Syst. Biol. 61(3):426–442, 2012

DOI:10.1093/sysbio/syr123
Advance Access publication on January 5, 2012

Miocene Dispersal Drives Island Radiations in the Palm Tribe Trachycarpeae (Arecaceae)

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Received 18 May 2011; reviews returned 21 August 2011; accepted 19 November 2011
Associate Editor: Mark Fishbein

Abstract.—The study of three island groups of the palm tribe Trachycarpeae (Arecaceae/Palmae) permits both the analysis of each independent radiation and comparisons across the tribe to address general processes that drive island diversification. Phylogenetic relationships of Trachycarpeae were inferred from three plastid and three low-copy nuclear genes. The incongruent topological position of *Brahea* in *CISP5* was hypothesized to be caused by a gene duplication event and was addressed using uninode coding. The resulting phylogenetic trees were well-resolved and the genera were all highly supported except for *Johannesteijsmannia* and *Serenoa*. Divergence time analysis estimated the stem of the tribe to be approximately 86 Ma and the crown to be 38 Ma, indicating that significant extinction may have occurred along this branch. Historical biogeographic analysis suggested that Trachycarpeae are of southern North American, Central American, or Caribbean origin and supports previous hypotheses of a Laurasian origin. The biogeography and disjunctions within the tribe were interpreted with respect to divergence times, the fossil record, and geological factors such as the formation of the Greater Antilles—Aves Ridge, the Bering and the North Atlantic land bridges, tectonic movement in Southeast Asia, climatic shifts between the Eocene and Pliocene, and volcanism in the Pacific basin. In considering the three major island radiations within Trachycarpeae, Miocene dispersal appears to have been the driving force in allopatric speciation and is highlighted here as an emerging pattern across the tree of life. [*Copernicia*; island radiation; *Licuala*; *Livistona*; Miocene; molecular dating; *Pritchardia*.]

Oceanic island ecosystems have long been recognized as natural laboratories for studying evolution because of their discrete geographical nature and diversity of species and habitats (Darwin 1876; Carlquist 1974; Grant and Grant, 2002; Savolainen et al. 2006). Many island systems have high levels of endemism and are classified as biodiversity "hotspots" (Mittermeier et al. 2000), including the Caribbean, Polynesian/Micronesian, and Sundaland/Wallacean biogeographic regions (Myers et al. 2000). Island taxa have provided outstanding examples of species radiations (e.g., Baldwin and Sanderson 1998; Losos and Ricklefs 2009) that permit the testing of evolutionary hypotheses about diversification using a combination of phylogenetics, divergence time estimation, and historical biogeographic inference. Recent advances in analytical methods have shown that dispersal is a key factor involved in diversification ("dispersification"; Moore and Donoghue 2007) and has led to renewed interest in oceanic dispersal and historical biogeography (e.g., Calsbeek and Smith 2003; De Quieroz 2005; Ree and Smith 2008).

The palms (Arecaceae) are an ideal group for the application of phylogenetic methods to address questions of biogeographic origin and radiation (e.g., Couvreur, Forest et al. 2011). The family is widespread and yet shows high rates of endemism at varied spatial scales (Eiserhardt et al. 2011; Baker and Couvreur, in press). In addition, palms have an abundant fossil record that dates back to the Cretaceous (Daghlian 1981; Muller 1981; Herendeen and Crane 1995) and includes fossils that can be linked with high confidence to specific extant lineages based on morphological synapomorphies (Harley 2006; Dransfield et al. 2008). Previous divergence time estimations yielded varied results but have led to a consensus that palms diverged from other commelinid monocots (Angiosperm Phylogeny III; Bremer et al. 2009) in the Middle Cretaceous after the initial breakup of Gondwana (Bremer 2000; Wilkström et al. 2001; Janssen and Bremer 2004). A number of narrative biogeographic scenarios have been proposed for palms (summarized in Dransfield et al. 2008), but the most recent analyses based on maximum likelihood (ML) methods suggest that palms diversified initially in Laurasia (Couvreur, Forest et al. 2011).

Trachycarpeae (subfamily Coryphoideae; 19 genera and ca. 269 species; Dransfield et al. 2008; Bacon and Baker 2011; Henderson and Bacon 2011) are outstanding within the palms because they display one of the widest distributions of all tribes in the family. This pattern together with distributions of other palm groups, such as tribe Areceae, supports the hypothesis that palms are capable of dispersing long distances over sea (Baker and Couvreur, in press). Indeed, palms are widespread in island systems that can only have been reached by transoceanic dispersal. Although floating palm seeds are well-known in a few species (e.g., the coconut, *Cocos nucifera*), this behavior is exceptional. Dispersal of palm seeds over long distances is most likely mediated by birds (Zona and Henderson 1989).

The monophyly of Trachycarpeae is highly supported, but the relationships within the tribe have been recognized as among the most significant ambiguities remaining within the family because of poor phylogenetic resolution and low branch support (Asmussen et al. 2006; Dransfield et al. 2008; Baker et al. 2009). The tribe is divided into two subtribes based, in part,

on gynoecial structure (Dransfield et al. 2008; Rudall et al. 2011), but due to a lack of phylogenetic evidence seven syncarpous genera of the Trachycarpeae from the Americas and the Pacific have not been placed in subtribes within the latest palm classification (*Acoelorrhaphe*, *Brahea*, *Colpothrinax*, *Copernicia*, *Pritchardia*, *Serenoa*, *Washingtonia*; Dransfield et al. 2005). Trachycarpeae have a complex biogeographic distribution characterized by disjunctions as well as island radiations (Fig. 1; Dransfield et al. 2008). It has been suggested that the extant distribution of Trachycarpeae is of Laurasian origin and that lineages have dispersed repeatedly into the Southern Hemisphere and over long distances onto new island and continental locations (Dransfield et al. 2008). Subtribe Rhapidinae of Trachycarpeae is distributed in eastern Asia with a disjunct monotypic genus, *Chamaerops*, found in Mediterranean regions of Europe and North Africa, as well as a monotypic *Rhapidophyllum*, which is found in the southeastern United States. Subtribe Livistoninae of Trachycarpeae is predominantly found in tropical Asia, though four of its six genera span Wallace's Line (Dransfield 1987). One of the genera, *Livistona*, is remarkable for its disjunct distribution between Asia and Australia, with a further disjunct species, *L. carinensis*, endemic to the Horn of Africa and southern Arabia (Dowe 2009; Bacon and Baker 2011). In a recent study, Crisp et al. (2010; see also Dransfield 1987) hypothesized that *Livistona* is a recent immigrant to Australia from a Miocene (17–10 Ma) dispersal event of eastern Asia origin but were unable to address the African disjunction due to inadequate taxon sampling.

Within Trachycarpeae, there are three cases of species radiation in island systems. Nineteen *Copernicia* species occur in the Caribbean, primarily in Cuba, and three other species are found in South America (Govaerts and Dransfield 2005). Because the Caribbean has been a tectonically active region for more than 100 myr (Burke 1998), there have been opportunities for both vicariance and dispersal. Ecological speciation may also have been important in the Cuban *Copernicia* radiation as many of the species are specialized to serpentine soils (Henderson et al. 1995; Brady et al. 2005). Second, *Licuala* is one of the largest palm genera comprising approximately 170 species (Barfod A. S., personal communication 2010) that are distributed throughout eastern Asia, Southeast Asia, and Australasia. *Licuala* displays a pronounced bimodal distribution of species diversity across Wallace's Line, with high diversity in the Sunda region and New Guinea and low diversity in Wallacea (Dransfield 1987). Lastly, *Pritchardia* includes 27 species of the central Pacific and the Hawaiian Archipelago (Hodel 2007, 2009). Although species boundaries within *Pritchardia* have been difficult to estimate in the past, it has been hypothesized that the formation of the volcanic archipelago itself has driven speciation (Hodel 2007) in the same manner as other Hawaiian lineages (Gillespie 2004). Available phylogenetic evidence, though poorly supported, indicates that *Pritchardia* is most closely related to North American members of the Trachycarpeae (Baker et al. 2009), suggesting that the tribe may have dispersed into the Pacific from both the east, in the case of *Pritchardia*, and the west, as in Livistoninae.

Here, we aim to gain broad insight into island radiations by examining each of the island clades of Trachycarpeae and comparing patterns across them to identify correlates of their diversification. We use a highly sampled phylogenetic tree based on data from both the nuclear and plastid genomes to reconstruct the generic relationships of Trachycarpeae. Having calibrated the phylogeny with confidently identified and dated fossil information, we estimate divergence times

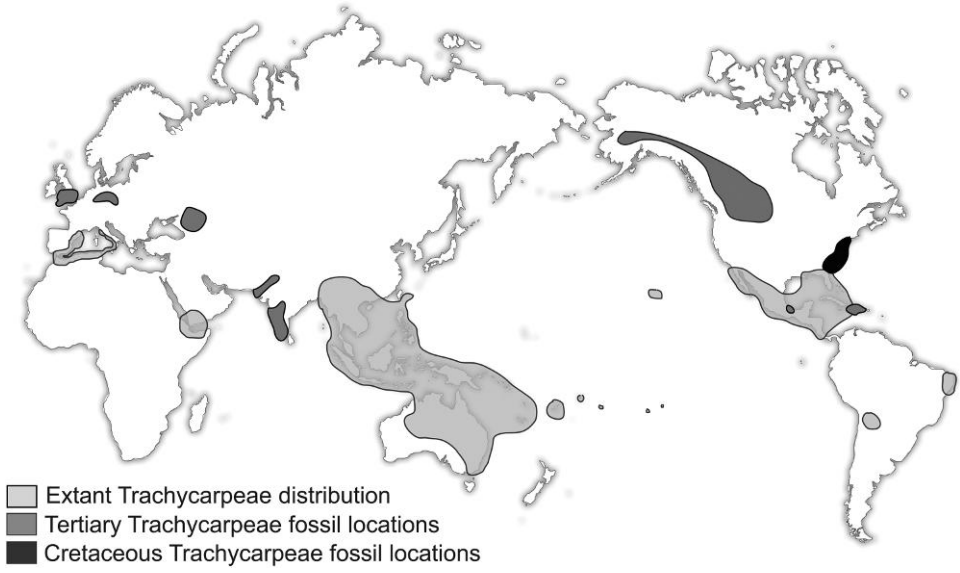

FIGURE 1. Map showing the extant, Tertiary, and Cretaceous distributions of Trachycarpeae. Fossil distributions are based on published fossil records attributable to the tribe but not unequivocally identified and are likely to be an incomplete estimation of past ranges.

and reconstruct ancestral distributions to infer the historical biogeography of the tribe. Our specific goals are to infer the timing and geographic origin of the lineages of Trachycarpeae, to explore the processes behind disjunct distributions, and to understand which geological and climatic events influenced each of the three island radiations. We assess general emerging patterns across the island clades and the roles that dispersal and geology have played in island radiations.

Materials and Methods

Taxon Sampling and DNA Sequencing

One hundred and thirteen species were sampled (online Appendix; available on Dryad, DOI:10.5061/dryad.2jc763qt) including all genera of Trachycarpeae and 10 outgroups. Each of the remaining seven tribes of subfamily Coryphoideae was represented among the outgroups as were subfamilies Arecoideae (*Geonoma*) and Ceroxyloideae (*Aphandra*) based on their sister-group relationship to Coryphoideae inferred in the complete genus-level family-wide analysis of Baker et al. (2009). We sampled 19–100% of species in each ingroup genus and on average genera were represented by 66% of their known species. More than one accession was sampled for some species yielding a total of 146 terminals included in the simultaneous analysis.

Genomic DNA was extracted following Alexander et al. (2007) and 720 new sequences were generated for protein-coding regions of *matK*, a coding region of *ndhF*, and coding and intergenic spacer regions of *trnD–trnT*, as well as three exon-anchored intron-spanning nuclear loci (*CISP4*, *CISP5*, and *RPB2*; Table 1). The *matK* data were generated from single amplifications using primers *matK*-19F and *matK*-1862R, with both *matK*-300F and *matK*-809F used as internal sequencing primers (Steele and Vilgalys 1994; Asmussen et al. 2006). Amplifications of *trnD-trnT* followed Hahn (2002), *ndhF* followed Cuenca and Asmussen-Lange (2007), *CISPs 4* and *5* followed Bacon et al. (2008), and *RPB2* followed Roncal et al. (2005). Amplified products were purified using Qiagen PCR purification kits and sequenced either by the Cancer Research Center at the University of Chicago (Chicago, IL) or Macrogen (Korea). All sequences generated for this study were deposited in GenBank under accession numbers HQ20241 to HQ20961.

Phylogenetic Analysis

Alignments were obtained using default parameters in MUSCLE v3.6 (Edgar, 2004) and manual adjustments were performed in MacClade v4.03 (Maddison and Maddison 2001) following Simmons (2004). Only parsimony-informative (PI) gaps were scored from unambiguously aligned regions using modified complex indel coding (Simmons and Ochoterena 2000; Müller 2006). Each of the six loci was analyzed independently to resolve their respective gene trees, which were compared to check for mutually well-supported contradictory signal that may have been caused by differential selection, hybridization, incomplete lineage sorting, recombination, and/or unrecognized paralogy (Doyle 1992). Default parameters in the Recombination Detection Program (RDP; Martin and Rybicki 2000) and Geneconv (Sawyer 1989) were used to test for recombination within each locus. Uninode coding was used to address a hypothesized gene duplication event in the *CISP5* locus (Simmons et al. 2000; Simmons and Freudenstein 2002). After inferring the duplication event, the unambiguously optimized character states (i.e., all possible character states that can be optimized at the node) were determined using MacClade for the internal node of the gene tree that represents the inferred duplication event, which is treated as the hypothetical ancestor. The uninode hypothetical ancestor sequence was not included in ML analyses because it violates the assumption that all characters have proportional branch lengths across all lineages (Chang 1996). After visual assessment of gene tree incongruence and respective support values, simultaneous analyses of all characters were performed (Kluge 1989; Nixon and Carpenter 1996; TreeBase study accession 11401).

Maximum parsimony (MP) tree searches and jackknife (JK; Farris et al. 1996) analyses were conducted for each data matrix in PAUP* v4.0b10 (Swofford 2001). ML (Felsenstein 1973) analyses were performed on the CIPRES portal using the RAxML-III algorithm

Table 1. Data matrix and parsimony tree statistics of each analysis, includes gap characters

Matrix	No. of terminals	No. of chars.	No. of PI chars.	% missing/ inapp. chars.	MPT length	No. of MPTs	No. of JK/BS clades ⩾ 50%	Average JK/BS support (%)	CI	RI
CISP4	114	1120	267	33	798	6880	61/78	83/81	0.65	0.91
CISP5	109	2646	249	43	544	9190	32/30	80/77	0.84	0.96
RPB2	107	930	272	20	843	9980	32/75	83/83	0.71	0.92
nDNA (*CISPs 4* and *5*, *RPB2*)	129	4696	801	46	2319	2190	85/89	84/84	0.70	0.92
matK	114	1830	146	6	395	9630	45/64	77/78	0.72	0.90
ndhF	139	970	77	8	186	10000	35/52	78/78	0.79	0.96
trnDT	133	886	78	17	256	380	33/43	79/74	0.54	0.88
Plastid (*matK*, *ndhF*, *trnDT*)	146	3686	301	23	861	850	65/89	81/82	0.65	0.91
Simultaneous parsimony	146	8283	1102	28	3208	4660	95/109	84/84	0.68	0.91

Notes: CI = ensemble consistency index (Kluge and Farris 1969) on the most parsimonious tree(s) for the parsimony-informative characters; RI = ensemble retention index (Farris 1989); chars. = characters; inapp. chars. = inapplicable characters; MPT = most parsimonious trees.

(Stamatakis et al. 2005). ML bootstrap (BS; Felsenstein 1985) analyses were also conducted using RAxML (Stamatakis et al. 2008). The Akaike Information Criterion (AIC) (Akaike 1974), as implemented in jModeltest v0.1.1 (Posada 2008), was used to compare and select the best-fit model for each data matrix following Pol (2004) and Posada and Buckley (2004). Because not all models applied by jModeltest are implemented in RAxML, more parameterized models were used when the model selected by the AIC was not available. Following Yang (2006) and Stamatakis et al. (2008), only the gamma distribution (Yang 1993) was estimated and not invariant sites (Reeves 1992). Congruence between the MP and ML analyses was visualized using TreeGraph2 where contradictory branch support is mapped by splitting branches into subtrees to find the highest conflicting support (Stöver and Müller 2010).

Divergence Time Estimation

Bayesian relaxed clock dating.—Higher Bayes factors (Nylander et al. 2004) were recovered in BEAST v1.4.8 (Drummond et al. 2006) for a relaxed rather than a strict clock model and the relaxed model was used to estimate divergence times in Trachycarpeae. The simultaneous data set was partitioned by locus, nucleotide substitution models were unlinked among partitions, and the GTR + Γ model was used based on the jModeltest results. A Yule tree prior, linked plastid clock models, and default operators were also defined in the BEAST .xml input. The lognormal distribution has been shown to be the most appropriate for modeling paleontological information because lineage origination should not postdate the fossil occurrence (Ho 2007; Ho and Phillips 2009). Lognormal prior distributions were set on three palm fossil calibrations. To test for convergence, analyses were run until the effective sample sizes of all parameters exceeded 200 and a 10% burn-in was removed (Drummond et al. 2006; Drummond and Rambaut 2007). Manual cross-validation of BEAST results was conducted by iteratively comparing ages reconstructed across particular nodes of the tree for the seven possible combinations of the three fossils to detect the narrowest credible set of estimated ages (Table 2). Although divergence time estimation may be biased due to an inappropriate model of among linkage group variation and a coalescent species tree is likely to give more accurate results for multiple unlinked partitions when compared with simultaneous analysis (e.g., McCormack et al. 2010), our sampling of one or two individuals per species and six loci is insufficient to determine the coalescent species tree for Trachycarpeae (Knowles 2010).

Fossil calibrations.—The use of multiple calibration points that are internal and external to the ingroup is expected to provide more realistic and less error-prone divergence time estimates than single calibrations (Brochu 2004; Müller and Reisz 2005; Marjanović and Laurin 2007). Following these guidelines, we used fossil information to constrain three stem nodes (sensu Magallón and Sanderson 2001) inferred in the Bayesian topology. The use of calibrations at stem nodes is appropriate because fossils are incomplete and often do not display sufficient synapomorphies to be positioned at crown nodes. All fossil calibrations provided are minimum ages and potentially are underestimations (see Heads 2011). Means (1.7) and standard

TABLE 2. Cross-validation of crown age estimates (Ma) for selected nodes tracked with effective sample size values in BEAST

		Extant taxa					Fossil taxa			
Calibration		HI *Pritchardia*	*Saribus*	*Copernicia*	*Livistona*	Rhapidinae	Trachycarpeae	*Palaeoraphe*	*Hyphaene*	*Sabalites*
PAL	Mean	1.76	6.13	8.61	9.01	10.54	20.11	17.78	13.75	28.47
	95% lower	0.75	3.51	5.09	5.77	7.53	16.00	15.05	7.44	20.26
	95% upper	3.00	8.96	12.49	12.41	13.74	24.64	20.93	20.76	37.59
HYP	Mean	4.63	15.92	22.57	23.57	27.57	52.40	46.50	27.93	76.64
	95% lower	1.52	7.01	9.84	11.16	14.47	26.16	23.66	25.14	42.97
	95% upper	8.70	26.48	38.46	38.17	43.82	84.31	74.13	31.20	117.81
SAB	Mean	5.30	18.13	25.80	26.72	31.13	59.83	53.07	42.27	87.22
	95% lower	2.21	10.45	15.26	16.95	22.13	45.18	39.35	25.36	84.29
	95% upper	8.92	26.37	37.34	36.57	40.86	74.78	66.64	59.06	90.63
PAL-HYP	Mean	2.15	7.71	10.64	11.20	13.01	23.46	20.54	27.08	42.51
	95% lower	0.95	4.61	6.45	7.21	9.37	17.87	16.39	24.80	32.76
	95% upper	3.63	10.93	15.72	15.24	16.87	30.16	25.40	29.53	53.11
PAL-SAB	Mean	3.31	10.89	15.87	15.99	18.61	34.66	28.57	35.95	86.60
	95% lower	1.37	5.91	8.68	9.72	12.36	22.93	20.11	16.79	84.07
	95% upper	5.71	16.23	23.78	22.85	25.34	47.82	38.12	87.59	89.46
HYP-SAB	Mean	5.30	18.40	25.74	26.91	31.67	60.58	53.71	28.06	87.23
	95% lower	2.25	10.56	15.50	17.12	22.76	45.85	40.13	25.20	84.28
	95% upper	9.03	26.64	37.00	37.02	41.36	76.44	68.12	31.26	90.65
PAL-HYP-SAB	Mean	3.50	11.71	17.09	14.65	20.09	37.74	30.90	27.76	86.65
	95% lower	1.42	6.40	9.74	9.17	13.91	25.11	22.14	25.07	84.18
	95% upper	5.88	17.02	25.38	20.84	26.77	51.05	40.38	30.84	89.61

Notes: The 95% HPD credible sets are indicated and the calibration points are *Palaeoraphe dominicana* (PAL), *Hyphaene kappelmanii* (HYP), and *Sabalities carolinensis* (SAB). HI = Hawaii.

deviations (0.3) of the lognormal distribution were consistent across calibration points and the zero offset value was set to the mean fossil ages described below.

The costapalmate leaf compression *Sabalites carolinensis* (SAB; Berry 1914) is the oldest palm fossil that can be unequivocally allocated to a taxonomic group within palms (subfamily Coryphoideae). We placed the constraint at the stem node of the Coryphoideae, for which palmate leaf-shape is a synapomorphy (Dransfield et al. 2008). The substrate where *S. carolinensis* was found dates to the Late Coniacian-Early Santonian (Fig. 1; Harley 2006) and the mean of the lognormal distribution for this fossil was 86.7 Ma. The amber-preserved flowers of *Palaeoraphe dominicana* (PAL; Poinar 2002) share floral characteristics with *Acoelorrhaphe* and *Colpothrinax* and particularly *Brahea*. However, there is insufficient evidence to link it directly to any of these genera and the phylogeny does not place the three genera as immediate relatives. We allocated the fossil to the stem node of *Brahea* that separates *Copernicia*, *Pritchardia*, and *Washingtonia* from the rest of Trachycarpeae based on synapomorphies including furrows on the petals, distinct sepals, and the size and shape of the anthers using a lognormal distribution mean of 17.5 Ma based on Iturralde-Vincent and MacPhee (1996). The fossil petiole of *Hyphaene kappelmanii* (HYP; Pan et al. 2006) is identified based on the large, upturned spines, flattened, broad spine bases, and the distinctive arcuate shape of the petiole edge between the spines. These characteristics link the fossil with a high degree of confidence to *Hyphaene* in tribe Borasseae. We used the fossil as a constraint on the stem node of *Borassus* with a lognormal distribution mean of 27.5 Ma.

Ancestral Range Reconstruction

Ancestral range patterns were inferred using 11 geographic areas: (A) Africa and Arabia; (B) New Caledonia; (C) Papuasia (New Guinea and the Solomon Islands); (D) South America; (E) India to Thailand (excluding peninsular Thailand), Japan, and China; (F) Malesia (including peninsular Thailand, excluding Papuasia); (G) central Pacific; (H) Hawaii; (I) southern North America, Central America, and the Caribbean; (J) Mediterranean Europe; and (K) Australia. Biogeographic areas were based on areas of endemism in the tribe while attempting to minimize the total number of areas (Sanmartín and Ronquist 2004). A likelihood framework for examining historical range shifts was implemented using the Dispersal-Extinction-Cladogenesis method (DEC; Ree et al. 2005) in Lagrange (www.reelab.net/largrange). DEC has been suggested to be a robust method of inferring historical biogeography because it takes into account divergence time estimates (Ree and Smith 2008). We used the ultrametric tree generated by BEAST to infer ancestral distributions with a uniform dispersal matrix. Uniform probabilities of dispersal across all 11 areas and throughout the duration of the Neogene may be unrealistic but were preferred over specifying a more parameterized dispersal matrix.

RESULTS

Incongruence and Simultaneous Analysis

The nuclear regions *CISP5* and *RPB2* resolved a non-monophyletic *Brahea*, which was inconsistent with results from the other gene trees (online Figs. 1 and 3 vs. online Figs. 2 and 4). The *RPB2* result was poorly supported (52% BS/<50% JK; online Fig. 3), whereas the *CISP5* result was well-supported (five branches with >75% JK/BS separate the two *Brahea* clades; online Fig. 1). Recombination was not detected in any of the loci using two tests as implemented in RDP and Geneconv. After accounting for hypothesized paralogy in *CISP5* using uninode coding, the topology estimated in BEAST (online Figs. 5 and 6) was in agreement with those resulting from MP and ML analyses of the simultaneous data set (Figs. 2 and 3) except for four instances (i) the relationships among *Copernicia*, *Pritchardia*, and *Washingtonia* (Fig. 4); (ii) the relationships amongst *Lanonia*, *Livistona*, and *Johannesteijmannia*; (iii) the position of *Colpothrinax*; and (iv) the position of *Washingtonia*. Manual BEAST fossil cross-validation shows variation in divergence time estimation (Table 2), with the best hypothesis based on the narrowest credible set from all three fossil calibrations interacting in one analysis (PAL-HYP-SAB; Table 3; Ho and Phillips 2009).

Divergence Times and Historical Biogeography in Trachycarpeae

Lagrange recovered dispersal and extinction rates of Trachycarpeae to be 0.003 and 0.004 per myr, respectively. Likelihood scores were not significantly different between multiple reconstructions within the confidence window of two log-likelihood units for 15 nodes (Table 4). Figure 5 shows the most likely scenario of range inheritance on a summarized dated phylogeny of Trachycarpeae genera and biogeographic groups of interest within certain genera. Dispersal resulting in range expansion was common throughout the tree during the Miocene, when a majority of the 17 dispersal events were inferred to have occurred. There were 13 local extinction events, which were inferred when a daughter lineage inherited a different range from its parent (range expansion prior to extinction).

Origins of Trachycarpeae.—Based on Lagrange analyses, the crown node of Trachycarpeae was unequivocally inferred to have originated in biogeographic region "I" (southern North America, Central America, or the Caribbean). The BEAST analyses estimated that

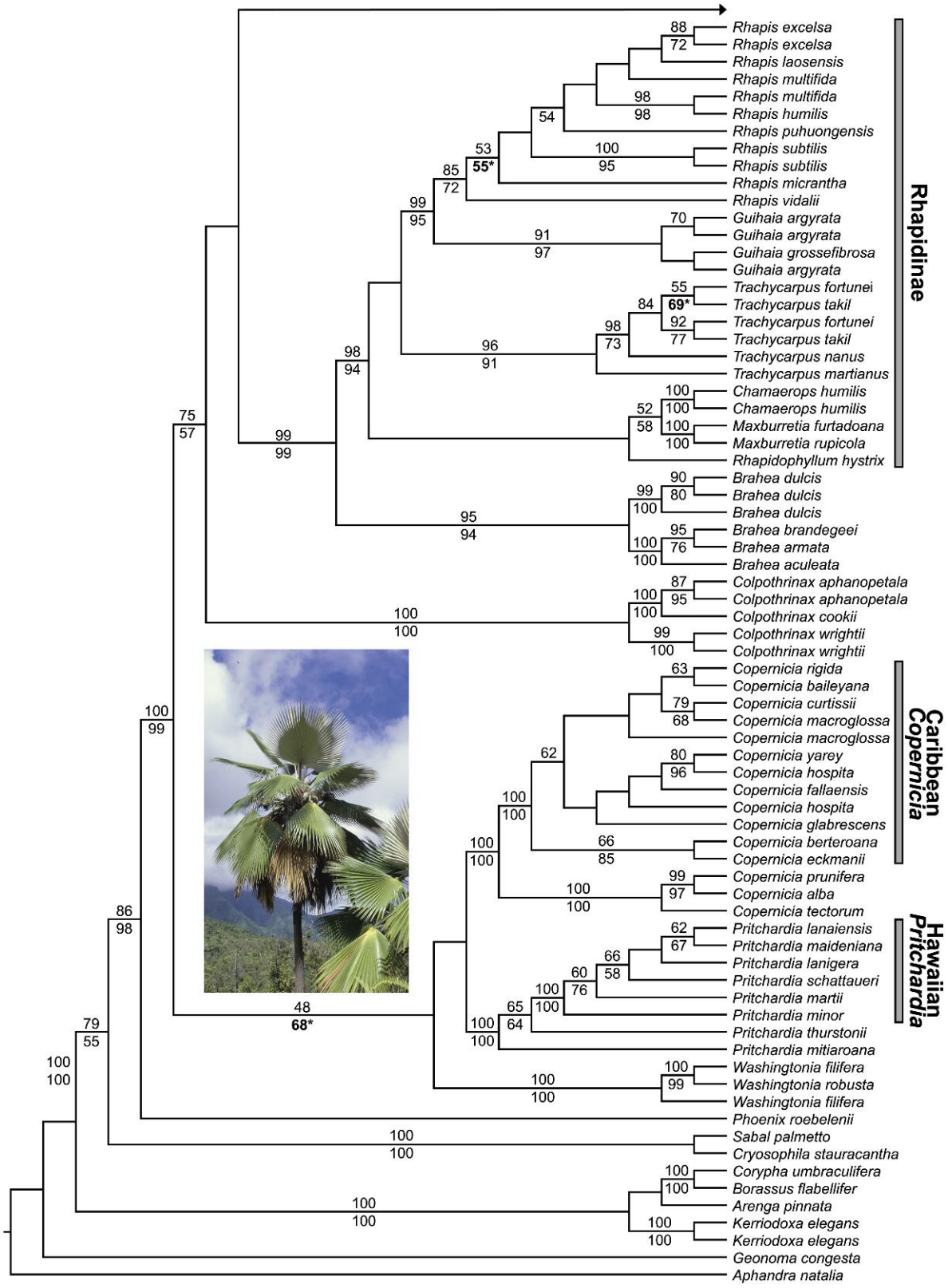

FIGURE 2. Basal portion of the simultaneous-analysis ML BS tree with likelihood BS values above each branch and parsimony JK values below each branch with only values ⩾50% shown for both measures. Clades in the likelihood BS tree that were contradicted by clades in the parsimony JK tree are indicated with bold font and asterisks, with JK support for the highest contradictory parsimony clade listed. *Pritchardia viscosa* from Kauai, HI is shown (photo courtesy of J. Dransfield).

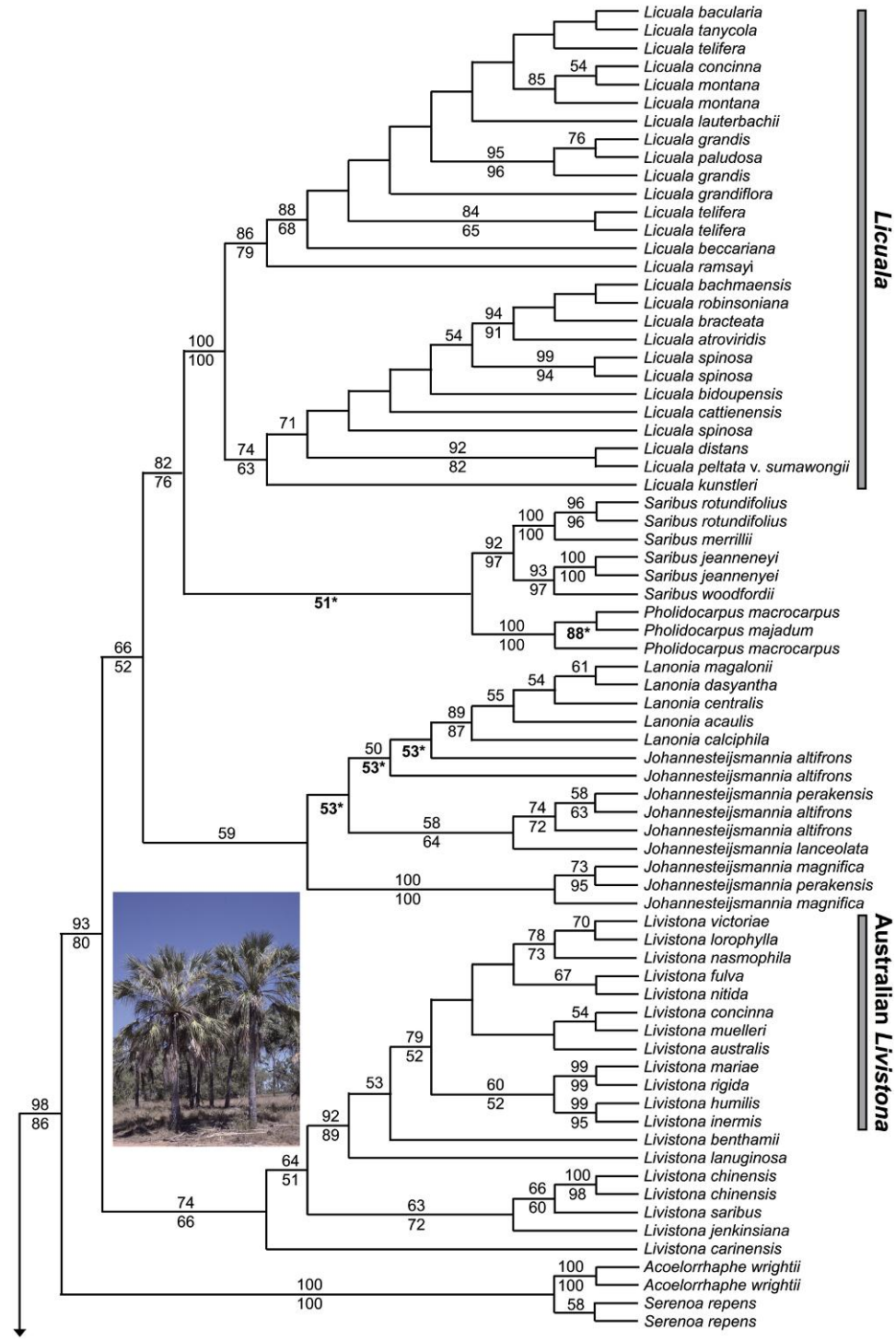

FIGURE 3. Distal portion of the ML simultaneous-analysis BS tree that comprises Livistoninae and its sister clade of *Serenoa* and *Acoelorrhaphe*. Support values and incongruence indicated as in Figure 2. *Livistona lanuginosa* from Queensland, Australia is shown (photo courtesy of J. Dransfield).

the stem node age of Trachycarpeae was 86.65 Ma [95% highest posterior density (HPD) 89.61–84.18 Ma], whereas the crown node of Trachycarpeae was estimated at 37.74 Ma (95% HPD 51.05–25.11 Ma; online Fig. 5).

Disjunct distributions.—We used both divergence time and biogeographical analyses to interpret the climatic and geological processes that resulted in disjunct distributions in both Livistoninae and Rhapidinae. In both subtribes southern North America, Central America, or

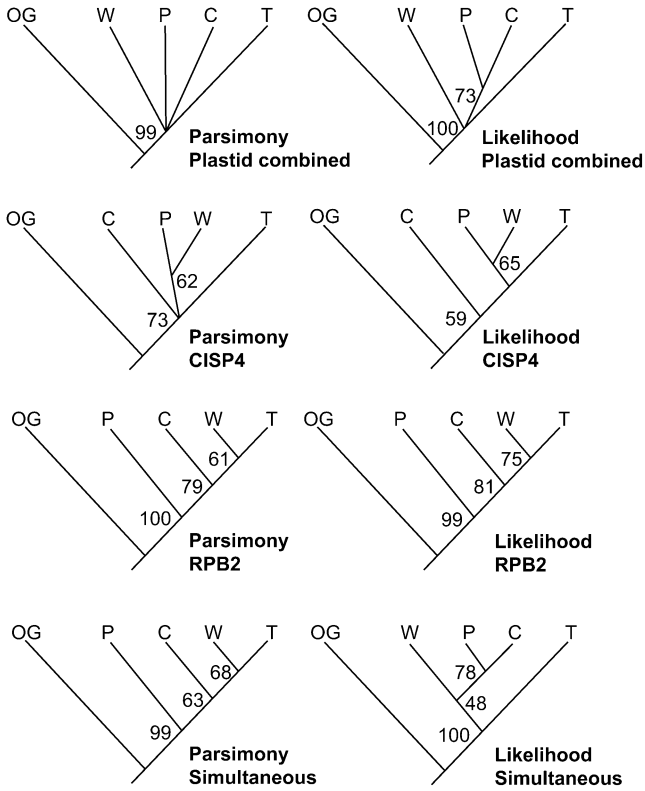

FIGURE 4. Parsimony versus likelihood reconstructions of plastid combined, *CISP4*, *RPB2*, and simultaneous analyses displaying variation in the resolution of *Pritchardia* (P), *Copernicia* (C), and *Washingtonia* (W) with respect to the outgroups (OG) and the remaining Trachycarpeae (T) members. Support for each clade is based on BS for likelihood and JK for parsimony.

the Caribbean ("I") was inferred for the stem node distributions that dated to 26.04 and 24.08 Ma, respectively (95% HPD 34.25–18.49 Ma and 32.66–17.26 Ma; Fig. 5; Table 3). Dispersal events then occurred in these lineages as their geographic distributions expanded during the Middle to Late Miocene (Fig. 5).

TABLE 3. Crown and stem node estimations in Ma for clades of interest based on three fossil calibrations

	Stem			Crown		
Genus	Mean	Upper	Lower	Mean	Upper	Lower
Acoelorrhaphe	9.73	16.46	4.34	0.38	1.21	0
Brahea	24.80	32.66	17.26	15.5	24.31	7.19
Chamaerops	17.31	23.62	11.40	6.20	10.57	2.34
Colpothrinax	28.56	37.49*	20.17*	7.87	14.44	2.74
Copernicia	32.10	44.73	20.13	17.09	25.38	9.74
Caribbean *Copernicia*	17.09	25.38	9.74	6.88	10.58	3.80
Guihaia	14.65	20.08	9.53	3.92	7.01	1.32
Johannesteijsmannia	21.63	28.73	15.41	7.44	11.57	3.86
Licuala	19.63	26.26	13.68	13.34	18.35	8.64
Lanonia	13.91	20.86*	7.85*	6.28	11.85	1.60
Livistona	18.84	25.22	12.24	14.65	20.84	9.17
Livistoninae	26.04	34.25	18.49	23.29	16.32	30.70
Maxburretia	17.31	23.62	11.40	5.30	9.39	1.81
Pholidocarpus	17.97	24.27	11.98	3.29	6.31	0.92
Pritchardia	32.10	44.73	20.13	10.57	17.05	5.13
Hawaiian *Pritchardia*	8.04	13.06	3.61	3.50	5.88	1.42
Rhapidinae	24.80	32.66	17.26	20.09	26.77	13.91
Rhapidophyllum	20.09	26.77	13.91	18.40	24.80	12.46
Rhapis	14.65	20.08	9.53	11.30	16.11	6.97
Saribus	17.97	24.27	11.98	11.71	17.02	6.40
Serenoa	9.73	16.46	4.34	7.97	14.06	3.06
Trachycarpeae	86.65	89.61	84.18	37.74	51.05	25.11
Trachycarpus	18.84	24.82*	12.68*	12.16	19.01	5.69
Washingtonia	34.43	45.73	24.45	5.41	10.91	1.44

Notes: The mean as well as the credible set (95% HPD) are listed as Ma and nodes that are supported by <0.50 posterior probabilities are indicated with *.

TABLE 4. Alternative ancestral range reconstructions for crown nodes of Trachycarpeae

Node	Area(s) inferred	-lnL	Rel. Prob.	Node	Area(s) inferred	-lnL	Rel. Prob.
Papuasian + Australian *Licuala*	CEFG–K	224.3	0.2877	Livistoninae + *Serenoa* + *Acoelorrhaphe*	E–I	224.0	0.3879
	E–K	224.4	0.2453		F–I	244.1	0.3484
	F–K	224.6	0.2063		K–I	225.5	0.1860
	E	226.0	0.0498		I	225.9	0.0543
Above + Sunda *Licuala*	EF–E	224.2	0.2956	"A" *Livistona* + *Lanonia*	E–A	223.5	0.6458
	F	224.5	0.2159		E	224.4	0.2410
	K–F	224.7	0.1793	*Serenoa* + *Acoelorrhaphe*	I	223.3	0.7197
	C–F	224.9	0.1535		I–DI	224.3	0.2633
	FK–F	225.9	0.0564	*Chamaerops* + *Maxburretia*	J-F	224.7	0.1776
Licuala, *Saribus* + *Pholidocarpus*	F	223.7	0.5072		I	224.9	0.1554
	EF–F	224.4	0.2613		J	224.9	0.1532
	FK–F	225.5	0.0814		F	224.9	0.1449
Above + *Johannesteijsmannia*	F	223.6	0.5753		J–I	225.1	0.1194
	EF–F	224.3	0.2726		I–F	225.2	0.1126
	BCG–F	224.2	0.2969		E	226.6	0.0286
Saribus + *Pholidocarpus*	F	224.3	0.2753	Above + *Rhapidophyllum*	I	224.0	0.3666
	C–F	224.7	0.1821		J–I	224.5	0.2274
	B–F	224.8	0.1689		F–I	224.5	0.2198
Livistoninae	F–E	224.1	0.3347		E–I	225.8	0.0622
	E	224.7	0.1882	Rhapidinae + *Brahea*	I	223.3	0.7855
	F	225.3	0.1013		EI–I	224.7	0.1943
	EF–E	225.4	0.0903	*Copernicia* + *Pritchardia*	I	223.7	0.5079
	F–K	226.0	0.0517		I–G	224.4	0.2496
Livistona + *Lanonia*	E	223.7	0.4860		I–H	224.9	0.1556
	EK–E	224.5	0.2374	*Pritchardia*	H–G	223.6	0.5570
	E–AE	225.2	0.1147		G	224.1	0.3499

Notes: Alternative reconstructions are within 2 log likelihood units of the ML estimate where area abbreviations are provided in Figure 5. Relative probability (Rel. Prob.) of the global likelihood for the optimal optimization is given (in gray shading) and compared with the alternative(s). The first of the two distributions for each node leads to the upper daughter branch and the second to the lower daughter branch in Figure 5. The Arabian and African biogeographic region is abbreviated as "A"; Livistoninae comprise *Licuala*, *Saribus*, *Pholidocarpus*, *Johannesteijsmannia*, *Livistona*, and the *Licuala* segregate; and Rhapidinae comprises *Rhapis*, *Guihaia*, *Trachycarpus*, *Chamaerops*, *Maxburretia*, and *Rhapidophyllum*.

Island radiations.—The stem and crown nodes of *Copernicia* were inferred to be distributed in southern North America, Central America, or the Caribbean ("I"; Fig. 5). Following the crown node divergence of *Copernicia*, the genus was found to have colonized South America. The mean estimated divergence time of the *Copernicia* stem node was 32.10 Ma (95% HPD 44.73–20.13 Ma) and the emergence of the extant radiation of Caribbean *Copernicia* lineages dated to 6.88 Ma (95% HPD 10.58–3.80Ma; online Fig. 5). The stem and crown nodes of *Licuala* were inferred to have an origin in Malesia ("F") and although there were alternative reconstructions for these nodes, they all included "F" within the range estimated (Table 4). Four dispersals were inferred within *Licuala* and the range of this genus expanded into areas "C" (Papuasia), "E" (India to Thailand, Japan, and China), "G" (western Pacific), and "K" (Australia). BEAST estimated the mean stem node of *Licuala* in the Miocene at 19.63 Ma (95% HPD 26.26–13.68 Ma), whereas the crown group dated to 13.34 Ma (95% HPD 18.35–8.64 Ma; online Fig. 6). Our data support a North American, Central American, or Caribbean ("I") ancestral *Pritchardia* stem distribution, which was followed by dispersal to the central Pacific ("G"; Fig. 5). A subsequent single colonization of *Pritchardia* to Hawaii from the central Pacific was inferred from a dispersal event followed by local extinction (Fig. 5). The stem node age of *Pritchardia* was estimated at 32.10 Ma (95% HPD 44.73–20.13 Ma), the crown node age at 10.57 Ma (95% HPD 17.05–5.13 Ma), and the diversification of the Hawaiian *Pritchardia*

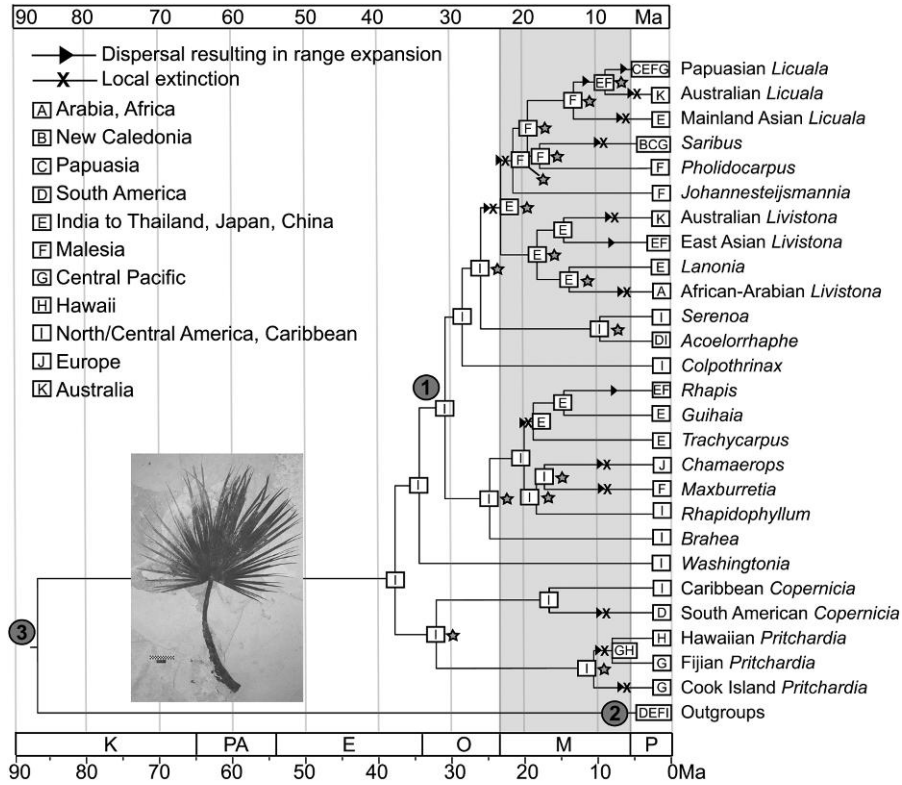

FIGURE 5. Ancestral range reconstruction for Trachycarpeae using Lagrange. Reconstructions are shown as boxes at each node and nodes with alternative reconstructions (within 2 log likelihood units of the maximum) are indicated with a star. Two modes of range inheritance (range expansion and local extinction) are indicated as symbols on branches of the phylogeny (see Results section). For clarity, selected sister terminals from a single area have been pruned from the chronogram. The three fossil calibrations, marked 1 (*Palaeoraphe*), 2 (*Hyphaene*), and 3 (*Sabalites*), are indicated with their placements on the tree.

lineage at 3.50 Ma (95% HPD 5.88–1.42 Ma; online Fig. 5).

DISCUSSION

Our data from the palm tribe Trachycarpeae permitted the examination of island radiations within three genera and subsequent comparison across genera to detect general processes driving island diversification. Based on the evidence from *Copernicia*, *Licuala*, and *Pritchardia*, we hypothesize that the island distributions result from dispersal events and that lineages subsequently diversified by allopatric and ecological speciation. Furthermore, these three island lineages appear to have been heavily influenced by dispersal during times of major geological and climatic events in the Miocene. Although there may be limitations to the methods used (e.g., gene tree incongruence, minimum age constraints, error in fossil age determinations, fixed geographic ranges through time), our estimates, in concert, likely detect mechanisms of island diversification that correspond to geological and climatic history.

Incongruence and Simultaneous Analysis

The non-monophyly of *Brahea* resolved in the nuclear region *CISP5* was the only well-supported case of incongruence between the separate gene trees (online Fig. 1 vs. online Figs. 2–4). Incongruence between loci could be due to hybridization, selection, recombination, incomplete lineage sorting, or paralogy (e.g., Doyle 1992). We suggest that hybridization is not responsible for the *Brahea* resolution because admixture would likely be widespread in the genome and not be restricted to short intron regions while being absent from the other independently segregating coalescent genes. Also, hybridization events across widely divergent lineages would have to be invoked to account for the topological conflicts. Although a comprehensive assessment of hybridization in palms is lacking, there is no evidence to support its occurrence in *Brahea* (Quero 1992; Henderson et al. 1995; Dransfield et al. 2008). We do not believe differential selection on *CISP5* to have caused incongruence because five well-supported (>75% JK/BS) branches separate the two *Brahea* clades and there would have to be extreme levels of selection to cause the topology. Second, the *CISP5* locus primarily spans intron sequence and therefore major shifts in selection pressures are unlikely. Furthermore, significant signal for recombination was not detected in any of the loci based on two exploratory analyses. Incomplete lineage sorting is a more difficult alternative to reject, but we believe the amount of ancestral

polymorphism that would need to have been present in the most recent common ancestor to form highly supported and divergent clades is unlikely.

We hypothesize that differential sampling of paralogous copies of the *CISP5* gene caused the *Brahea* incongruence among the coalescent genes. Our hypothesis is that a duplication event occurred on the branch leading to Trachycarpeae plus its sister group, Phoeniceae (online Fig. 1). If our paralogy hypothesis is correct, we infer at least (i) a loss of Paralog 2 prior to divergence of the lineage that gave rise to the taxa sampled in Fig. 3; (ii) a loss of Paralog 1 prior to divergence of the lineage that gave rise to the Rhapidinae (after the divergence of *Rhapidophyllum*); (iii) a loss of Paralog 2 in the lineage that gave rise to *Pritchardia*; and (iv) depending on the relationships among *Colpthrinax*, *Copernicia*, *Pritchardia*, and *Washingtonia*, at least one additional loss of Paralog 2 in this/these lineage(s). High divergence on the branch length leading to the ingroup members of the basal *Brahea* clade (0.178), which is more than twice the average of all the other branch lengths on the tree (0.066; online Fig. 1) is extremely unlikely to be accounted for by lineage sorting given that Paralogs 1 and 2 would have had to been present as alternative alleles at a single locus in the ancestor of Trachycarpeae. Although our results may raise some uncertainty, *Brahea* is a widely recognized genus that is readily distinguished morphologically from other American fan palms (Henderson et al. 1995) and its monophyly is strongly supported by *CISP4* and our simultaneous analyses. Nevertheless, the group merits closer phylogenetic scrutiny with denser sampling using more loci and more *Brahea* species and individuals.

After accounting for paralogy in *CISP5* using uninode coding, the topology estimated in BEAST (online Figs. 5 and 6) was in agreement with those resulting from MP and ML analyses of the simultaneous data set (Figs. 2 and 3) except for the relationships among *Copernicia*, *Pritchardia*, and *Washingtonia*. We hypothesize that these differences are caused by where the long outgroup branch attached to the ingroup (Fig. 4). Both the MP and ML *RPB2* partitions resolved *Pritchardia* as sister to the rest of the Trachycarpeae (100% BS/99% JK), whereas *CISP4* had low support for *Copernicia* being sister to the rest of Trachycarpeae (ML) or the placement of the genus was unresolved (MP). The plastid gene tree was effectively unresolved due to short branches and character conflict between PI characters. In the simultaneous analysis, MP resolved *Pritchardia* as sister to the rest of the Trachycarpeae with 63% JK, whereas ML resolved the root of Trachycarpeae between the clade of (*Washingtonia* [*Copernicia*, *Pritchardia*]) and the rest of the extant Trachycarpeae. These changes in topology (for ML) and support (for MP) are both consistent with long-branch attraction for the nuclear partition, which is overturned (in the simultaneous ML analysis) or reduced (in the simultaneous MP analysis) by the slower evolving plastid partition (Fig. 4; Wolfe et al. 1987).

Divergence Times and Historical Biogeography in Trachycarpeae

Divergence time estimation can be biased by various factors, including, but not limited to, the accuracy of dating fossil strata, error in assigning fossils to taxa and nodes, poorly supported nodes in the topology, the choice and definition of priors, and issues with estimating rates of molecular evolution (Nixon 1996; Graur and Martin 2004; Gandolfo et al. 2008). Additionally, because the timing of gene divergence necessarily predates the actual speciation event (unless gene flow accompanies species divergence; Edwards and Beerli 2000; Carstens and Knowles 2007), divergence times based on a simultaneous approach may be biased toward older dates (McCormack et al. 2010). But if the sources of error are properly accounted for, general statements can be made about biogeographic events that encompass large scale and relatively slow processes over long periods of time (Ho and Phillips 2009).

Increasing the number of calibration points allows for a greater exploration of among-lineage rate diversification (Ho 2007). It has also been suggested that the inclusion of more fossils, and increased uncertainty therein, outweighs the risk of single calibrations that undoubtedly lead to biases (Ho and Phillips 2009). We therefore chose to focus our interpretation on the analysis based on three fossil calibration points. When cross-validating our general hypothesis, we note that with fewer calibration points much more variation is recovered in dates and the ranges of the credible sets were wider (Table 2). In addition, it is more difficult to estimate dates for nodes that are distant from calibrated nodes (e.g., Linder et al. 2005) as seen when comparing the *Palaeoraphe* calibration point estimation for *Hyphaene* to the estimation using *Sabalites* or *Palaeoraphe-Sabalites*. Finally, our data show a close correspondence between the ages estimated for Hawaiian taxa and the ages of the islands themselves based on potassium–argon dating (Kauai 5.1 Ma, Oahu 3–2.6 Ma, Maui Nui 2.2–1.2 Ma, and Hawaii 0.5–0 Ma; online Fig. 5; Table 3; Clague and Dalrymple 1987). Our data are also consistent with the divergence time estimates of Crisp et al. (2010) for *Livistona* and Trachycarpeae (∼29 to 16 Ma and 41 to 23 Ma, respectively).

American origins of the Trachycarpeae.—Trachycarpeae have been proposed to be of Laurasian origin because all but 2 genera (*Pritchardia* and *Copernicia*) are found on Laurasian landmasses and 10 of the remaining genera are strictly Laurasian in distribution (Dransfield et al. 2008). The Lagrange results unequivocally support a Laurasian origin and proposes a more specific biogeographic region "I" (North America, Central America, or the Caribbean) for the crown of Trachycarpeae. Furthermore, BEAST estimated the origin of the crown node of Trachycarpeae in the Late Eocene (40–34 Ma) and indicates a long evolutionary period (>40 myr) where significant extinction may have occurred (Fig. 5, online Fig. 5).

Disjunct distributions.—We hypothesize that the disjunct distributions of extant Trachycarpeae lineages are likely the result of boreotropical forest expansion and subsequent retraction caused by tectonic plate movement and associated climate change (e.g., Donoghue and Smith 2004). The floristic affinity between eastern North America and eastern Asia has been recognized since the time of Linnaeus (see Boufford and Spongberg 1983), and the continuity of boreotropical forests was caused by two land bridges that connected regions in the Northern Hemisphere, the Bering Land Bridge (BLB) and the North Atlantic Land Bridge (NALB). The BLB linked western North America and Eastern Asia and the NALB connected eastern North America with Europe and Asia. Abundant palm fossil occurrences indicate that forests of tropical affinity spread across much of North America (e.g., Berry 1937) and Europe (Chandler 1978; Dransfield et al. 2008 and references therein) in the Eocene and Oligocene periods, during which time lineages of Trachycarpeae may have expanded their ranges into new habitats. In the Miocene (23.8–5.3 Ma) boreotropical forests began to retract due to climatic cooling and drying events and became relictual fragments that were further isolated by the rise of grassland systems (e.g., Millar 1993; Morley 2000). Global climate shifts throughout the Oligocene and Miocene caused boreotropical assemblages to be restricted to refugia in China, Southeast Asia, and in the Americas, whereas fewer lineages survived in southern European and northern African refugia (Tiffney 1985a).

One example of a disjunct pattern in Trachycarpeae is the Rhapidinae. *Brahea* is sister to the subtribe and both *Brahea* and *Rhapidophyllum* are distributed in southern North America ("I"), *Chamaerops* is found in Mediterranean regions of Europe ("J"), *Maxburretia* is distributed in Malesia ("F"), *Guihaia* and *Trachycarpus* are found in mainland areas of Asia ("E"), and *Rhapis* is distributed in both Asia and Malesia ("E" and "F"). Divergence between *Brahea* and the Rhapidinae genera occurred at a mean age of 24.80 Ma and migration and further lineage diversification increased at the crown node age of 20.09 Ma (online Fig. 5). This is consistent with the assertion of Tiffney (1985a) that the Miocene was an important period for the evolution of the disjunction between North America and Asia. Tiffney (1985b) postulated that migration across the NALB was possible during the Paleocene and Eocene and that by the Miocene, some species still filtered across through a series of stepping-stones. Recent work has shown that floristic migration was still prevalent even in the Late Miocene (Tiffney 2008; Denk et al. 2010). As the Miocene progressed, boreotropical regions began to physically split apart more and severe climatic changes caused further fragmentation (Zachos et al. 2001). Fossil evidence of the Rhapidinae also corroborates our hypothesis of disjunctions corresponding to the submersion of both the BLB (e.g., putative Rhapidinae fossil occurrences in Alaska, Hollick 1936, the Middle Eocene chert of British Columbia, Canada [*Rhapidophyllum* and *Brahea*; Erwin and Stockey 1991], and north-central USA [Wyoming; A. Aase, personal communication 2010]) and the NALB [e.g., fossils attributed to extant *Trachycarpus* identified in Lower Eocene deposits of the London Clay (Chandler 1978), in Miocene Czech Republic fossil beds (see Dransfield et al. 2008), and in Oligocene and Miocene substrates of Russia (Takhtajan 1958)]. Though such taxonomic assignments to fossils should be treated with caution and alternative biogeographic reconstruction are likely at certain nodes, these findings are consistent with our hypothesis that the disjunction in Rhapidinae is attributable to migration across both the BLB and NALB combined with subsequent radiation in Asia and extinction in intervening areas outside of boreotropical refugia along the migratory path.

Livistona includes a single Afro-Arabian species that is sister to the rest of the genus (27 species) and a clade of 18 Australian species that is sister to an Asian clade of 9 species (Dowe 2009; Bacon and Baker 2011). Dransfield (1987) postulated a Laurasian origin for the tribe and further suggested that the Australian *Livistona* originated from a Sundaland colonizer. Recent long distance dispersal across Wallace's Line, as suggested by Dransfield (1987), has been corroborated with molecular data (Crisp et al. 2010). Furthermore, fragmentation of ranges in Australia due to climatic changes and ecological shifts may have led to rapid speciation (Crisp et al. 2010). Our data are consistent with the finding that *Livistona* is a recent lineage in Australia with a mean age of 18.84–14.65 Ma between the stem and the crown nodes, respectively (online Fig. 6) and a dispersal event from region "E" (India to Thailand, Japan, and China) into Australia ("K") and Malesia ("F"; Fig. 5). The study of Crisp et al. (2010) included only limited sampling of non-Australian *Livistona* species and, as a result, did not find support for a non-monophyletic *Livistona* sensu Dransfield et al. (2008). We have used our more densely sampled results to recircumscribe *Livistona* by removing several taxa into the resurrected *Saribus* (Bacon and Baker 2011) and drawing attention to the absence of *Livistona* from Wallacea (Lesser Sunda Islands, Moluccas, Sulawesi), a disjunction that had not been previously appreciated.

Island Dispersal and Diversification

The Copernicia radiation and the Greater Antilles-Aves Ridge.—Land bridges and island chains between North and South America existed periodically from the Late Cretaceous to the Oligocene, including the Greater Antilles-Aves Ridge land bridge (GAARlandia; Iturralde-Vinent and MacPhee 1999). GAARlandia is hypothesized to have comprised large closely spaced islands or possibly a continuous peninsula that linked South America to the Greater Antillean Islands and southern Mexico in the Eocene–Oligocene transition (35–33 Ma; Iturralde-Vinent 2006). The GAARlandia connection predated the Panama land bridge and is known to have influenced biogeographic patterns in many lineages (Cody et al. 2010) such as sloths (McPhee et al. 2000)

and South American trees (Pennington and Dick 2004). GAARlandia has further been suggested to be biogeographically important in other palm groups as well, including a Caribbean diversification pattern proposed for *Gaussia* (Chamaedoreae; Cuenca et al. 2008) and to explain the dispersal of the *Calyptronoma-Calyptrogyne* ancestor to the Caribbean (Geonomateae; Roncal et al. 2010). We propose that the GAARlandia land bridge enabled *Copernicia* species to colonize the Caribbean and areas of South America from northern regions (Fig. 5).

Our results for *Copernicia* are consistent with the GAARlandia hypothesis because the stem node mean age estimated at 32.10 Ma and an upper 95% HPD of 44.73 Ma, which is within the time frame proposed for the GAARlandia land bridge (online Fig. 5). The crown lineage of the South American *Copernicia* was also inferred to have undergone a Miocene dispersal event, which may represent the movement of ancestral lineages across the land bridge to South America (Fig. 5). The crown node of the Caribbean crown lineage emerged at a mean age of 6.88 Ma (Late Miocene) and corresponds to the timing of the isolation of islands due to active tectonic disruption and the subsidence of the land bridge due to increased sea levels (Iturralde-Vinent and MacPhee 1999). High diversification rates in Cuban *Copernicia* may be attributed to frequent allopatric speciation from repeated geological change of the island and the region and/or may be driven by ecological speciation based on the formation of serpentine soils in the generic center of diversity (Henderson et al. 1995; Brady et al. 2005).

The Licuala radiation and geologically mediated speciation.—We inferred the stem age of Livistoninae as 26.04 Ma (online Fig. 6) and to have been distributed in biogeographic region "I" (Fig. 5), whereas the crown node was estimated at 23.29 Ma and inferred to have been distributed in Malesia ("E"; Fig. 5; Table 4). Leading up to the Oligocene, newly formed islands that were derived from the extrusion of Indochina to the southeast were further broken up during the Late Eocene and Early Oligocene (39–30 Ma; Morley 2000). These islands underwent more geological restructuring from 25 Ma onward (Hall 2002). Formation of modern Malesia by the final juxtaposition of the Sunda and Sahul shelves in the mid-Miocene is well established (~16 to 12 Ma; Audley-Charles et al. 1981; Morley 1998), and we propose that the newly reformed region spurred the radiation of genera such as *Licuala* via allopatric speciation. Lagrange inferred dispersal events on each of the three branches leading to major *Licuala* groups, two of which were followed by local extinction (Fig. 5). The inferred stem age for *Licuala* is 19.63 Ma and the crown age is estimated at a mean of 13.34 Ma, which closely corresponds to the timing of the final positioning of islands in Malesia. Furthermore, although Lagrange reconstructed three alternative stem origins for *Licuala*, all included Malesia ("F"; Table 4).

Dransfield (1981, 1987) hypothesized that the bimodal distribution of *Licuala*, where species diversity is high on either side of Wallace's Line and low in intervening Wallacea, stems from colonizations of both eastern and western origin and/or to Pleistocene climatic shifts that caused extinction within Wallacea. With one exception (*L. paludosa*), our data resolved two clades within *Licuala*, one east and one west of Wallace's Line. Taking the phylogenetic and divergence times results together, our data substantiate the hypothesis that the bimodal distribution of *Licuala* is most likely due to Miocene diversification and further show the pattern to be driven by migration associated with the final formation of Malesia.

The Pritchardia radiation from a recent and single colonization event.—The stem node of *Pritchardia*, shared with its sister group *Copernicia*, was inferred to be 32.10 Ma. The ancestral area of this node was inferred to be in North America, Central America, or the Caribbean (region "I", Fig. 5). The general pattern of Hawaiian angiosperm radiations having a North American origin has recently been reviewed by Baldwin and Wagner (2010) and is here illustrated in *Pritchardia*. The mean crown age was estimated at 10.57 Ma and corresponds to the timing of major speciation events in *Pritchardia* responsible for modern diversity in the genus. The geological history of Fiji is complex owing to its proximity to the Australian-Pacific plate boundary (Neall and Trewick 2008), but the oldest exposed land surfaces on Fiji are reported to date from 20 to 5 Ma (Evenhuis and Bickel 2005) for which our inferred age for *P. thurstonii* is consistent (8.04 Ma; Fig. 5). The geological history of the Cook-Austral Chain is even more ambiguous (Neall and Trewick 2008), but it is believed to be older than Fiji based on the geology of the Pacific basin as a whole, which also corresponds to our data on the reconstruction of the Cook Island endemic *P. mitiaroana* (10.56 Ma). These results further support the hypothesis that the Trachycarpeae colonized the Pacific on two fronts, from the west, as seen in *Pritchardia*, and from the east, as seen in Livistoninae.

The mean age estimated for the Hawaiian *Pritchardia* clade is 3.50 Ma and appears to follow a general species-to-time ratio (26 species; Table 2) that is comparable to other Hawaiian plant lineages such as *Schiedia* (29 species, 4.92 Ma; Frajman et al. 2009) and the silversword alliance (30 species, 5.1 Ma; Baldwin and Sanderson 1998). The Hawaiian radiation of *Pritchardia* shows a progressive pattern (sensu Wagner and Funk 1995) where the earliest divergences are represented on the oldest islands and subsequent divergences trace down the island chain as new islands were formed. As seen in Figure 2, *P. minor* is at the base of the Hawaiian clade and is distributed on the oldest island of Kauai, in contrast to the divergent *P. maideniana*, which is found on the youngest island of Hawaii. The exception in our reconstruction, *P. lanaiensis*, may represent a back dispersal from younger to older islands. It

appears that the availability of new habitat on emerging islands for dispersal and population expansion, and subsequent allopatric speciation due to the volcanic nature of the archipelago, has spurred the radiation of *Pritchardia* species (online Fig. 5).

Miocene dispersals and adaptive radiation in island systems.—In addition to pronounced warming periods in the Miocene (Zachos et al. 2001) that resulted in a phase of northern expansion of tropical forests worldwide (Morley 2000), there were a range of global geological events that also contributed to increased rates of dispersal and diversification across many paleogeographic areas (Tiffney 1984; Morley 1998, 2003). The closing of the Tethys Sea, the uplift of Panama and the closure of the Central American Seaway, the collision of the Sunda and Sahul plates forming Wallace's Line, and the rise of major mountain ranges such as the Alps, the Himalayas (proposed to have uplifted in phases, one of which occurred in the Middle Miocene), the New Guinea highlands, and the Andes, all had dramatic effects on world climate, global oceanic currents, biotic distributions, and speciation mechanisms. Through studies of species that track tropical forest evolution, such as palms (Morley 2000; Couvreur, Forest et al. 2011), we can gain insight into general patterns that underlie the earth's biodiversity and the processes that shape it.

A general trend emerging from our data is that the Miocene was a key period of dispersal for lineages of Trachycarpeae. The genera that were inferred to have high dispersal rates in the Miocene (*Copernicia*, *Licuala*, and *Pritchardia*) are species-rich and distributed in island systems (the Caribbean, Southeast Asia, and central Pacific, respectively; Fig. 5). Notably, many other tropical and subtropical plant taxa from across the angiosperm phylogeny are reported to have pronounced rates of dispersal in the Miocene (e.g., Renner 2004; Clark et al. 2009; Clayton et al. 2009; del Hoyo et al. 2009; Li et al. 2009; Thiv et al. 2010; Couvreur, Pirie et al. 2011; Emadzade and Hörandl 2011). The overarching pattern of Miocene influence on species diversification has also been detected in insects (McKenna and Farrel 2006; Solomon et al. 2008; Aduse-Poku et al. 2009; Davis and Scholtz 2010; Ribera et al. 2011), arthropods (Sotelo et al. 2009), mollusks (Nekola et al. 2009), reptiles (Daza et al. 2009; Kornilios et al. 2010), fish (Schwarzer et al. 2009; Bellwood et al. 2010), birds (Bunce et al. 2009; Patané et al. 2009), and mammals (Douady et al. 2003; Patou et al. 2009; Malekian et al. 2010). Surprisingly, patterns of Miocene dispersal have also been detected in bacteria (Pearson et al. 2009) and, taken together, indicate a general pattern across the tree of life.

Supplementary Material

Supplementary material, including data files and/or online-only appendices, can be found in the Dryad data repository (DOI:10.5061/dryad.2jc763qt).

Funding

This work was supported by the National Tropical Botanical Garden (McBryde Graduate Student Fellowship); a National Science Foundation Doctoral Dissertation Improvement Grant [DEB-1010731] award; the Montgomery Botanical Center (Research Associateship); an International Palm Society Endowment Grant to C.D.B.; a Royal Botanic Garden, Kew Bentham-Moxon Trust Grant to C.D.B and W.J.B.; and a National Science Foundation Grant [DEB-0639792] to M.P.S.

Acknowledgments

We thank Ronald DeBry, Mark Fishbein, and anonymous reviewers for suggestions that greatly improved the manuscript; Fairchild Tropical Botanical Garden, Lyon Arboretum, Montgomery Botanical Center, the National Tropical Botanical Garden, the Royal Botanic Garden, Kew, Patrick Alexander, John Dowe, Andrew Henderson, Look Su Lee, and Li-Bing Zhang for DNA samples; Julissa Roncal for unpublished sequences; and Anders Barfod, Thomas Couvreur, John Dransfield, Aaron Pan, John Paul, Richard Ree, and Warren Wagner for helpful discussions.

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