMCP clade of Buerki et al., 2012); however, relationships among these last three genera remain to be shown. *Pandanus* was previously classified into eight subgenera by Stone (1974). Two of these, *Martellidendron* and *Acrostigma* (now *Benstonea*), were elevated to generic rank (Callmander et al., 2003, 2012). The chloroplast phylogeny estimate of Buerki et al. (2012) recovered two subclades within *Pandanus* and their results suggest that up to five of the remaining subgenera recognized by Stone may not form monophyletic groups.

The Pandanaceae is distributed throughout the Paleotropics from West Africa to the islands of the eastern Pacific (Fig. 1). With the exception of *Martellidendron*, which is endemic to Madagascar and the Seychelles, the genera have overlapping distributions centered on Malesia, a region which includes Indonesia, Borneo, the Philippines, and New Guinea. This region perhaps represents the most complex geological history on the planet due to the convergence of landforms of Gondwanan, Laurasian, and Pacific plate

origin (Hall, 2002, 2009; Hill and Hall, 2002). *Sararanga* is narrowly distributed in the Philippines, the Solomon Islands, northern mainland New Guinea, and on the nearby Yepen and Manus islands (Stone, 1961). *Freycinetia* has a center of diversity in New Guinea and Indonesia and its distribution reaches Hawai'i and Micronesia indicating that part of its range at least has been achieved through LDD (Stone, 1967a, 1968, 1969). *Benstonea* is distributed from India to Fiji with the majority of species found in Borneo (Callmander et al., 2012). While the first *Pandanus* subclade, “subclade 1” has a distribution similar to that of *Benstonea*, the second *Pandanus* subclade, “subclade 2” has achieved the widest extant distribution among Pandanaceae lineages reaching Africa, Madagascar, much of Southeast Asia, and nearly all of the islands of the tropical Indo-Pacific (Buerki et al., 2012; Stone, 1974).

The biogeography of the family has been previously discussed under an assumption of an East-Gondwana origin with sub-familial lineages resulting from the breakup of the supercontinent during the Cretaceous (Callmander and Laivao, 2002; Callmander et al., 2003; Nadaf and Zanan, 2012; Stone, 1976a). However, there have been no explicit biogeographical analyses of the family and it is unclear what role Gondwana-derived vicariance or potentially recent long-distance-dispersal (LDD) have played in the historical biogeography of the family. Further, recent fossil discoveries, fossil reassignments, and available age estimates for the family cast some doubt on a Gondwana origin.

The Gondwana supercontinent formed in the Southern Hemisphere prior to the Cambrian from the fusion of several continental blocks (see McLoughlin (2001) for a chronology of the Gondwana breakup summarized below). In the Early Jurassic, the supercontinent began to break up starting with rifts between West Gondwana and East Gondwana which became fully separated by 130 Ma. West-Gondwana split into South America and Africa with the two becoming isolated by 105 Ma. The breakup of East-Gondwana isolated Madagascar by 65 Ma and the Indian subcontinent was isolated from 65 Ma until it fused with Laurasia at c.43 Ma. Antarctica, and Australia finally separated by 35.5 Ma resulting in the set of southern hemisphere continents that we recognize today.

The oldest Pandanaceae fossils are not found on Gondwanan landmasses, instead they are leaf fragments assigned to the genus *Pandanites* Tuzson from Maastrichtian (66.0–72.1 Ma) strata from North America and from Early Campanian (79–83.6 Ma) strata in Austria and Romania (Kvaček and Herman, 2004; Popa et al., 2011). *Pandanites* exhibit a suite of characters including lateral

nerves resulting in an ‘M’-shaped leaf cross-section, apical drip tip, spiral leaf arrangement, marginal prickles, parallel veins, and tetracytic stomata which allies this taxon to the Pandanaceae (Kvaček and Herman, 2004).

Several more recent fossils have affinities with Pandanaceae. *Pandanus eocenicus* Guleria & Lakhanpal from Early Eocene strata (41.2–56.0 Ma) of Gujarat, India may be Pandanaceae although the fossils lack the characters to place them in the family with certainty. Leaf fragments described as *Pandanus helicopus* Kurz. from the Neogene (2.6–23.0 Ma) of Sumatra are likely assignable to the Pandanaceae; however, like *P. eocenicus*, the taxon is not definitively assignable to *Pandanus* due to the lack of reproductive material (Kvaček and Herman, 2004). Two fossil pollen genera, *Dryptopollenites* Stover in Stover & Partridge and *Lateropora* Pocknall & Mildenhall are present in the fossil records of Australia and New Zealand beginning in the Paleocene (56–59 Ma) and are thought to have affinities with *Freycinetia* although this awaits a more detailed comparative analysis (Macphail et al., 1994). The fossil genus *Megaporites* Krutzsch described from Miocene (5.3–23.0 Ma) Taiwan is also believed to have affinities with *Freycinetia* (Huang, 1980). Late Miocene to recent fossil pollen attributed to *Pandanus* has been found from throughout Southeast Asia and Islands of the Pacific (Jarzen, 1983; Leopold, 1969). Fossil impressions of *P. tectorius* fruit (>1.2 Ma) were found in a rejuvenation stage lava flow along the north coast of the island of Kauai, Hawaii with subsequent Holocene *Pandanus* pollen and macro sub-fossil specimens found in deposits along the south coast of that island (Burney et al., 2001; Burney, 2002).

Several other fossil taxa previously assigned to the Pandanaceae from Gondwana-derived continents including *Pandanaceoxylon* Patil & Datar from Cretaceous (66.0–145.0 Ma) India and *Viracarpone* Sahní and *Pandanusocarpon* Bonde from the Eocene (33.9–56.0 Ma) of India are not attributable to the Pandanaceae due to a lack of synapomorphic characters and these have been assigned to other extant families (Bonde, 2005; Cox et al., 1995; Herman and Kvaček, 2010).

Age estimates for the family are incongruous. Janssen and Bremer (2004) estimated the origin of the Pandanaceae at 98 Ma using a plastid sequence-based phylogeny estimate of the monocots and a calibration based on the crown age of the monocots as calculated by Bremer (2000). However, in an analysis based on 36 fossil calibration points scattered throughout the angiosperm lineage, Bell et al. (2010) calculated the age of the family at

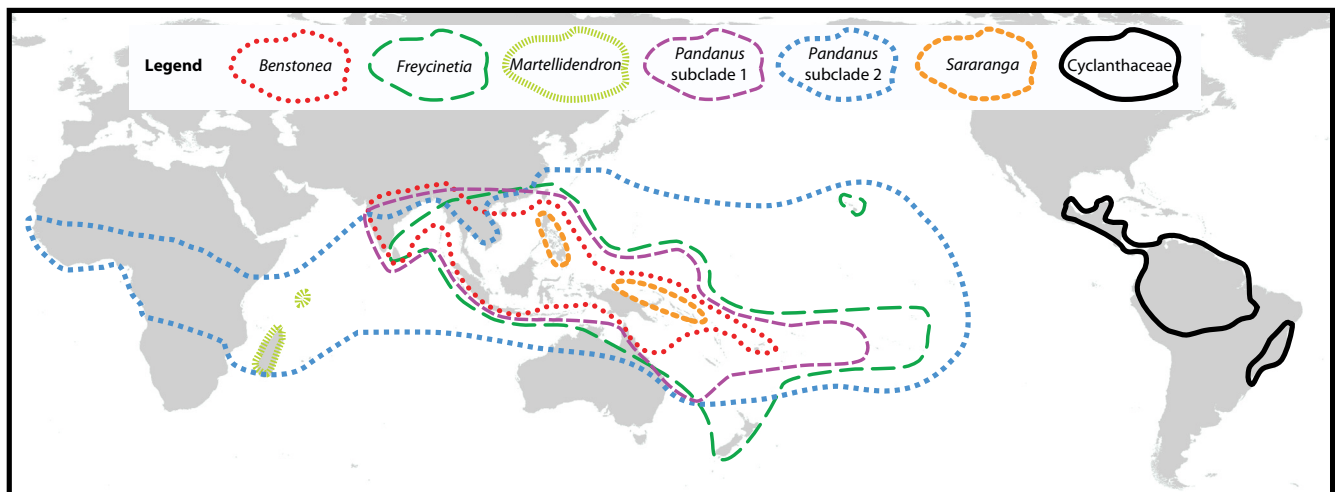


Fig. 1. Natural extant distributions of the genera of the Pandanaceae, including the two *Pandanus* subclades, and the Cyclanthaceae. Red, *Benstonea* Callm. & Buerki; Dark green, *Freycinetia* Gaudich.; Light green, *Martellidendron* (Martelli) Callm. & Chassot; Blue, *Pandanus* Parkinson subclade 1; Purple, *Pandanus* subclade 2; Orange, *Sararanga* Hemsl.; Black, Cyclanthaceae Poit. ex A. Rich. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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