DISSERTATION

TRACHYCARPEAE PALMS AS MODELS TO UNDERSTAND PATTERNS OF ISLAND BIOGEOGRAPHY AND DIVERSIFICATION

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

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Fort Collins, Colorado

Summer 2011

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ABSTRACT

TRACHYCARPEAE PALMS AS MODELS TO UNDERSTAND PATTERNS OF ISLAND BIOGEOGRAPHY AND DIVERSIFICATION

Palms are iconic members of tropical flora and are representative of the vast diversity found in rain forests across the world. Outside of being fundamental for forest structure and function and for human well-being in many tropical countries, palms also emerge as models for evolutionary studies. Because of their long history, rich fossil record, and dispersal ability, palms have been suggested to track forest evolution and change through time. In this dissertation, I use various molecular and analytical techniques to show that palms are an excellent model for understanding patterns of biogeography and diversification in tropical forests. Results show that Miocene dispersal was a driving force in island diversification across the world from the Caribbean, to Southeast Asia, to Hawaii. Data also support that differential shifts in diversification are key to shaping diversity patterns on Southeast Asian islands and across Wallace's Line. At finer scales, results show the importance of hybridization in the diversification of island lineages. Together, this research defines important conclusions from Trachycarpeae palms and extends them to the understanding of islands and to tropical forests in general.

ACKNOWLEDGEMENTS

I would like to acknowledge my family and friends for their support over the last five years. Particularly my parents, brother, and most of all, my husband Geovanni Romero, were fundamental in my completion of this dissertation and it is an accomplishment for them as well. I also thank my advisor, Mark Simmons, for whose confidence in my abilities enabled me to pursue my interests. His guidance was fundamental to my development as a systematic botanist and his patience was always appreciated. I am also indebted to Warren Wagner, my committee member and National Tropical Botanical Garden McBryde Fellowship and Smithsonian Institution Pre-Doctoral Fellowship supervisor. His knowledge of the Hawaiian flora and island biogeography instilled in me a great enthusiasm for these fascinating subjects that I plan to continue working on. I also thank my other committee members, Amy Angert and John McKay, for increasing my knowledge in areas new to me and pushing me to think broadly about my project and results. I would also like to acknowledge the support of the palm community, including William Baker, Anders Barford, Angelica Cibiran Jaramillo, Thomas Couvreur, John Dransfield, Don Hodel, James Horn, and Julissa Roncal, whose insights shaped my work. Also, many in Hawaii were elemental in the success of this work, including Ane Bakutis, Davis Burney, Susan Ching, David Lorence, Leland Miyano, Hank Oppenheimer, Steve Perlman, Natalia Tangalin, Chipper Wichman, and Ken Wood.

DEDICATION

This dissertation is dedicated to André Maurício Vieira de Carvalho (1951-2002), who introduced me to the world of botany and who is never forgotten.

TABLE OF CONTENTS

Chapter 1. Introduction

Palms are iconic members of tropical flora and are representative of the vast diversity found in rainforests across the globe. Palms exhibit a variety of life forms (Tomlinson et al. 2010), show evidence for rich island radiations (Bacon et al. in review1*), and form an essential basis for human life, especially in tropical, rural, and generally poor communities (e.g., Pederson and Balslev 1992). Palms are considered keystone species (Johnson 1996) as they play especially important roles in the structure and function of tropical forests and are known to harbor mycorrhizal associations (Fisher and Jayachandran 1999). Palm seeds can be water (fresh and salt) tolerant and in some species, even the fruits are resistant (Dransfield et al. 2008). Although traditionally viewed as having low dispersal capabilities (Dransfield 1981; Uhl and Dransfield 1987), more recent studies have shown that palms do disperse widely (e.g., Kristiansen et al. 2009). Dispersal ability, the effects geological and climatic events have on distributions, and molecular phylogenies aid in the inference of dispersal and vicariance events (Bacon et al. in review2*).

The goal of this chapter is to review the molecular systematics and biogeography of Trachycarpeae, the focal taxonomic group of this dissertation, and briefly discuss the palm fossil record. I also provide an overview of the subsequent dissertation chapters and conclude by demonstrating that palms are an excellent model system for the understanding of biogeography and diversification on islands and for the evolution of

tropical forests. At one level, palms are an ancient lineage with wide-ranging dispersal agents and trace major geographical and climatic shifts. At another level, niche specialization, the small range sizes of some palms, and high ecological heterogeneity in the regions where they are found can lead to the evolution of an ecosystem, such as tropical rainforests.

Overview of Trachycarpeae

The taxonomic focus of this dissertation is the Trachycarpeae tribe of Coryphoideae (Arecaceae). Trachycarpeae comprise 19 genera (Dransfield et al. 2008; Bacon and Baker in press*; Henderson and Bacon in press*) and ca. 269 species and are a monophyletic group (Uhl et al. 1995; Asmussen and Chase 2001; Hahn, 2002; Asmussen et al. 2006; Baker et al. 2009). The tribe is divided into two subtribes based on gynoecial structure; Rhapidinae have carpels that are free throughout their length (apocarpous), whereas Livistoninae carpels are free at the base, but apically united by their styles (syncarpous). Due to a lack of phylogenetic evidence and the desire to recognize subtribes based on carpel form, seven syncarpous genera of the Trachycarpeae (Fig. 1; *Acoelorrhaphe, Brahea, Colpothrinax, Copernicia, Pritchardia, Serenoa, Washingtonia*) from the Americas and the Pacific have not been placed in subtribes according to the latest palm classification system (Dransfield et al. 2005). Trachycarpeae encompass various biogeographic and diversification patterns highly suited for evolutionary studies. The phylogenetic relationships within the tribe have remained tenuous and few studies have

included more than exemplar taxa (but see Roncal et al. 2008; Crisp et al. 2010). Robust phylogenetic relationships are fundamental for conservation efforts, as well as for pattern-based evolutionary analyses such as biogeography.

Fig. 1. Examples of unplaced Trachycarpeae palms *Pritchardia*, *Acoelorrhaphe*, *Serenoa*, and *Washingtonia* in their native habitats. Images by permission from J. Dransfield.

Divergence time estimation in palms has resulted in different absolute ages (Bremer, 2000; Wilkstrom et al. 2001; Janssen and Bremer 2004; Couvreur et al. in press*) but have led to a consensus that palms diverged from other commelinid monocots in the Middle Cretaceous after the initial breakup of Gondwana. From fossil evidence and phylogenetic studies, it has been proposed that the Coryphoideae subfamily originated in the Northern Hemisphere and diversified in the boreotropics through the Late Cretaceous and Tertiary (Morley 2000; Dransfield et al. 2008). Family-wide analyses of the palms further indicate that the extant distribution of Trachycarpeae is of a Laurasian origin followed by dispersals into the Southern Hemisphere and over long distances onto new

island and continental locations (Dransfield 1987; Dransfield et al. 2008; Baker et al. 2009). The divergence times of Trachycarpeae have not been addressed and form the basis for Chapter 2.

Review of the Fossil Record and its Implications on Biogeography

Palms have a rich fossil record dating from the Late Cretaceous onwards. Although the record is unusually rich among the angiosperms, only a small fraction of palms fossils can be identified to specific taxonomic groups with confidence. While some fossils assigned to Arecaceae occur earlier, *Sabalites carolinensis* is the oldest unequivocal palm fossil (Berry 1914). The substrate from where the *Sabalites* fossil was found dates to the late Coniacian (88.3 Ma) to the early Santonian (85.1 Ma) of the Late Cretaceous of South Carolina, USA (Berry 1914). The *Sabalites* fossil has been attributed to the stem lineage of the Coryphoideae, for which palmate leaf-shape is a synapomorphy (Harley 2006). A stem lineage is the most inclusive monophyletic group that comprises the extant members of a clade and the extinct lineages that diverged from the lineage leading to the crown group (*sensu* Magallón and Sanderson 2001). Other palm subfamilies appear in the fossil record during the Late Cretaceous and, although fossil identifications are not infallible, most of the generic diversity arose during the Tertiary in worldwide fossil deposits (reviewed in Dransfield et al. 2008).

More than 12 fossils have been identified within the Trachycarpeae (Dransfield et al. 2008), but only the fossil flowers of *Palaeoraphe dominicana* have been accepted with confidence as closely related to a specific extant palm group (Poinar 2002). *Palaeoraphe* flowers are preserved in Dominican amber (Early Miocene; Iturralde-

Vincent and McPhee 1996) and share floral characteristics with *Brahea*, *Acoelorrhaphe* and *Colpothrinax*. Most morphological synapomorphies are shared with *Brahea*, including furrows on the petals, distinct sepals, and the size and shape of the anthers. This fossil taxon is distinct from *Brahea* because of its ridged carpels, recurved tips of the styles and reflexed petals opposite the stamens (Dransfield et al. 2008).

Miocene Dispersal Drives Island Radiations in Trachycarpeae

The first chapter of this dissertation uses DNA sequence data from the nuclear (two loci) and chloroplast genomes (three loci) from 146 individuals of Trachycarpeae palms and dates the phylogeny using three palm fossils- *Sabalites carolinensis* (Berry 1914), *Palaeoraphe dominicana* (Poinar 2002), and *Hyphaene kappelmanii* (Pan et al. 2006). Phylogenetic, divergence times, and historical-biogeographic analyses were used to understand subtribal and inter-generic relationships, disjunct distributions, and the diversification of three cases of island radiations in the tribe (*Copernicia* in the Caribbean, *Licuala* in Southeast Asia, and *Pritchardia* in the South Pacific).

The results supported previous studies that Trachycarpeae is a monophyletic group and the data generally resolved inter-generic relationships within the tribe (Bacon et al. in review1*). Two extreme examples of disjunct distribution in Trachycarpeae were examined. First, *Livistona* is primarily distributed in eastern and southeastern Asia and Australia, but *L. carinensis* is found in the Horn of Africa and southern Arabia. Secondly, Rhapidinae are distributed in eastern Asia with disjunct species found in Mediterranean regions of Europe and North Africa, as well as in the southeastern United States. The results were unclear as to whether *Livistona* originated in eastern Asia or in Africa and

Arabia region because of the ambiguous optimizations between the parsimony and likelihood versus the Bayesian results. The disjunction in Rhapidinae was attributed with high statistical support to migration events across the North Atlantic Land Bridge combined with subsequent radiation in Asia and extinction in intervening areas outside of boreotropical refugia.

Outside of the inference of key geological and climatic processes driving the distributions of island groups of Trachycarpeae, a general trend emerging from the data is that the Miocene was a key period of dispersal and allopatric speciation. The genera that were inferred to have the highest dispersal rates during the Miocene (*Copernicia*, *Licuala*, *Pritchardia*) are species-rich and distributed in insular systems (Caribbean, Southeast Asia, and South Pacific). Markedly, many other tropical and subtropical plant taxa from across the angiosperm phylogeny are reported to have pronounced rates of dispersal in the Miocene (Renner 2004; Clark et al. 2009; Clayton et al. 2009; del Hoyo et al. 2009; Li et al. 2009; Thiv et al. 2010). Taken together, these results demonstrate that palms can be excellent models to understand general patterns of diversification and biogeography of angiosperms on islands and of tropical forest in general.

Disparities in Species Diversity: Dispersal and Diversification Rates across Wallace's Line

Disparity in species diversity is most commonly seen in the differences between the tropical and north temperate floras (tropical-temperate disparity; Middlebach et al. 2007) or in palm species richness between South America and Africa (neo- versus paleotropics; Bjorholm et al. 2006). A unique form of disparity in species diversity is

characterized by high species richness in Sunda and Sahul regions of southeast Asia, coupled with remarkably low diversity in Wallacea (Sulawesi, the Moluccas, and the Lesser Sunda Islands collectively; Dransfield 1981, 1987). Understanding the origin of this bimodal pattern may increase the understanding of which evolutionary processes have generated the vast biodiversity in Southeast Asia where three of the worlds "hottest" biodiversity hotspots are located (Myers et al. 2004). This bimodal pattern has been reported in grasses (Baker et al. 1998), Caesalpinoid legumes, sedges, and diptocarps (van Welzen and Slik 2009) and although not unique to the angiosperms (e.g., hawkmoths, Beck et al. 2006), the pattern has been suggested to be the most pronounced in the palm family (Dransfield 1981, 1987; Baker et al. 1998; Baker and Couvreur in press*). A time-calibrated phylogeny and models of historical biogeography and diversification rates were used to test whether dispersal ability and shifts in diversification contributed to shape the bimodal pattern in the Livistoninae subtribe.

A close correspondance was detected between the fossil history of the group (e.g., Conran and Rosefields 2003) and the divergence times and ancestral ranges estimated from the phylogeny. Furthermore, the dispersal events of Livistoninae lineages corresponded to major tectonic events such as the collision of the Asian and Australian plates and a (potentially temporary) dispersal corridor that was formed from eastern Asia into areas east of Wallace's Line. Furthermore, to test the hypothesis that increased diversification rates in species that dispersed across Wallace's Line contributed to shaping the bimodal distribution pattern in Livistoninae, a rate increase would need to be detected in the vicinity of at least one of the three instances of dispersal to the Sahul region on the phylogeny. Based on the diversification rate analysis, a significant increase in net

diversification rate was detected at the stem node of the New Guinean *Licuala*. Simulations allowed for the determination that it was unlikely that the other clades originating in the same credible interval of the New Guinean *Licuala* were the result of the same diversification regime. The increase in diversification rate in *Licuala* was shown to have accentuated the bimodal pattern by elevating the number of palm species found on either side of Wallacea.

The fossil history and estimated divergence times for early divergent Livistoninae show the influence of tectonic activity at the Asian-Australian tectonic plate boundary and that the dispersal of *Licuala* to New Guinea corresponds to the timing of island formation and mountain uplift. Plant lineages such as palms, legumes, and Annonaceae (e.g., Morley 2000; Couvreur et al. 2011) have been suggested to be excellent systems to understand the evolution of tropical forests because their physiological requirements largely restrict them to these biomes (e.g., Bjorholm et al. 2006). Furthermore, these plant lineages have been identified in the earliest known fossil record of tropical rainforests (e.g., Wing et al. 2009). Recent studies in *Pseudovaria* closely mirror the biogeographic movements (Annonaceae; Su and Saunders 2010) of Livistoninae and are likely concordant with the evolutionary change of southeast Asian rainforests as a whole.

Evaluating Multiple Criteria for Species Delimitation: an Empirical Example Using Hawaiian Palms (Arecaceae: Pritchardia)

Robust species delimitations are the building block of conservation, evolutionary, and systematics studies, but they can be difficult to estimate in certain cases, particularly in rapid radiations and in island systems where hybridization is generally more common

(Carlquist 1970). The criteria used to distinguish evolutionary lineages differ based on the perceived importance of the various characteristics of evolving populations, from reproductive isolation (Mayr 1963) to the existence of diagnostic characters (Cracraft 1983; Nixon and Wheeler 1990) and the occupation of distinct niches (Van Valen 1976). de Querioz (1998, 2007) has suggested that despite the historical focus on differing species-delimitation criteria, all species concepts share the same root, that species are separately evolving lineages. Because species-delimitation criteria arise at different times during cladogenesis, it is the accumulation of evidence and the satisfaction of multiple criteria (general lineage species concept) that leads to stable, less controversial, species circumscriptions.

The general lineage species concept was applied to Hawaiian *Pritchardia* palms, an important group for species evaluation because the genus is a conservation priority for the state of Hawaii with 15 threatened or endangered species according to the IUCN Red List. Not only is accurate estimation of species limits essential to conservation, it is also important for the understanding of diversification and radiation of Hawaiian *Pritchardia*. Three criteria, the phylogenetic species concepts I and II and the genotypic cluster species concept, were used to test whether currently recognized species merit taxonomic recognition as evolutionary lineages is discussed with respect to the accumulation of evidence in favor of their delimitation.

Data from four plastid and three nuclear genes, five variable microsatellite loci, and 19 morphological characters resulted in differing assessments of distinct lineages and are hypothesized to be caused by differing evolutionary rates between data sources. Additionally, taxonomic entities may be confounded because of the effects of incomplete

lineage sorting and/or gene flow. A coalescent species tree explicitly modeled incomplete lineage sorting and was largely congruent with the simultaneous analysis, consistent with the idea that the tempo of the *Pritchardia* radiation likely causes the lack of resolution amongst lineages. Furthermore, gene flow amongst populations of sympatric *Pritchardia* lineages likely explains the admixture between those groups. Delimiting Hawaiian *Pritchardia* species remains difficult but the ability to understand the influence of evolutionary processes, incomplete lineage sorting from the coalescent species tree and hybridization from the microsatellite and sequence data allows for mechanisms driving *Pritchardia* species diversity to be inferred.

Conclusions

In the absence of a complete fossil record for tropical rainforests, analysis of large pantropical groups that are characteristic of tropical rainforests can provide important insights into the formation of tropical biomes. In this respect, the palm family is an ideal study system. First, palms are among the most important components of tropical rainforests worldwide in terms of species diversity (~2400 species), abundance of individuals, and impact on the environment (Kahn and de Granville 1992; Phillips et al. 2002). Furthermore, over 95% of their species diversity is restricted to tropical rainforests (Dransfield et al. 2008). Water and energy-related variables are strong determinants of palm diversity (Bjorholm et al. 2006; Kreft et al. 2006) and fundamental anatomical constraints prevent palms from colonizing cold environments (Tomlinson 1979, 2006). Second, the known history of palms extends far back into the Cretaceous, (ca. 100 Ma) and ancestral biome and area reconstructions show strong support for early palm lineages

diversifying in tropical rainforest-like environments at northern latitudes (Couvreur et al. in press*). Using two important characteristics of the palm family, fossil history and physiological constraints, show how palms emerge as a model group for the study of the origin and diversification of tropical rainforests.

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Chapter 2: Miocene Dispersal Drives Island Radiations in the Palm Tribe Trachycarpeae (Arecaceae)

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. 2004). 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 2008a).

The palms (Arecaceae) are an ideal group for the application of phylogenetic methods to address questions of biogeographic origin and radiation (e.g., Couvreur et al. in press). The family is widespread and yet shows high rates of endemism at varied spatial scales (Baker and Couvreur in press). In addition, palms have an abundant fossil

record that dates back to the Cretaceous (Daghlian 1981; Muller 1981; Herendeen & Crane 1995) and includes fossils that can be linked with confidence to specific extant lineages based on morphological synapomorphies (Harley 2006; Dransfield et al. 2008). Previous divergence time estimation studies have yielded varied results but have led to a consensus that palms diverged from other commelinid monocots (APG 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 methods suggest that palms diverged initially in Laurasia (Couvreur et al. in press).

Trachycarpeae (subfamily Coryphoideae; 19 genera and ca. 269 species; Dransfield et al. 2008; Bacon and Baker in press; Henderson and Bacon in press) are unique within the palms because they display one of the widest distributions of all tribes in the family as well as several dramatic island radiations. This distribution pattern offers an opportunity to explore each of the radiations individually, as well as compare their patterns of diversification in a global context. 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. in press), 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). The Rhapidinae are 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. The Livistoninae are predominantly found in tropical Asia, though four of its six genera span Wallace's Line (Dransfield et al. 2008; Henderson and Bacon in press; Bacon et al. unpubl.). *Livistona* is remarkable for its disjunct distribution between Asia and Australia, with a further disjunct species, *L. carinensis*, native to the Horn of Africa and southern Arabia (Dowe 2009; Bacon and Baker in press). In a recent study, Crisp et al. (2010; see also Dransfield 1987) hypothesized that *Livistona* is a recent Australian immigrant from eastern Asia but were unable to address the African disjunction due to inadequate sampling.

Within Trachycarpeae there are three cases of species radiation in island systems. There are 19 *Copernicia* species in the Caribbean, primarily in Cuba, and three other species distributed in South America (Govaerts and Dransfield 2005). Because the Caribbean has been a tectonically active region for more than 100 million years (Burke1998), there have been opportunities for both vicariance and dispersal. Ecological speciation may also have been important in the Cuban *Copernicia* radiation as many of

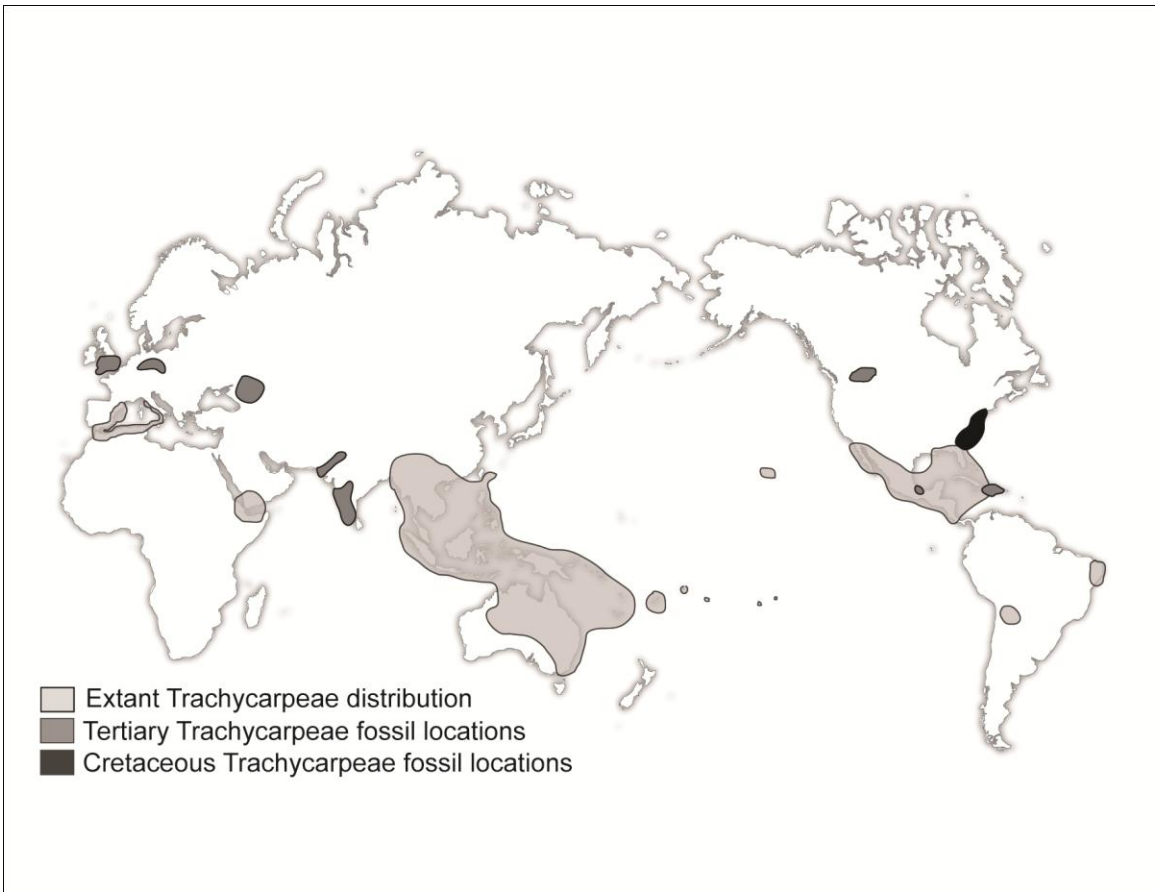

Fig. 1. Map showing the extant, Tertiary, and Cretaceous distributions of Trachycarpeae. Fossil distributions are based on published fossil records attributable to the tribe, but not unequivocally identified and are likely to be an incomplete estimation of past ranges.

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 ca. 170 species (Barford pers. comm. 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; Bacon et al. unpubl.; Baker and Couvreur in press). Lastly, *Pritchardia* includes 27 species of the southwest Pacific and the Hawaiian

Archipelago (Hodel 2007, 2009). Although species boundaries within *Pritchardia* have been difficult to estimate in the past, it has been suggested that the formation of the volcanic archipelago itself has driven speciation in the same manner as other Hawaiian lineages (Hodel 2007, Bacon unpubl. data). 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 Trachycarpeae may have dispersed into the Pacific from both the east, in the case of *Pritchardia*, and the west, as in Livistoninae.

We aim to gain broad insight into island radiations by examining each of the Trachycarpeae island clades and comparing patterns across them to identify correlates of their diversification. We use a highly sampled phylogenetic tree based on representation from both the nuclear and plastid genomes to reconstruct the generic relationships of Trachycarpeae. Using the phylogeny calibrated with confidently identified and dated fossil information, we estimate divergence times and reconstruct ancestral distributions to infer the historical biogeography of the tribe. Our specific goals are to test the timing and geographic origin of Trachycarpeae lineages, to explore the processes involved in the formation of disjunct distributions, and to understand which geological and climatic events were fundamental in spurring the three sets of island radiations across Trachycarpeae. We assess general emerging patterns across Trachycarpeae island clades and the roles that dispersal and geology have played in island distributions and the species radiations found in these biodiverse systems.

Materials and Methods

TAXON SAMPLING AND DNA SEQUENCING

One hundred and thirteen species were sampled (Appendix 1) including all genera of Trachycarpeae and 10 outgroups. The remaining seven tribes of subfamily Coryphoideae were represented among the outgroups, as were subfamilies Arecoideae (*Geonoma*) and Ceroxyloideae (*Aphandra*) based on their inferred sister group relationship to Coryphoideae from the broader-scale analysis by 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 and intron 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

Table 1. Parsimony data matrix and tree statistics of each analysis that includes gap characters. "PI" = parsimony informative; "MPT" = most parsimonious tree; “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).

Matrix	# terminals	# chars.	# PI chars.	% missing / inapp. chars.	MPT length	# of MPTs	# of JK / BS ≥ 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

purified using Qiagen PCR purification kits and sequenced either by the Cancer Research generated for this study were deposited in GenBank under accession numbers HQ20241 to HQ20961 (Appendix 1).

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 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 hybridization, differential selection, incomplete lineage sorting, 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 were determined in MacClade for the internal node of the gene tree that represents the inferred duplication event, which is treated as the hypothetical ancestor. For single gene duplications, as with CISP5, the species-tree matrix contains three times as many characters, but the same or a slightly lower (due to ambiguous optimization of character states at the hypothetical

ancestor) minimal number of steps as the gene-tree matrix. Subsequent likelihood matrices did not include the uninode hypothetical ancestor sequence 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, a simultaneous analysis of all characters was 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). Maximum likelihood (ML; Felsenstein 1973) analyses were performed on the CIPRES portal using the RAxML-III algorithm (Stamatakis et al. 2005). ML bootstrap (BS; Felsenstein 1985) analyses were also conducted using RAxML (Stamatakis et al. 2008). The Akaike Information Criterion (Akaike 1974), as implemented in jModeltest v0.1.1 (Posada 2008), was used to compare and to 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 applied when the model selected by the AIC was not available. Following Yang (2006) and Stamatakis (2008), invariant-site models (Reeves 1992) were not considered because models that incorporated the gamma distribution (Yang 1993) were estimated. 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.– Significantly higher Bayes Factors (Nylander et al. 2004) were recovered for a relaxed rather than a strict clock model and BEAST v1.4.8 (Drummond et al. 2006) was used to implement a relaxed clock estimate of divergence times in Trachycarpeae. The simultaneous dataset was partitioned by locus, nucleotide substitution models were unlinked amongst 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 post-date the fossil occurrence (Ho 2007; Ho and Phillips 2009). Lognormal prior distributions were set on three palm fossil calibrations. To test for MCMC chain convergence analyses were run until the effective sample sizes (ESS) of all parameters exceeded 200 and a 10% burn-in was removed (Drummond et al. 2006; Drummond and Rambaut 2007). 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 to older dates 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 to simultaneous analysis (e.g., McCormack et al. 2010), our sampling of one individual per species and five loci is insufficient to determine the coalescent species tree for Trachycarpeae (Knowles 2010).

Calibration points.– 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). 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 (e.g., Heads 2011).

Fossil taxa.– 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 of the Coryphoideae, for which palmate leaf-shape is a synapomorphy (Dransfield et al. 2008). The substrate where *S. carolinensis* was found dates to 88.3 - 85.1 Ma (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 *Brahea*, *Acoelorrhaphe* and *Colpothrinax*, 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 clade comprising *Colpothrinax* and the rest of the Trachycarpeae (Fig. 2) 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 McPhee (1996). The fossil petiole of *Hyphaene kappelmanii* (HYP; Pan et al. 2006)

Table 2. Cross-validation of crown age estimates (million years ago, Ma) for selected crown nodes tracked with ESS values in BEAST. The 95% HPD credible sets are indicated and the calibration points are *Palaeoraphe dominicana* (PAL), *Hyphaene kappelmanii* (HYP), and *Sabalities carolinensis* (SAB).

		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	24.80	27.76	86.65
	95% lower	1.42	6.40	9.74	9.17	17.26	25.11	17.26	25.07	84.18
	95% upper	5.88	17.02	25.38	20.84	32.66	51.05	32.66	30.84	89.61

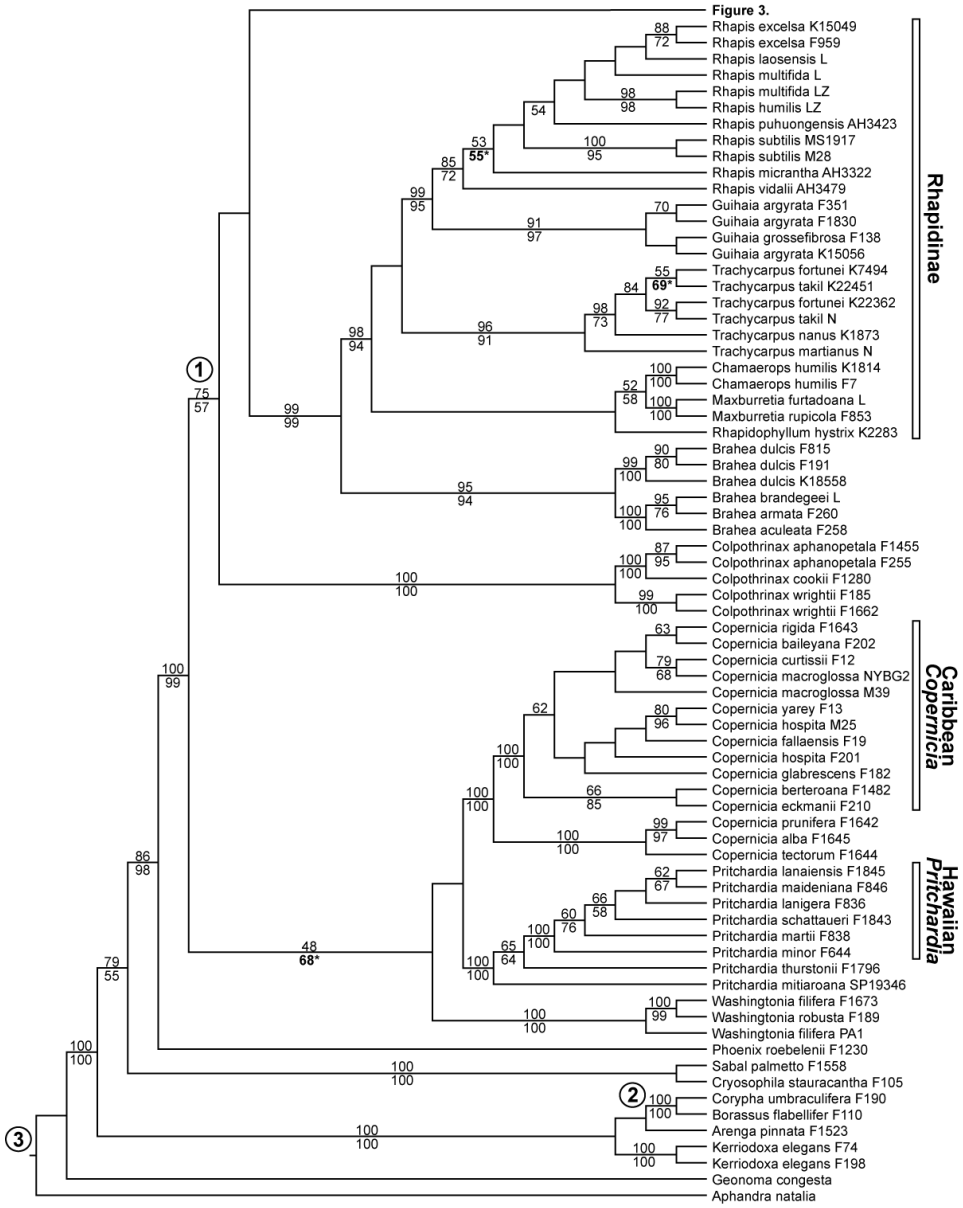

Fig. 2. Basal portion of the simultaneous-analysis maximum likelihood BS tree with likelihood BS values above each branch and parsimony JK values below each branch with only values ≥ 50% shown for both measures. Clades in the likelihood BS tree that were contradicted by clades in the parsimony JK tree are indicated with bold font and asterisks, with JK support for the highest contradictory parsimony clade listed. The three fossil calibrations, marked 1 (PAL), 2 (HYP), and 3 (SAB), are indicated with their placements on the tree.

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) southwest 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 (Ree and Smith 2008b). DEC has been suggested to be a robust method of inferring historical biogeography because it takes into account divergence time estimates (Ree and Smith 2008a). We used the ultrametric tree generated by BEAST to infer ancestral distributions with a uniform dispersal matrix.

Results

INCONGRUENCE AND SIMULTANEOUS ANALYSIS

Brahea was resolved in two highly distinct, well-supported clades in the CISP5 gene tree (Suppl. Fig. 1 versus Suppl. Figs. 2-4). Incongruence between these 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 it is unlikely that it would be detected in CISP5 only and not in any of the other three coalescent genes (cpDNA, CISP4, RPB2). Also, multiple hybridization events would have to be invoked to account for the topological conflicts. We do not believe differential selection on CISP5 to have caused incongruence because five well-supported (>75% JK/BS) branches separate the two clades that include *Brahea*. For the selection scenario, there would have to be extreme levels of convergent selection to cause the topology. Secondly, the CISP5 locus is a non-coding region and therefore major shifts in selection pressures are unlikely. Recombination was not detected in any of the loci using the two tests in RDP and Geneconv. 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. The branch length leading to the ingroup members of the basal *Brahea* clade is 0.178 and is more than twice the average of all the other branch lengths on the tree (0.066; Suppl. Fig. 1). Our hypothesis for the cause of gene tree incongruence is paralogy and that a duplication event occurred on the branch leading to Trachycarpeae plus its sister group, Phoeniceae.

DIVERGENCE TIMES AND HISTORICAL BIOGEOGRAPHY IN TRACHYCARPEAE

The topology estimated in BEAST (Suppl. Figs. 6 and 7) was in agreement with those resulting from MP and ML analyses of the simultaneous dataset (Figs. 2 and 3) except for 1) the position of *Lanonia* as nested within *Livistona* [0.44 posterior probability (PP)], rather than unresolved in MP (with *Johannesteijmannia* and a clade of *Licuala*, *Saribus*, and *Pholidocarpus*) and nested within *Johannesteijmannia* in ML (15% BS), 2) *Colpothrinax* resolved as sister to the clade of Livistoninae + *Acoelorrhaphe* + *Serenoa* in the BEAST analysis (0.20 PP), but as sister to *Brahea* and the remaining divergent Trachycarpeae in the MP and ML trees (57% JK / 75% BS), and 3) the position of *Washingtonia*, which is sister to the rest of the Trachycarpeae in the Bayesian (0.69 PP) and MP tree (68% JK), but is sister to the clade of *Copernicia* and *Pritchardia* in the ML tree (48% BS). As seen from the branch support values, none of the three cases were mutually well supported by the MP/ML versus Bayesian trees. BEAST fossil cross-validation results show variation in divergence time estimation, with the best hypothesis based on the narrowest credible set from all three fossil calibrations interacting in one analysis (PAL-HYP-SAB; Table 2; Ho and Phillips 2009).

Origins of Trachycarpeae.– Based on Lagrange analyses, ancestral Trachycarpeae lineages were unequivocally inferred to have originated in biogeographic region "I" (southern North America, Central America, or the Caribbean) and both the stem node representing early diversification and the crown node representing major divergences within the subtribe unequivocally reconstructed "I". The BEAST analyses

estimated that the mean stem node age of Trachycarpeae was 86.65 Ma (95% HPD 89.61-84.18Ma), whereas the crown node of Trachycarpeae was estimated at 37.74 Ma (95% HPD 51.05-25.11 Ma; Suppl. Fig. 6).

Disjunct distributions.– We used both divergence time and biogeographical analyses to understand the climatic and geological processes that formed disjunct distributions in both Livistoninae and Rhapidinae. In both subtribes, Lagrange inferred southern North America, Central America, or the Caribbean for the stem node distributions ('I'; Fig. 4). Dispersal events were then inferred in these lineages as their geographic distributions were expanded during the mid to Late Miocene (Fig. 4, Table 3). Due to subsequent forest contraction and climate change, extant disjunct lineages were likely stranded in relic forest fragments (e.g., *Livistona carinensis* in Africa and Arabia, *Chamaerops* in the Mediterranean, and *Rhapidophyllum* in southeastern USA).

Island radiations.– Lagrange inferred the stem and crown nodes of *Copernicia* to be distributed in southern North America, Central America, or the Caribbean ('I'; Fig. 4). The crown node of *Copernicia* was inferred to have undergone a dispersal event, representing the colonization of South America from a southern North American, Central American, or Caribbean ancestor lineage. The mean estimated divergence time of the *Copernicia* stem node was inferred to be at 32.10 Ma (95% HPD 44.73-20.13 Ma) and the emergence of the Caribbean *Copernicia* dated to 6.88 Ma (95% HPD 10.58-3.80Ma; Suppl. Fig. 6). The stem and crown nodes of *Licuala* were reconstructed to have an origin

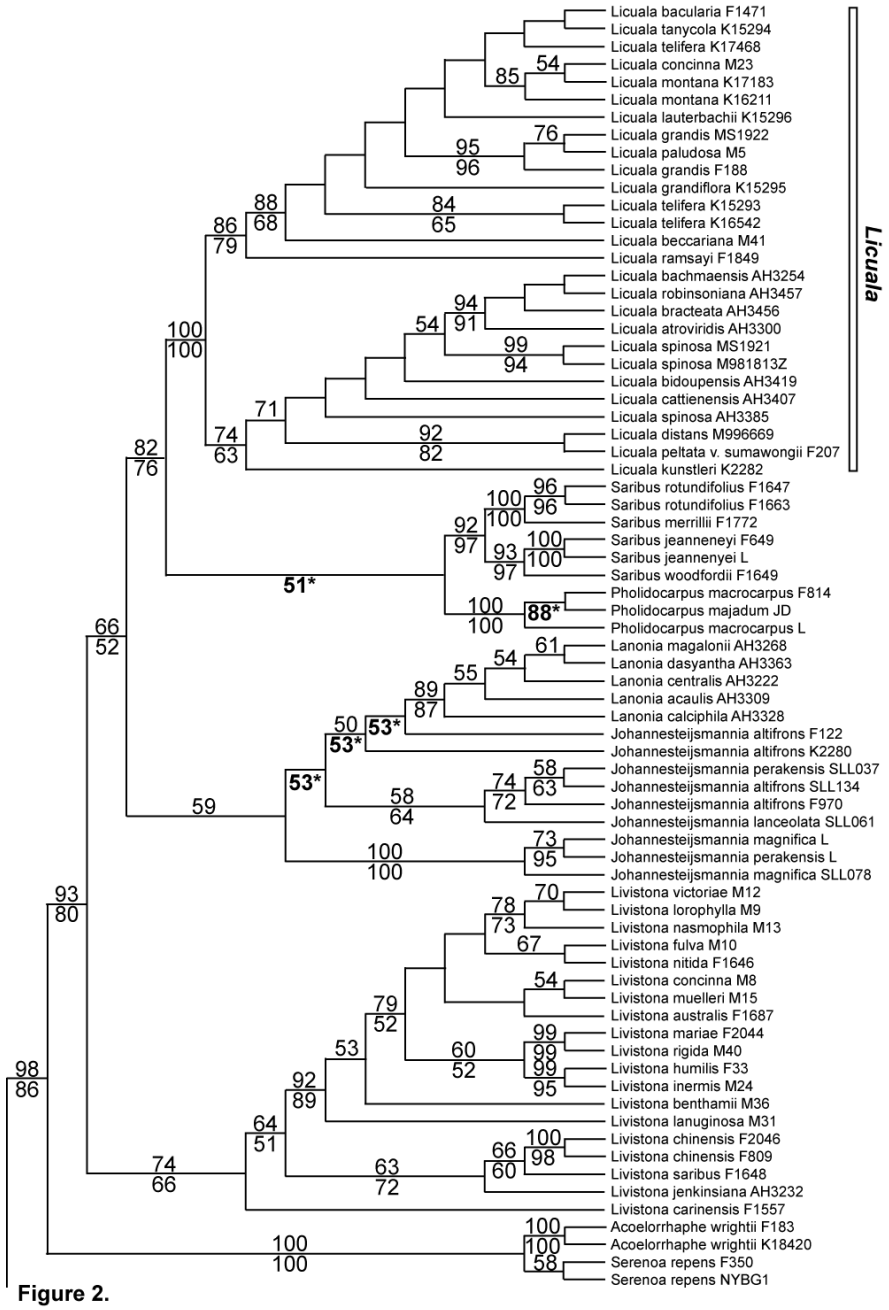

Figure 2.

Fig. 3. Distal portion of the maximum likelihood simultaneous-analysis BS tree comprised of Livistoninae and its sister clade of *Serenoa* and *Acoelorrhaphe*. Support values and incongruence indicated as in Fig. 2.

Table 3. Crown and stem node divergence times estimations in millions of years (Ma) for each of the monophyletic tribes and genera and particular clades of interest based on the calibration of all three fossils (see Table 2). The mean as well as the credible set (95% HPD) are listed as millions of years (Ma) and nodes that are supported by <0.50 PP are indicated with *.

	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
Segregate *Licuala*	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

in Malesia ("F") and although there were alternative reconstructions for this node, they all included "F" within the range estimated (Table 4). Four dispersals were reconstructed within *Licuala* and the range of this genus expanded from India to Thailand, Japan, and China ("E") to across Wallace's Line in Australia ("K") and New Guinea ("C"). 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; Suppl. Fig. 7). Our data support a North American, Central American, or Caribbean ("I") ancestral *Pritchardia* stem distribution, which was followed by dispersal to the southwest Pacific ("G"; Fig. 4). A subsequent single colonization of *Pritchardia* to Hawaii from the southwest Pacific was inferred from a dispersal event followed by local extinction (Fig. 4). The stem node age of *Pritchardia* was estimated at 32.10 Ma (95% HPD 44.73-20.13 Ma) and the crown node age at 10.57 Ma (95% HPD 17.05-5.13 Ma), and the diversification of the Hawaiian *Pritchardia* lineage at 3.50 Ma (95% HPD 5.88-1.43 Ma; Suppl. Fig. 6).

Discussion

Our data from the palm tribe Trachycarpeae allowed individual 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*, the island distributions result from dispersal events where lineages likely diversified *in situ* by allopatric and ecological speciation. Furthermore, these three island lineages appear to have been highly impacted by dispersal during times of major geological and climatic events in the Miocene. Although there are limitations to

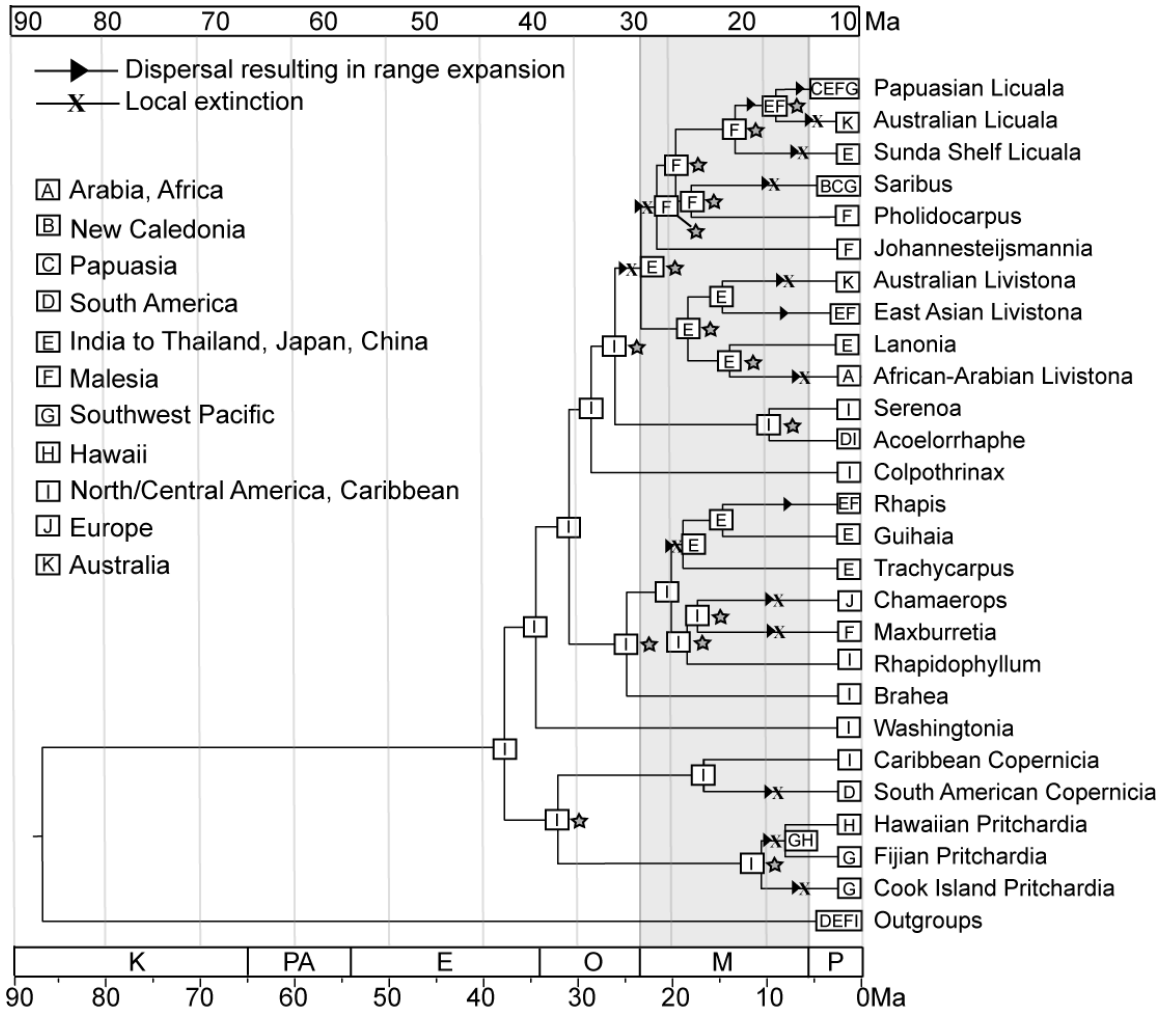

Fig. 4. Ancestral range reconstruction for Trachycarpeae using Lagrange. Reconstructions are shown as boxes at each node and nodes with alternative reconstructions (within 2 log likelihood units of the maximum) are indicated with a star. Two modes of range inheritance (range expansion and local extinction) are indicated as symbols on branches of the phylogeny (see Results). For clarity, selected sister terminals from a single area have been pruned from the chronogram.

the methods used (e.g., gene tree incongruence, minimum age constraints, error in fossil age determinations), our estimates, in concert, detect mechanisms of island diversification that correspond to geological and climatic history.

INCONGRUENCE AND SIMULTANEOUS ANALYSIS

Incongruence between gene trees was detected in the data, particularly with the nuclear region CISP5 (Suppl. Figs. 1, 3, 4). Selection is unlikely to apply to the CISP5 data that are derived from noncoding DNA. Significant signal for recombination was not detected in any of the loci based on two exploratory analyses. For hybridization to be viable alternative hypothesis hybridization events across widely divergent lineages are required and we can therefore rule it out as a potential cause of incongruence. 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). Furthermore, we believe the amount of ancestral polymorphism required in the most recent common ancestor to form highly supported and divergent clades is very unlikely. We suggest that differential sampling of paralogous copies of the CISP5 gene caused the *Brahea* incongruence between CISP5 and the other coalescent genes.

After accounting for paralogy in CISP5 using uninode coding (Suppl. Fig. 5), the main disparity between MP and ML topologies (Figs. 2 and 3) was the relationship among *Copernicia*, *Pritchardia*, and *Washingtonia*, which was caused by differences in where the long outgroup branch attached to the ingroup (Fig. 5). Both the MP and ML RPB2 partitions resolved *Pritchardia* as sister to the rest of the Trachycarpeae (100%

Table 4. Alternative distributions for nodes within two log likelihood units of the maximum likelihood estimate. Relative probability of the global likelihood for the optimal optimization is given (in gray shading) and compared to the alternative(s). The first of the distributions leads to the upper branch and the second to the lower daughter branch in Fig. 4. *Pholidocarpus*, *Johannesteijsmannia* and the Arabia - Africa region are abbreviated as Pholido, Johan, and "A"; Livistoninae comprise *Licuala*, *Saribus*, *Pholidocarpus*, *Johannesteijsmannia*, *Livistona*, and *Lanonia*; and Rhapidinae comprises *Rhapis*, *Guihaia*, *Trachycarpus*, *Chamaerops*, *Maxburretia*, and *Rhapidophyllum*.

Node	Area(s) inferred	-lnL	Rel. Prob.	Node	Area(s) inferred	-lnL	Rel. Prob.
Papuasian + Australian *Licuala*	C-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	0.0186
	E	226.0	0.0498		I	225.9	0.0543
Above + Sunda *Licuala*	E-EF	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* + Pholido	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 + Johan	F	223.6	0.5753		J-I	225.1	0.1194
	EF-F	224.3	0.2726		I-F	225.2	0.1126
Saribus + Pholido	G-F	224.2	0.2969		E	226.6	0.0286
	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 + *Licuala* segregate	E	223.7	0.0486		I-H	224.9	0.1556
	EK-E	224.5	0.2374	*Pritchardia*	GH-G	223.6	0.5570
	E-AE	225.2	0.1147		G	224.1	0.3499

BS/99% JK), whereas the CISP4 partitions had low support for *Copernicia* being sister to the rest of Trachycarpeae (ML) or the genus was unresolved (MP). The plastid partitions were effectively unresolved due to short branches and character conflict. 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. 5; 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 particular 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 comes after the actual speciation event (unless gene flow accompanies species divergence; Edwards and Beerli 2000; Carstens and Knowles 2007), divergence times based on a concatenated approach may be biased towards 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).

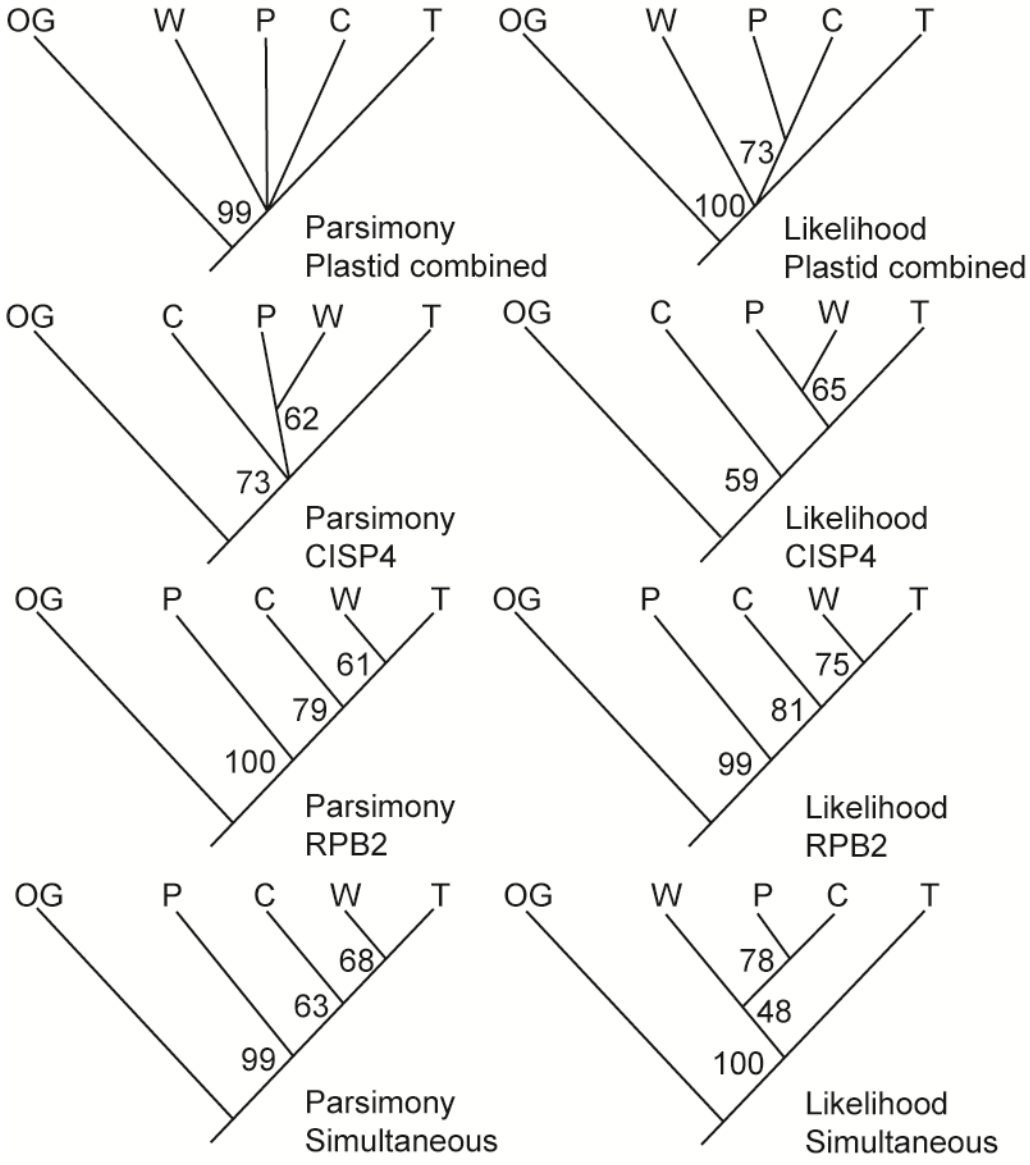

Fig. 5. Parsimony versus likelihood reconstructions of plastid combined, CISP4, RPB2, and simultaneous analyses displaying variation in the resolution of *Pritchardia* (P), *Copernicia* (C), and *Washingtonia* (W) with respect to the outgroups (OG) and the remaining Trachycarpeae (T) members. Support for each clade is based on BS for likelihood and JK for parsimony.

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 the analysis based on three fossil calibration points as our working hypothesis on which we base further discussion. 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 correlation 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; Table 3; Clague and Dalrymple 1987). Our data are also consistent with Crisp et al.'s (2010) divergence time estimates for *Livistona* and Trachycarpeae (~29-16 Ma and 41-23 Ma, respectively).

American origins of the Trachycarpeae.– Trachycarpeae have been proposed to be of Laurasian origin because all but two genera (*Pritchardia* and *Copernicia*) are found on Laurasian landmasses and ten of the remaining genera are strictly Laurasian in distribution (Dransfield et al. 2008). Our interpretation of the Lagrange results unequivocally supports a Laurasian origin and proposes a more specific biogeographic

region ‘I’ (North America, Central America, or the Caribbean) for both the crown and stem 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 million years) where only one stem lineage survived (Fig. 4, Suppl. Fig. 6).

Disjunct distributions.– We hypothesize that the disjunct distributions of extant Trachycarpeae 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 reference therein) in the Eocene and Oligocene periods, during which time many Trachycarpeae species 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 few lineages survived in refugia in southern Europe and northern Africa (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 southeastern 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 diversification increased at the crown node age of 20.09 Ma (Suppl. Fig. 6). This is consistent with Tiffney's (1985a) assertion 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 (Denk et al. 2010). Boreotropical regions began to physically split apart more and severe climatic changes caused further fragmentation as the Miocene progressed (Zachos et al. 2001). Fossil evidence of the Rhapidinae also corroborates our hypothesis of disjunctions correlating to the NALB. For example, fossils attributed to extant *Trachycarpus* have been identified in Lower Eocene deposits of 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, these findings are consistent with our hypothesis that the disjunction in Rhapidinae can

be attributed to migration across the NALB combined with subsequent radiation in Asia and extinction in intervening areas outside of boreotropical refugia along the migratory path.

Livistona comprises 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 nine species (Dowe 2009; Bacon and Baker in press). Dransfield (1987) postulated a Laurasian origin for the tribe and further suggested that the Australian (Gondwana) *Livistona* must have 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 18.32-14.67 Ma between the stem and the crown nodes respectively (Suppl. Fig. 7) and a dispersal event from region "E" (India to Thailand, Japan, and China) into Australia ("K") and Malesia ("F"; Fig. 4). Our data are unclear as to whether the genus originated in biogeographic region "E" (India to Thailand, Japan, and China) or "A" (Africa and Arabia) because of the ambiguous optimizations between the MP – ML and BEAST analyses.

ISLAND DISPERSAL AND DIVERSIFICATION

The Copernicia *radiation and GAARlandia*.– 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 was made up of 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 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 colonization pattern proposed for *Gaussia* (Chamaedoreeae; 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 more northern regions (Fig. 4).

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 (Suppl. Fig. 6). 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. 4). The crown node of the Caribbean crown lineage emerged at a mean age of 6.88 Ma (Late Miocene) and correlates 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 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.*– Malesia was inferred to be the ancestral area of the crown node of Livistoninae ("F"; Fig. 4; Table 4) and the lineage origin was estimated at the mean stem age of 26.04 Ma (Suppl. Fig. 7). Leading up to this time period, 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 onwards (Hall 2002). Formation of modern Malesia by the final juxtaposition of the Sunda and Sahul shelves in the mid-Miocene is well established (~16-12 Ma; Audley-Charles et al. 1981; Morley 1998) and we propose that the newly reformed region created opportunities for the radiation of genera such as *Licuala* via allopatric speciation. Lagrange inferred dispersal events on each of the four branches leading to major *Licuala* groups, two of which were followed by local extinction (Fig. 4). The mean 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 biogeography of *Licuala*, where species diversity is high on either side of Wallace's Line and low in intervening Wallacea (Lesser Sunda Islands, Moluccas, Sulawesi), 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*; Fig. 3), our data resolved two clades within *Licuala*, one east and one west of Wallace's Line. Taking the phylogenetic and divergence time estimation together, our data substantiate the hypothesis that the bimodal distribution of *Licuala* is most likely due to Miocene diversification (Baker and Couvreur in press) and further show the pattern to be driven by migration associated with the final formation of Malesia. More recent data have corroborated this hypothesis and shown that Pleistocene climatic shifts and changes in net diversification rate have also contributed to this disparity in species diversity in Southeast Asia as exemplified in *Licuala* (Bacon et al. unpubl.).

The Pritchardia *radiation from a recent and single colonization event*.– The mean stem age of *Pritchardia* was inferred to be 32.1 Ma and approximates the timing of the divergence of *Pritchardia* from its sister group *Copernicia*. Lagrange inferred the stem node of *Pritchardia* as having ancestral lineages in North America, Central America, or the Caribbean (region "I", Fig. 4). The general pattern of Hawaiian angiosperm radiations of North American origin has recently been described by Baldwin and Wagner (2010) and is here illustrated in *Pritchardia*. The mean crown age was estimated at 10.57 Ma and correlates 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 20-5 Ma (Evenhuis and Bickel 2005) for which our inferred age for *P. thurstonii* is consistent (8.04 Ma; Fig. 4). 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*. 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 discussed above (NALB).

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 further colonizations 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 (Suppl. Fig. 7).

Miocene dispersals and adaptive radiation in island systems.– In addition to pronounced warming periods in the Miocene (Zachos 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, biotic distributions, and speciation mechanisms. Through studies of species that track tropical forest evolution, such as palms (Couvreur et al. in press; Morley 2000), 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*, *Pritchardia*) are species-rich and distributed in island systems (the Caribbean, Southeast Asia, and South Pacific respectively; Fig. 4). Notably, many other tropical and subtropical plant taxa from across the angiosperm phylogeny are reported to have pronounced rates of dispersal in the Miocene (Renner 2004; Clark et al. 2009; Clayton et al. 2009; del Hoyo et al. 2009; Li et al. 2009; Thiv et al. 2010; Couvreur et al. 2011; Emadzade and Hörnadl 2011; Bacon et al., unpubl.). 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 et al. 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.

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Appendix 1.

List of taxa sampled with taxonomic authorities, voucher information, and GenBank accession numbers for new sequences generated for this study.

Acoelorrhaphe wrightii H. Wendl.-FTG Live Collection P.2313 (DNA Bank 183); CISP4 HQ720844, CISP5 HQ720730, *matK* HQ720241, *ndhF* HQ720594, RPB2 HQ720485, *trnDT* HQ720464. ***Acoelorrhaphe wrightii*** H. Wendl.-Kew DNA Bank 18420; CISP4 HQ720845, CISP5 HQ720731, *matK* HQ720242, *ndhF* HQ720595, RPB2 HQ720486, *trnDT* HQ720465. ***Arenga pinnata*** (Wurmb) Merr.-FTG Live Collection 77313A (DNA Bank 1523); CISP4 HQ720846, *matK* HQ720243, *ndhF* HQ720596, RPB2 HQ720487, *trnDT* HQ720355. ***Borassus flabellifer*** L.-FTG Live Collection 84427A (DNA Bank 110); CISP4 HQ720847, CISP5 HQ720732, *matK* HQ720244, *ndhF* HQ720597, *trnDT* HQ720484. ***Brahea aculeata*** (Brandegee) H.E. Moore-FTG Live Collection 88218C (DNA Bank 258); CISP4 HQ720848, CISP5 HQ720733, *matK* HQ720245, *ndhF* HQ720598, RPB2 HQ720488, *trnDT* HQ720455. ***Brahea armata*** S. Watson-FTG Live Collection 70126G (DNA Bank 260); CISP4 HQ720849, CISP5 HQ720734, *matK* HQ720246, RPB2 HQ720489, *trnDT* HQ720453. ***Brahea brandegeei*** (Purpus) H.E. Moore-Lyon Live Collection 66.0284; CISP4 HQ720850, CISP5 HQ720735, *matK* HQ720247, *ndhF* HQ720599, RPB2 HQ720490, *trnDT* HQ720466. ***Brahea dulcis*** (Kunth) Mart.-FTG Live Collection 59978A (DNA Bank 815); CISP4 HQ720852, CISP5 HQ720737, *matK* HQ720249, *ndhF* HQ720601, RPB2 HQ720492, *trnDT* HQ720468. ***Brahea dulcis*** (Kunth) Mart.-*F. Forest 83* (K); CISP4 HQ720853, *matK* HQ720250, *ndhF* HQ720602, RPB2 HQ720493, *trnDT* HQ720469. ***Brahea dulcis***

(Kunth) Mart.-FTG Live Collection 59978B (DNA Bank 191); CISP4 HQ720851, CISP5 HQ720736, *matK* HQ720248, *ndhF* HQ720600, RPB2 HQ720491, *trnDT* HQ720467. ***Chamaerops humilis*** L.-*Barrow 76* (K); CISP4 HQ720855, CISP5 HQ720739, *matK* HQ720307, *ndhF* HQ720604, RPB2 HQ720495, *trnDT* HQ720434. ***Chamaerops humilis*** L.-FTG Live Collection RM157A (DNA Bank 7); CISP4 HQ720854, CISP5 HQ720738, *matK* HQ720251, *ndhF* HQ720603, RPB2 HQ720494, *trnDT* HQ720433. ***Colpothrinax aphanopetala*** R. Evans-FTG Live Collection 87660A (DNA Bank 255); CISP4 HQ720857, CISP5 HQ720741, *matK* HQ720253, *ndhF* HQ720606, RPB2 HQ720496, *trnDT* HQ720444. ***Colpothrinax aphanopetala*** R. Evans-FTG Live Collection 93488A (DNA Bank 1455); CISP4 HQ720856, CISP5 HQ720740, *matK* HQ720252, *ndhF* HQ720605, *trnDT* HQ720443. ***Colpothrinax cookii*** Read-FTG Live Collection 87660A (DNA Bank 1280); CISP4 HQ720858, CISP5 HQ720742, *matK* HQ720254, *ndhF* HQ720607, *trnDT* HQ720448. ***Colpothrinax wrightii*** Griseb. and H. Wendl. ex Voss-FTG Live Collection 81235D (DNA Bank 185); CISP4 HQ720860, CISP5 HQ720743, *matK* HQ720256, *ndhF* HQ720608, RPB2 HQ720497, *trnDT* HQ720449. ***Colpothrinax wrightii*** Griseb. and H. Wendl. ex Voss-FTG DNA Bank 1662; CISP4 HQ720859, CISP5 HQ720744, *matK* HQ720255, RPB2 HQ720498, *trnDT* HQ720445. ***Copernicia alba*** Morong-FTG DNA Bank 1645; CISP4 HQ720861, CISP5 HQ720745, *matK* HQ720257, *ndhF* HQ720609, RPB2 HQ720499, *trnDT* HQ720416. ***Copernicia baileyana*** Léon-FTG Live Collection 87581C (DNA Bank 202); CISP4 HQ720862, CISP5 HQ720746, *matK* HQ720258, *ndhF* HQ720610, RPB2 HQ720500, *trnDT* HQ720420. ***Copernicia berteroana*** Becc.-FTG Live Collection FG4715D (DNA Bank 1482); CISP4 HQ720863, CISP5 HQ720747, *matK* HQ720259, *ndhF* HQ720611,

RPB2 HQ720501, *trnDT* HQ720460. ***Copernicia curtissii*** Becc.-FTG Live Collection 6912 (DNA Bank 12); CISP4 HQ720864, CISP5 HQ720748, *matK* HQ720260, *ndhF* HQ720612, RPB2 HQ720502, *trnDT* HQ720430. ***Copernicia ekmanii*** Burret-FTG Live Collection 931115D (DNA Bank 210); CISP4 HQ720865, CISP5 HQ720749, *matK* HQ720261, *ndhF* HQ720613, RPB2 HQ720503, *trnDT* HQ720461. ***Copernicia fallaensis*** Léon-FTG Live Collection 88531H (DNA Bank 19); CISP4 HQ720866, CISP5 HQ720750, *matK* HQ720262, *ndhF* HQ720614, RPB2 HQ720504, *trnDT* HQ720431. ***Copernicia glabrescens*** H. Wendl.-FTG Live Collection 59873B (DNA Bank 182); CISP4 HQ720867, CISP5 HQ720751, *matK* HQ720263, *ndhF* HQ720615, RPB2 HQ720505, *trnDT* HQ720418. ***Copernicia hospita*** Mart.-FTG Live Collection FG4674B (DNA Bank 201); CISP4 HQ720869, CISP5 HQ720752, *ndhF* HQ720616, RPB2 HQ720506, *trnDT* HQ720428. ***Copernicia hospita*** Mart.-MBC Live Collection 94607; CISP4 HQ720868, CISP5 HQ720753, *matK* HQ720264, *ndhF* HQ720617, RPB2 HQ720507, *trnDT* HQ720427. ***Copernicia macroglossa*** H. Wendl. ex Becc.-MBC Live Collection 96373; CISP4 HQ720870, CISP5 HQ720754, *matK* HQ720265, *ndhF* HQ720618, RPB2 HQ720508, *trnDT* HQ720429. ***Copernicia macroglossa*** H. Wendl. ex Becc.-NYBG Live Collection 4121/95A; CISP4 HQ720871, CISP5 HQ720755, *matK* HQ720266, *ndhF* HQ720619, RPB2 HQ720509, *trnDT* HQ720426. ***Copernicia prunifera*** (Mill.) H.E. Moore-FTG DNA Bank 1642; CISP4 HQ720872, CISP5 HQ720756, *matK* HQ720267, *ndhF* HQ720620, RPB2 HQ720508, *trnDT* HQ720353. ***Copernicia rigida*** Britton and P. Wilson-FTG DNA Bank 1643; CISP4 HQ720873, CISP5 HQ720757, *matK* HQ720268, *ndhF* HQ720621, RPB2 HQ720511, *trnDT* HQ720421. ***Copernicia tectorum*** (Kunth) Mart.-FTG DNA Bank 1644; CISP4

HQ720874, CISP5 HQ720758, *matK* HQ720269, *ndhF* HQ720622, RPB2 HQ720512, *trnDT* HQ720482. ***Copernicia yarey*** Burret-FTG Live Collection 59971S (DNA Bank 13); CISP4 HQ720875, CISP5 HQ720759, *matK* HQ720270, *ndhF* HQ720623, RPB2 HQ720513, *trnDT* HQ720432. ***Corypha umbraculifera*** L.-FTG Live Collection FG1141H (DNA Bank 190); CISP4 HQ720876, CISP5 HQ720760, *matK* HQ720271, *ndhF* HQ720624, RPB2 HQ720514, *trnDT* HQ720483. ***Cryosophila stauracantha*** (Heynh.) R.J. Evans-FTG Live Collection 8089B (DNA Bank 105); CISP4 HQ720877, CISP5 HQ720761, *matK* HQ720272, *ndhF* HQ720625, *trnDT* HQ720481. ***Guihaia argyrata*** (S.K. Lee and F. N. Wei) S.K. Lee, F.N. Wei and J. Dransf.-FTG Live Collection 89278D (DNA Bank 351); CISP4 HQ720879, CISP5 HQ720763, *ndhF* HQ720627, *trnDT* HQ720451. ***Guihaia argyrata*** (S.K. Lee and F. N. Wei) S.K. Lee, F.N. Wei and J. Dransf.-FTG DNA Bank 1830; CISP4 HQ720878, CISP5 HQ720762, *matK* HQ720274, *ndhF* HQ720626, *trnDT* HQ720450. ***Guihaia argyrata*** (S.K. Lee and F. N. Wei) S.K. Lee, F.N. Wei and J. Dransf.-*W.J. Baker s.n.* (K); CISP4 HQ720880, CISP5 HQ720764, *matK* HQ720273, *ndhF* HQ720628, *trnDT* HQ720442. ***Guihaia grossefibrosa*** (Gagnep.) J. Dransf., S.K. Lee and F.N. Wei-FTG Live Collection 89936A (DNA Bank 138); CISP4 HQ720881, CISP5 HQ720765, *matK* HQ720275, *ndhF* HQ720629, *trnDT* HQ720452. ***Johannesteijsmannia altifrons*** (Rchb.f. and Zoll.) H.E. Moore-FTG DNA Bank 970; CISP5 HQ720767, RPB2 HQ720516, *trnDT* HQ720403. ***Johannesteijsmannia altifrons*** (Rchb.f. and Zoll.) H.E. Moore-FTG Live Collection 86547E (DNA Bank 122); CISP4 HQ720882, CISP5 HQ720766, *matK* HQ720277, *ndhF* HQ720629, RPB2 HQ720515, *trnDT* HQ720360. ***Johannesteijsmannia altifrons*** (Rchb.f. and Zoll.) H.E. Moore-1985-1515 (K); CISP4 HQ720883, *ndhF* HQ720631,

trnDT HQ720358. ***Johannesteijsmannia altifrons*** (Rchb.f. and Zoll.) H.E. Moore-*S.L. Look 134* (K); CISP4 HQ720884, CISP5 HQ720768, *matK* HQ720276, *ndhF* HQ720632, RPB2 HQ720517, *trnDT* HQ720402. ***Johannesteijsmannia lanceolata*** J. Dransf.-*S.L. Look 061* (K); CISP4 HQ720885, CISP5 HQ720769, *matK* HQ720278, *ndhF* HQ720633, RPB2 HQ720518, *trnDT* HQ720400. ***Johannesteijsmannia magnifica*** J. Dransf.-*S.L. Look 078* (K); CISP4 HQ720886, CISP5 HQ720771, *matK* HQ720279, *ndhF* HQ720635, RPB2 HQ720520, *trnDT* HQ720397. ***Johannesteijsmannia magnifica*** J. Dransf.-Lyon Live Collection 90.0308; CISP4 HQ720887, CISP5 HQ720770, *matK* HQ720280, *ndhF* HQ720634, RPB2 HQ720519, *trnDT* HQ720398. ***Johannesteijsmannia perakensis*** J. Dransf.-*S.L. Look 037* (K); CISP4 HQ720887, CISP5 HQ720772, *matK* HQ720282, *ndhF* HQ720636, RPB2 HQ720522, *trnDT* HQ720401. ***Johannesteijsmannia perakensis*** J. Dransf.-Lyon Live Collection 2006.0062; *matK* HQ720281, *ndhF* HQ720637, RPB2 HQ720521, *trnDT* HQ720399. ***Kerriodoxa elegans*** J. Dransf.-FTG Live Collection 86356B (DNA Bank 198); *matK* HQ720283, *ndhF* HQ720639, *trnDT* HQ720356. ***Kerriodoxa elegans*** J. Dransf.-FTG Live Collection 84213A (DNA Bank 74); CISP4 HQ720889, CISP5 HQ720773, *matK* HQ720284, *ndhF* HQ720638, RPB2 HQ720523, *trnDT* HQ720357. ***Lanonia acaulis*** Henderson, N.K. Ban, and N.Q. Dung-*A.J. Henderson 3309* (NY); *trnDT* HQ720359. ***Lanonia calciphila*** Becc.-*A.J. Henderson 3328* (NY). CISP4 HQ720892, *ndhF* HQ720646; ***Lanonia centralis*** Henderson, N.K. Ban, and N.Q. Dung-*A.J. Henderson 3222* (NY). *ndhF* HQ720647. ***Lanonia dasyantha*** Burret-*A.J. Henderson 3363* (NY). *ndhF* HQ720650, *trnDT* HQ720361. ***Lanonia magalonii*** Henderson, N.K. Ban, and N.Q. Dung-*A.J. Henderson 3268*, Vietnam (NY). *ndhF* HQ720661, *trnDT* HQ720362. ***Licuala atroviridis*** Henderson, N.K. Ban, and N.Q.

Dung-*A.J. Henderson 3300* (NY); *ndhF* HQ720640. ***Licuala bachmaensis*** Henderson, N.K. Ban, and N.Q. Dung-*A.J. Henderson 3254* (NY); *ndhF* HQ720641, *trnDT* HQ720393. ***Licuala bacularia*** Becc.-FTG Live Collection 951383N (DNA Bank 1471); CISP4 HQ720890, CISP5 HQ720775, *matK* HQ720285, *ndhF* HQ720642, RPB2 HQ720524, *trnDT* HQ720411. ***Licuala beccariana*** (K. Schum. and Lauterb.) Furtado-MBC Live Collection 96179.A; CISP5 HQ720775, *matK* HQ720286, *ndhF* HQ720643, RPB2 HQ720525, *trnDT* HQ720390. ***Licuala bidoupensis*** Henderson, N.K. Ban, and N.Q. Dung-*A.J. Henderson 3419* (NY); *ndhF* HQ720644, *trnDT* HQ720394. ***Licuala bracteata*** Gagnep.-*A.J. Henderson 3456* (NY); CISP4 HQ720891, *ndhF* HQ720645, *trnDT* HQ720395. ***Licuala cattienensis*** Henderson, N.K. Ban, and N.Q. Dung-*A.J. Henderson 3407* (NY); *ndhF* HQ720648, *trnDT* HQ720392. ***Licuala concinna*** Burret-MBC Live Collection 2000524.V; CISP4 HQ720893, CISP5 HQ720776, *ndhF* HQ720649, RPB2 HQ720526, *trnDT* HQ720382. ***Licuala distans*** Ridl.-MBC Live Collection 99669.BB; CISP4 HQ720894, CISP5 HQ720777, *matK* HQ720287, *ndhF* HQ720651, RPB2 HQ720527, *trnDT* HQ720381. ***Licuala grandiflora*** Ridl.-*J. Dransfield 7719* (K); CISP5 HQ720778, *ndhF* HQ720652. ***Licuala grandis*** H. Wendl.-*M.P. Simmons 1922* (MO); CISP4 HQ720896, CISP5 HQ720780, *ndhF* HQ720654, RPB2 HQ720529, *trnDT* HQ720387. ***Licuala grandis*** H. Wendl.-FTG Live Collection 6329D (DNA Bank 188); CISP4 HQ720895, CISP5 HQ720779, *matK* HQ720288, *ndhF* HQ720653, RPB2 HQ720528, *trnDT* HQ720389. ***Licuala kunstleri*** Becc.-1985-1497 (K); CISP4 HQ720897, CISP5 HQ720781, *matK* HQ720289, *ndhF* HQ720655, RPB2 HQ720530, *trnDT* HQ720386. ***Licuala lauterbachii*** Dammer and K. Schum.-*C.D. Heatubun 187* (K); CISP4 HQ720898, CISP5 HQ720782, *ndhF* HQ720656, RPB2

HQ720531, *trnDT* HQ720388. ***Licuala montana*** Dammer and K. Schum.-*W.J. Baker 576* (K); CISP4 HQ720899, *ndhF* HQ720657, RPB2 HQ720532, *trnDT* HQ720383. ***Licuala paludosa*** Griff.-MBC Live Collection 91374; CISP4 HQ720900, CISP5 HQ720783, *ndhF* HQ720658, *RPB2* HQ720533, *trnDT* HQ720391. ***Licuala peltata*** v. sumawongii Saw-FTG Live Collection 70320G (DNA Bank 207); CISP4 HQ720901, CISP5 HQ720784, *matK* HQ720290, *ndhF* HQ720659, RPB2 HQ720534, *trnDT* HQ720414. ***Licuala ramsayi*** (F. Muell.) Domin.-*J.W. Horn 4930* (PTBG); CISP4 HQ720902, CISP5 HQ720785, *matK* HQ720291, *ndhF* HQ720660, RPB2 HQ720535, *trnDT* HQ720396. ***Licuala robinsoniana*** Becc.-*A.J. Henderson 3457* (NY); *ndhF* HQ720662, *trnDT* HQ720415. ***Licuala spinosa*** Wurmb.-*A. J. Henderson 3385* (NY); *ndhF* HQ720663, RPB2 HQ720556. ***Licuala spinosa*** Wurmb.-MBC Live Collection 981813.Z; CISP4 HQ720903, CISP5 HQ720786, *matK* HQ720292, *ndhF* HQ720664, RPB2 HQ720536, *trnDT* HQ720384. ***Licuala spinosa*** Wurmb.-*M.P. Simmons 1921* (MO); CISP4 HQ720904, CISP5 HQ720787, *ndhF* HQ720665, RPB2 HQ720537, *trnDT* HQ720385. ***Licuala tanycola*** H.E. Moore-*Baker 1139* (K); CISP5 HQ720788, *matK* HQ720293, *ndhF* HQ720666, *trnDT* HQ720412. ***Licuala telifera*** Becc.-*Dransfield 7686* (K); CISP4 HQ720907, CISP5 HQ720789, *ndhF* HQ720669. ***Licuala telifera*** Becc.-*W.J. Baker 1054* (K); CISP4 HQ720905, *ndhF* HQ720667. ***Livistona australis*** (R. Br.) Mart.-*J.L. Dowe 313* (FTG); CISP4 HQ720908, CISP5 HQ720790, *matK* HQ720338, *ndhF* HQ720670, RPB2 HQ720538, *trnDT* HQ720370. ***Livistona benthamii*** F.M. Bailey-MBC Live Collection 69691.G; CISP5 HQ720791, *matK* HQ720345, *ndhF* HQ720671, RPB2 HQ720539, *trnDT* HQ720404. ***Livistona carinensis*** (Chiov.) J. Dransf.-FTG DNA Bank 1557; CISP4 HQ720909, CISP5 HQ720792, *matK* HQ720332, *ndhF* HQ720672,

RPB2 HQ720539, *trnDT* HQ720363. ***Livistona chinensis*** (Jacq.) R. Br. ex Mart.-FTG Live Collection 93982X (DNA Bank 809); CISP4 HQ720911, CISP5 HQ720793, *matK* HQ720331, *ndhF* HQ720674, RPB2 HQ720542. ***Livistona chinensis*** (Jacq.) R. Br. ex Mart.-FTG DNA Bank 2046; CISP4 HQ720910, CISP5 HQ720794, *matK* HQ720335, *ndhF* HQ720673, RPB2 HQ720541, *trnDT* HQ720413. ***Livistona concinna*** Dowe and Barford-MBC Live Collection 9659.H; CISP4 HQ720912, *matK* HQ720339, *ndhF* HQ720675, RPB2 HQ720543, *trnDT* HQ720369. ***Livistona fulva*** Rodd- MBC Live Collection 96212; CISP4 HQ720913, CISP5 HQ720795, *matK* HQ720341, *ndhF* HQ720676, RPB2 HQ720544. ***Livistona humilis*** R. Br.-FTG Live Collection 84202F (DNA Bank 33); CISP4 HQ720914, CISP5 HQ720796, *matK* HQ720333, *ndhF* HQ720677, RPB2 HQ720545, *trnDT* HQ720374. ***Livistona inermis*** R. Br.- MBC Live Collection 97973.G; CISP4 HQ720915, CISP5 HQ720797, *matK* HQ720342, *ndhF* HQ720678, RPB2 HQ720546, *trnDT* HQ720373. ***Livistona jenkinsiana*** Griff.- *A.J. Henderson 3232* (NY); CISP4 HQ720916, CISP5 HQ720798, *ndhF* HQ720679, RPB2 HQ720547, *trnDT* HQ720372. ***Livistona lanuginosa*** Rodd- MBC Live Collection 9670.B; CISP5 HQ720799, *ndhF* HQ720680, RPB2 HQ720548, *trnDT* HQ720375. ***Livistona lorophylla*** Becc.- MBC Live Collection 20011352.A; CISP4 HQ720917, CISP5 HQ720800, *matK* HQ720344, *ndhF* HQ720681, RPB2 HQ720549, *trnDT* HQ720365. ***Livistona mariae*** F. Muell.-*J. Doupe 353* (FTG); CISP4 HQ720918, CISP5 HQ720801, *matK* HQ720343, *ndhF* HQ720682, RPB2 HQ720550, *trnDT* HQ720376. ***Livistona muelleri*** F.M. Bailey- MBC Live Collection 9619.P; CISP4 HQ720919, CISP5 HQ720802, *matK* HQ720330, *ndhF* HQ720683, RPB2 HQ720551, *trnDT* HQ720368. ***Livistona nasmophila*** Dowe and D.L. Jones- MBC Live Collection 20011342.A; CISP4

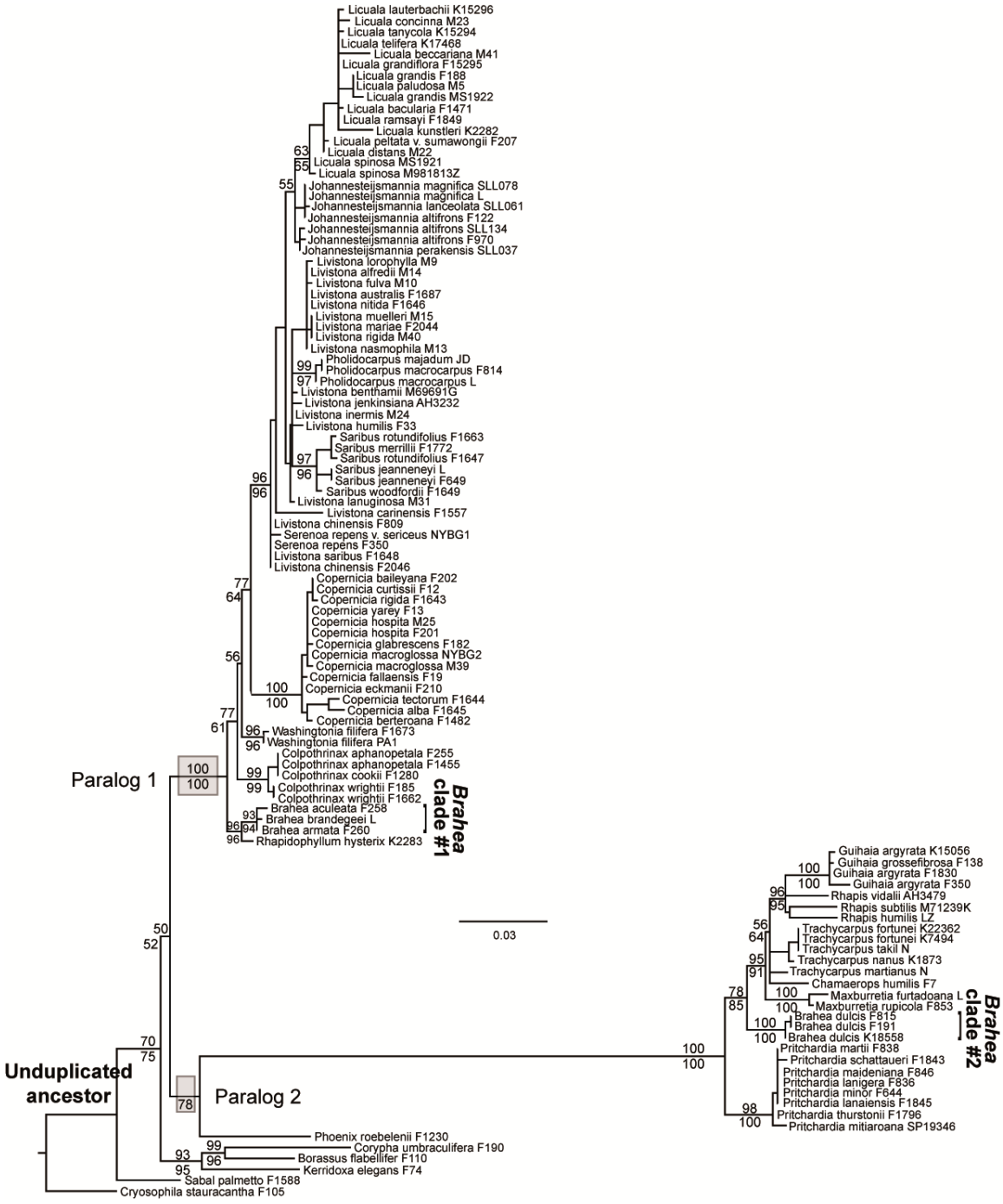
HQ720920, CISP5 HQ720803, *matK* HQ720334, *ndhF* HQ720684, RPB2 HQ720552, *trnDT* HQ720366. ***Livistona nitida*** Rodd-FTG DNA Bank 1646; CISP4 HQ720921, CISP5 HQ720804, *matK* HQ720340, *ndhF* HQ720685, RPB2 HQ720553, *trnDT* HQ720367. ***Livistona rigida*** Becc.- MBC Live Collection 91144.B; CISP5 HQ720805, *matK* HQ720337, *ndhF* HQ720686, RPB2 HQ720554, *trnDT* HQ720377. ***Livistona saribus*** (Lour.) Merr. ex A. Chev.-FTG DNA Bank 1648; CISP4 HQ720922, CISP5 HQ720806, *matK* HQ720336, *ndhF* HQ720687, RPB2 HQ720555, *trnDT* HQ720371. ***Livistona victoriae*** Rodd- MBC Live Collection 96265.H; *matK* HQ720306, *ndhF* HQ720688, *trnDT* HQ720364. ***Maxburretia furtadoana*** J. Dransf.-Lyon Live Collection 2000.0351; CISP4 HQ720923, CISP5 HQ720807, *matK* HQ720311, *ndhF* HQ720689, RPB2 HQ720557, *trnDT* HQ720441. ***Maxburretia rupicola*** (Ridl.) Furtado-FTG DNA Bank 853; CISP4 HQ720924, CISP5 HQ720808, *matK* HQ720297, *ndhF* HQ720690, RPB2 HQ720558, *trnDT* HQ720446. ***Phoenix roebelenii*** O'Brien-FTG Live Collection P.129B (DNA Bank 1230); CISP4 HQ720925, CISP5 HQ720809, *matK* HQ720352, *ndhF* HQ720691, RPB2 HQ720559, *trnDT* HQ720354. ***Pholidocarpus macrocarpus*** Becc.-FTG Live Collection 2002-0584A (DNA Bank 814); CISP4 HQ720926, CISP5 HQ720810, *matK* HQ720295, *ndhF* HQ720693, RPB2 HQ720560, *trnDT* HQ720405. ***Pholidocarpus macrocarpus*** Becc.-Lyon Live Collection 2000.0369; CISP4 HQ720927, CISP5 HQ720811, *matK* HQ720296, *ndhF* HQ720694, RPB2 HQ720561, *trnDT* HQ720406. ***Pholidocarpus majadum*** Becc.-*Dowe s.n.*; CISP4 HQ720928, CISP5 HQ720812, *matK* HQ720294, *ndhF* HQ720692, RPB2 HQ720562, *trnDT* HQ720407. ***Pritchardia lanaiensis*** Becc. and Rock-*S.P. Perlman 16385* (PTBG); CISP4 HQ720929, CISP5 HQ720813, *matK* HQ720298, *ndhF* HQ720695, RPB2 HQ720563, *trnDT*

HQ720422. ***Pritchardia lanigera*** Becc.-FTG DNA Bank 836; CISP4 HQ720930, CISP5 HQ720814, *matK* HQ720300, *ndhF* HQ720696, RPB2 HQ720564, *trnDT* HQ720423. ***Pritchardia maideniana*** Becc.-FTG DNA Bank 846; CISP4 HQ720931, CISP5 HQ720815, *matK* HQ720299, *ndhF* HQ720697, RPB2 HQ720565, *trnDT* HQ720419. ***Pritchardia martii*** (Gaudich.) H. Wendl.-FTG DNA Bank 838; CISP4 HQ720932, CISP5 HQ720816, *matK* HQ720301, *ndhF* HQ720698, RPB2 HQ720566, *trnDT* HQ720462. ***Pritchardia minor*** Becc.-FTG DNA Bank 644; CISP4 HQ720933, CISP5 HQ720817, *matK* HQ720302, RPB2 HQ720567, *trnDT* HQ720424. ***Pritchardia mitiaroana*** J. Dransf. and Y. Ehrh.-*S.P. Perlman 19346* (PTBG); CISP4 HQ720934, CISP5 HQ720818, *matK* HQ720304, *ndhF* HQ720699, RPB2 HQ720568, *trnDT* HQ720463. ***Pritchardia schattaueri*** Hodel-*J.W. Horn 4939* (PTBG); CISP4 HQ720935, CISP5 HQ720819, *matK* HQ720303, *ndhF* HQ720700, RPB2 HQ720569, *trnDT* HQ720425. ***Pritchardia thurstonii*** F. Muell. and Drude-FTG DNA Bank 1796; CISP4 HQ720936, CISP5 HQ720820, *matK* HQ720305, *ndhF* HQ720701, RPB2 HQ720570, *trnDT* HQ720417. ***Rhapidophyllum hystrix*** (Frazer ex Thouin) H. Wendl.-*Chase 2283* (K); CISP4 HQ720937, CISP5 HQ720821, *matK* HQ720323, *ndhF* HQ720702, RPB2 HQ720571, *trnDT* HQ720459. ***Rhapis excelsa*** (Thunb.) Henry-FTG DNA Bank 959; CISP4 HQ720938, *matK* HQ720320, *ndhF* HQ720703, RPB2 HQ720572, *trnDT* HQ720474. ***Rhapis excelsa*** (Thunb.) Henry-*Baker s.n.* (K); CISP4 HQ720939, *matK* HQ720321, *ndhF* HQ720704, RPB2 HQ720573, *trnDT* HQ720475. ***Rhapis humilis*** Blume-*L. B. Zhang s.n.*; CISP4 HQ720940, CISP5 HQ720822, *matK* HQ720308, *ndhF* HQ720705, RPB2 HQ720574, *trnDT* HQ720436. ***Rhapis laosensis*** Becc.-Lyon Live collection 98.0591; CISP4 HQ720941, CISP5 HQ720823, *matK* HQ720322, *ndhF*

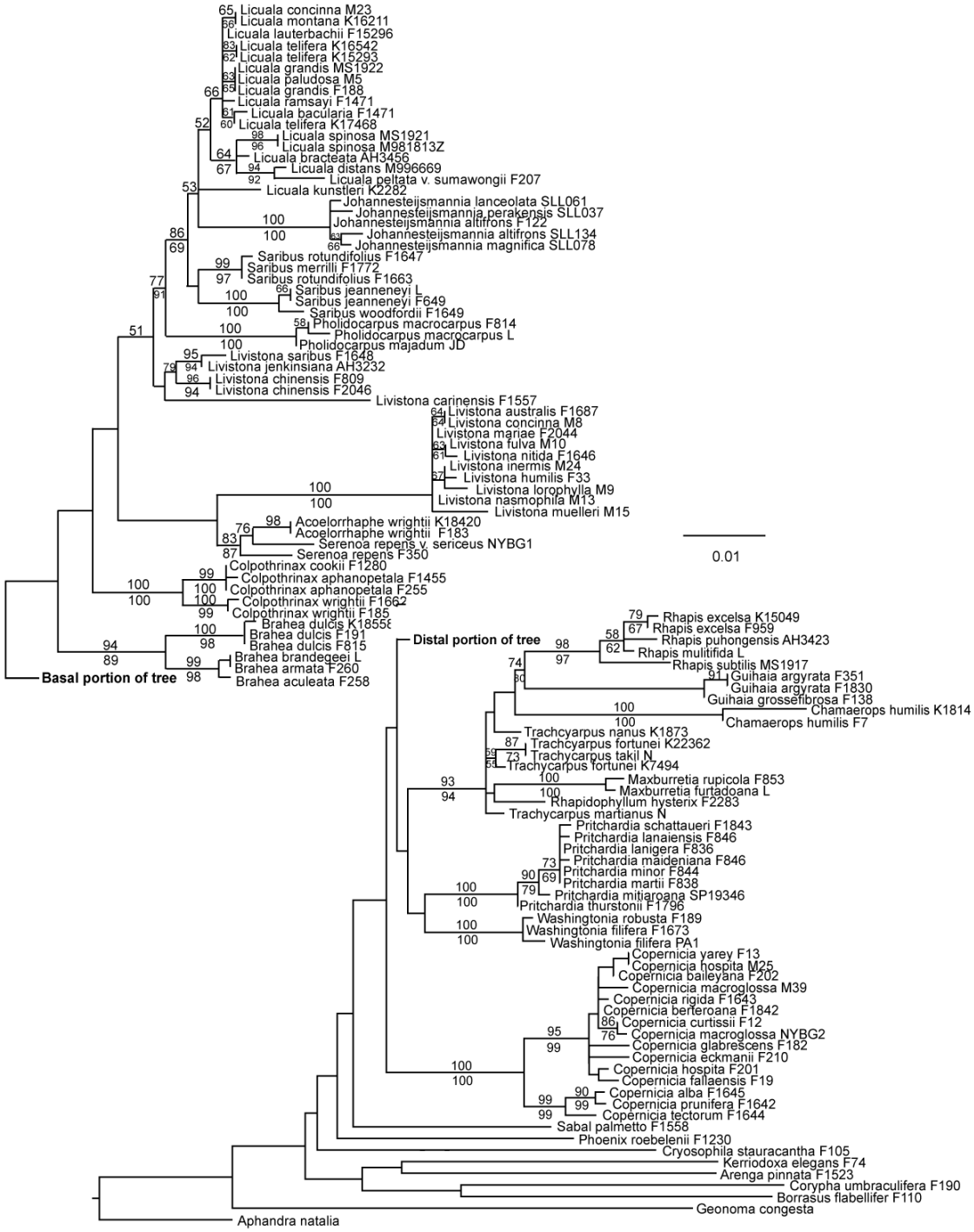
HQ720706, *trnDT* HQ720476. ***Rhapis multifida*** Burret-*Lyon s.n.*; CISP4 HQ720942, *matK* HQ720316, *ndhF* HQ720707, *trnDT* HQ720477. ***Rhapis multifida*** Burret-*L. B. Zhang s.n.*; *matK* HQ720319, *ndhF* HQ720708, RPB2 HQ720575, *trnDT* HQ720437. ***Rhapis puhuongensis*** M.S. Trudgen, T.P. Anh, and A.J. Henderson-*A.J. Henderson 3423* (NY); CISP4 HQ720943, *matK* HQ720318, *ndhF* HQ720709, RPB2 HQ720576, *trnDT* HQ720435. ***Rhapis subtilis*** Becc.-MBC Live Collection 71239.K; CISP5 HQ720824, *matK* HQ720309, *ndhF* HQ720710, *trnDT* HQ720471. ***Rhapis subtilis*** Becc.-*M.P. Simmons 1917* (MO); CISP4 HQ720944, CISP5 HQ720825, *matK* HQ720310, *ndhF* HQ720711, RPB2 HQ720577, *trnDT* HQ720472. ***Rhapis vidalii*** Aver., H.T. Nguyen and L.K. Phan-*A.J. Henderson 3479* (NY); CISP5 HQ720826, *matK* HQ720317, *ndhF* HQ720712, *trnDT* HQ720473. ***Sabal palmetto*** (Walter) Lodd. ex Schult. and Schult. f.-FTG DNA Bank 1588; CISP4 HQ720945, CISP5 HQ720827, *matK* HQ720346, *ndhF* HQ720713, RPB2 HQ720578, *trnDT* HQ720458. ***Saribus jeanneneyi*** Becc.-FTG DNA Bank 649; CISP4 HQ720946, CISP5 HQ720828, *matK* HQ720347, *ndhF* HQ720714, RPB2 HQ720579, *trnDT* HQ720379. ***Saribus jeanneneyi*** Becc.-Lyon Live Collection 2000.0182; CISP4 HQ720947, CISP5 HQ720829, *matK* HQ720347, RPB2 HQ720580, *trnDT* HQ720380. ***Saribus merrillii*** Becc.-*J.W. Horn 4925* (FTG); CISP4 HQ720948, CISP5 HQ720830, *matK* HQ720348, *ndhF* HQ720715, RPB2 HQ720581, *trnDT* HQ720408. ***Saribus rotundifolius*** (Lam.) Mart.-FTG DNA Bank 1663; CISP4 HQ720949, CISP5 HQ720831, *matK* HQ720349, *ndhF* HQ720716, RPB2 HQ720583, *trnDT* HQ720409. ***Saribus rotundifolius*** (Lam.) Mart.-FTG DNA Bank 1647; CISP4 HQ720950, CISP5 HQ720832, *matK* HQ720350, *ndhF* HQ720717, RPB2 HQ720582, *trnDT* HQ720410. ***Saribus woodfordii*** Ridl.-FTG DNA Bank 1649; CISP4

HQ720951, CISP5 HQ720833, *matK* HQ720351, *ndhF* HQ720718, RPB2 HQ720584, *trnDT* HQ720378. ***Serenoa repens*** (W. Bartram) Small-FTG Live Collection 71522C (DNA Bank 350); CISP4 HQ720952, CISP5 HQ720834, *matK* HQ720326, *ndhF* HQ720719, RPB2 HQ720585, *trnDT* HQ720456. ***Serenoa repens*** (W. Bartram) Small-NYBG Live Collection 4131/95D; CISP4 HQ720953, CISP5 HQ720835, *matK* HQ720325, *ndhF* HQ720720, RPB2 HQ720586, *trnDT* HQ720454. ***Trachycarpus fortunei*** (Hook.) H. Wendl.-*Dransfield s.n.* (K); CISP4 HQ720955, CISP5 HQ720836, *matK* HQ720313, *ndhF* HQ720722, RPB2 HQ720587, *trnDT* HQ720479. ***Trachycarpus fortunei*** (Hook.) H. Wendl.-*Chase 22362* (K); CISP4 HQ720954, CISP5 HQ720837, *matK* HQ720315, *ndhF* HQ720721, RPB2 HQ720588, *trnDT* HQ720439. ***Trachycarpus martianus*** (Wall. ex Mart.) H. Wendl.-NTBG Live Collection 70531; CISP4 HQ720956, CISP5 HQ720838, *matK* HQ720324, *ndhF* HQ720723, *trnDT* HQ720438. ***Trachycarpus nanus*** Becc.- *Chase 1873* (K); CISP4 HQ720957, CISP5 HQ720839, *matK* HQ720312, *ndhF* HQ720724, RPB2 HQ720589, *trnDT* HQ720478. ***Trachycarpus takil*** Becc.-*NTBG Live Collection s.n.*; CISP4 HQ720958, CISP5 HQ720840, *ndhF* HQ720726, RPB2 HQ720590, *trnDT* HQ720440. ***Trachycarpus takil*** Becc.-*Gibbons s.n.* (K); *matK* HQ720314, *ndhF* HQ720725, *trnDT* HQ720480. ***Washingtonia filifera*** (Linden ex André) H. Wendl.-FTG DNA Bank 1673; CISP4 HQ720959, CISP5 HQ720841, *matK* HQ720328, *ndhF* HQ720727, RPB2 HQ720591, *trnDT* HQ720457. ***Washingtonia filifera*** (Linden ex André) H. Wendl.-*P.A. Alexander s.n.*; CISP4 HQ720960, CISP5 HQ720842, *matK* HQ720327, *ndhF* HQ720728, RPB2 HQ720592, *trnDT* HQ720470. ***Washingtonia robusta*** H. Wendl.-FTG Live Collection 71439B (DNA Bank 189);

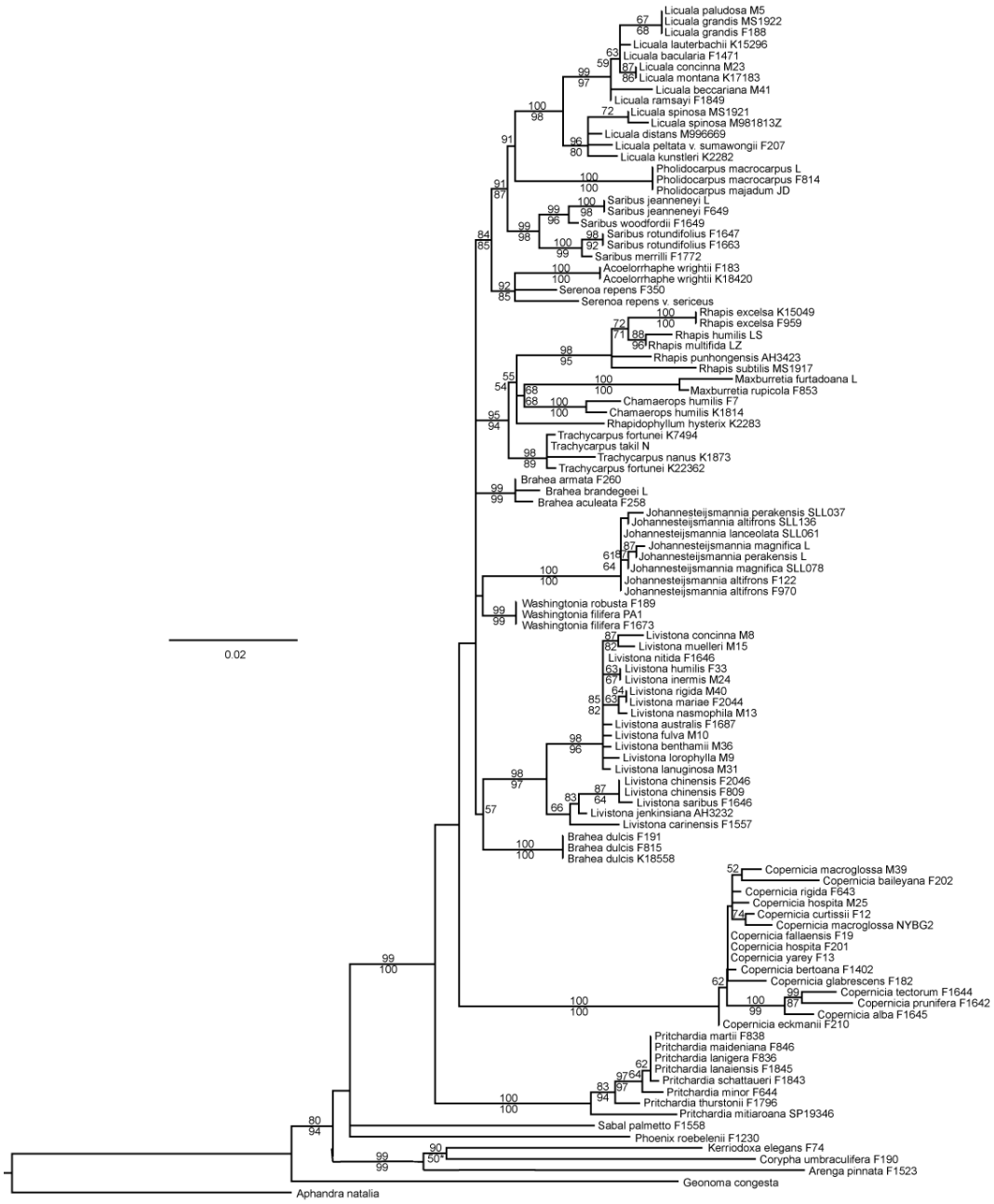
CISP4 HQ720961, CISP5 HQ720843, *matK* HQ720329, *ndhF* HQ720729, RPB2 HQ720593, *trnDT* HQ720447.



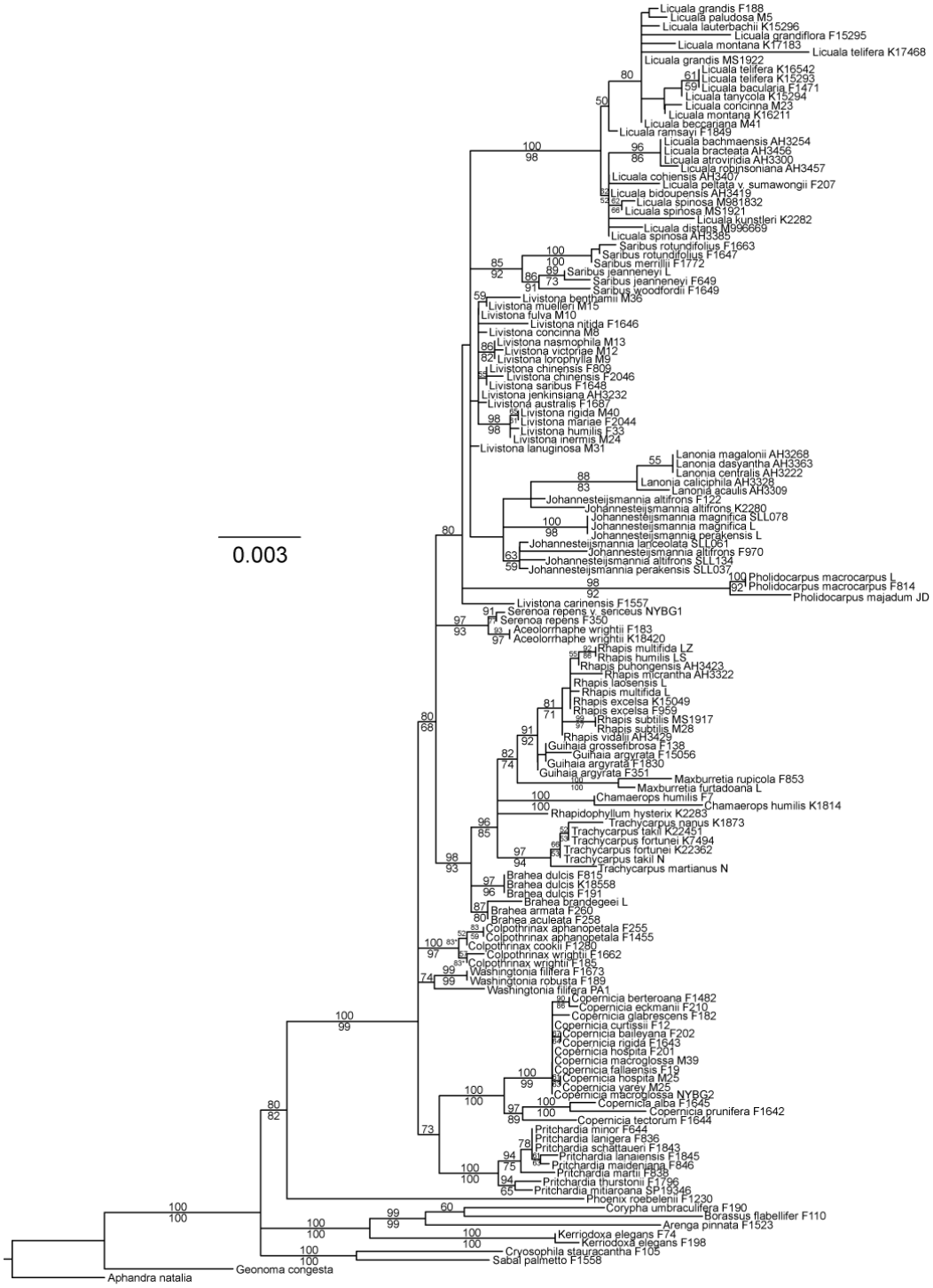
Supplemental figure 1. CISP5 bootstrapped maximum likelihood gene tree before uninode coding. Indicated are both inferred paralogs and the unduplicated ancestor sequences, for which the hypothetical ancestor sequence was derived in MacClade (see methods section.).



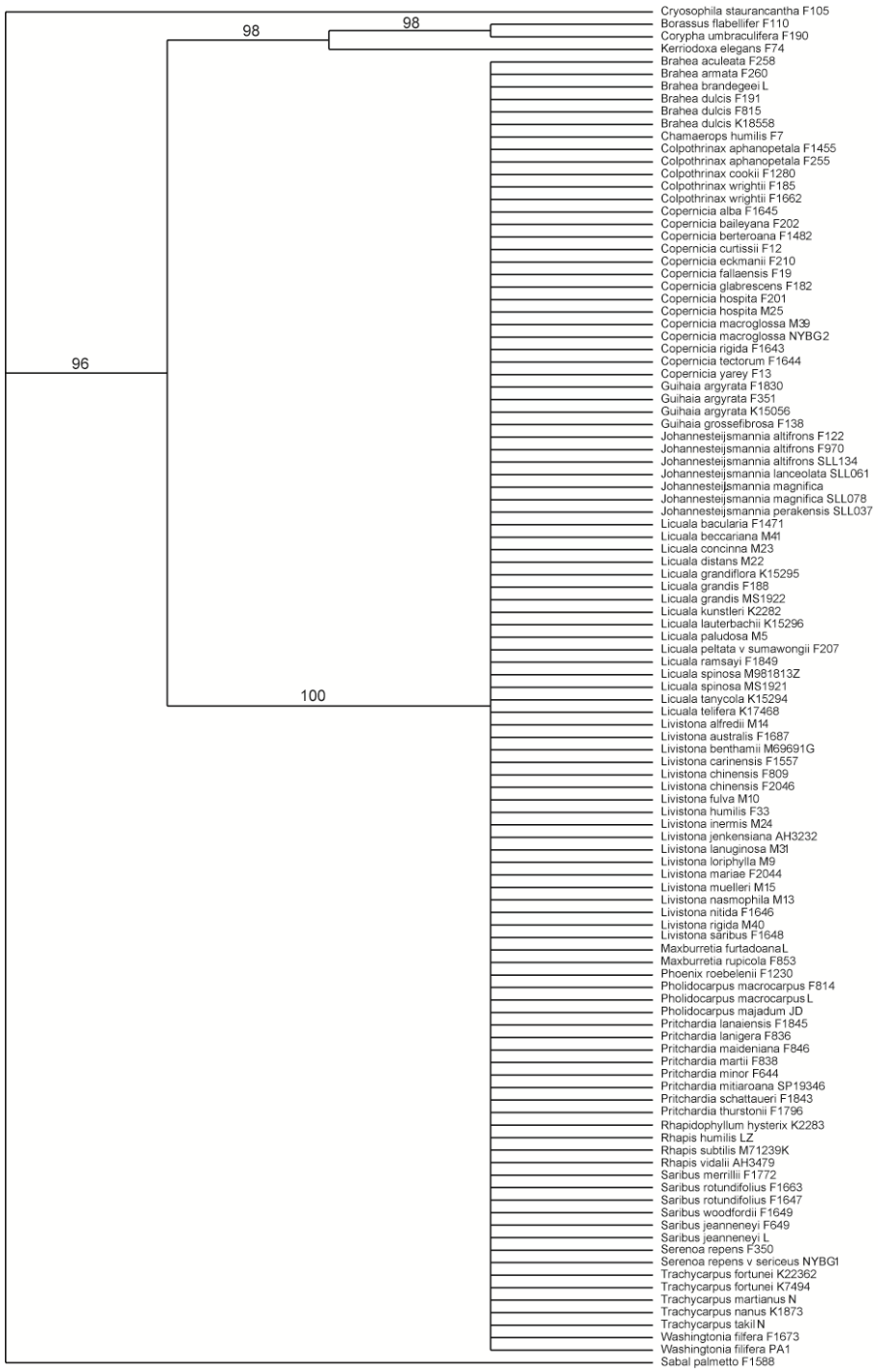
Supplemental figure 2. CISP4 bootstrapped maximum likelihood gene tree where support values ≥ 50% are shown with BS above and JK support below each branch.



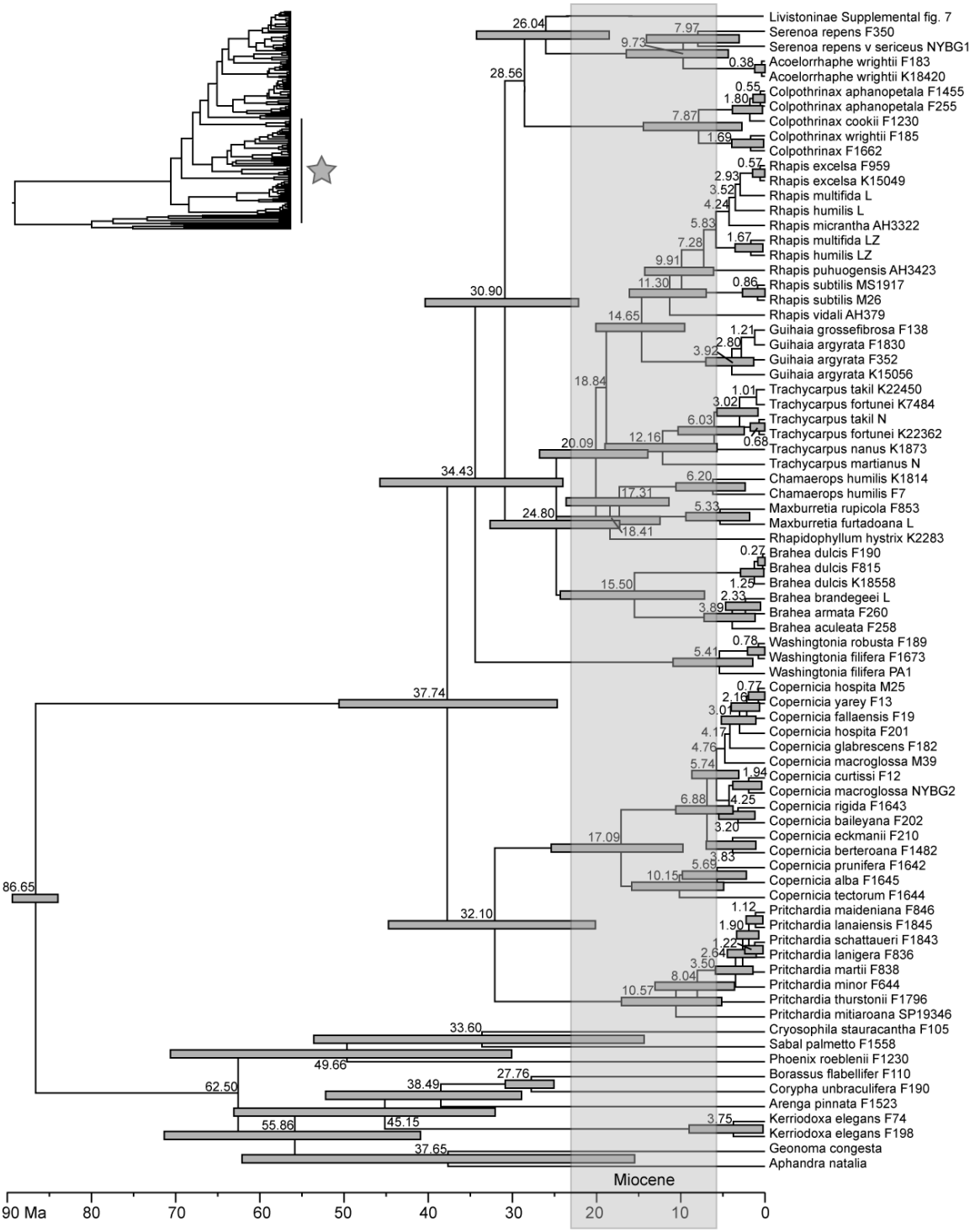
Supplemental figure 3. RPB2 bootstrapped maximum likelihood gene tree. Clades in the likelihood BS tree that were contradicted by clades in the parsimony JK tree are indicated with asterisks, with JK support for the highest contradictory parsimony clade listed.



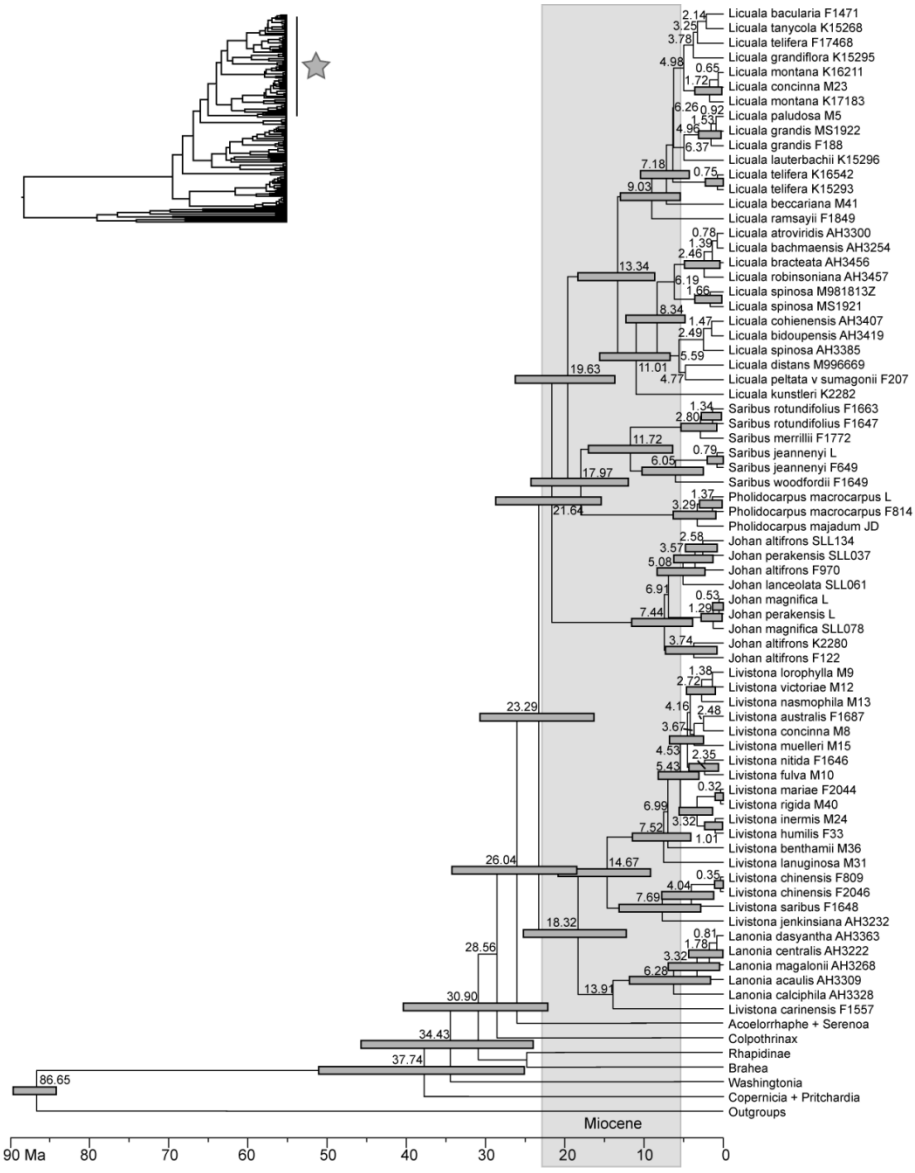
Supplemental figure 4. Plastid combined bootstrapped maximum likelihood gene tree of *matK*, *ndhF*, and *trnDT* with support values and incongruence indicated as in Supplemental figure 3.



Supplemental figure 5. Parsimony strict consensus tree of the uninode coded CISP5 with JK values ≥ 50% above each branch.



Supplemental figure 6. Basal portion of BEAST derived Bayesian tree showing minimum mean ages and 95% HPD credible set for all nodes. Nodes with no credible set bars indicate that they were supported by less than 0.50 posterior probabilities.



Supplemental figure 7. Distal portion of BEAST derived Bayesian tree showing minimum mean ages and 95% HPD credible set for all nodes. Nodes with no credible set bars indicate that they were supported by less than 0.50 posterior probabilities. *Johannesteijsmannia* is abbreviated as Johan.

Chapter 3. Disparities in Species Diversity: Dispersal and Diversification Rates across Wallace's Line

Since Darwin (1859) and Wallace (1878), many biologists have hypothesized about the causal mechanisms behind disparities in species diversity. Broad patterns of species diversity have been the focus of most studies and examples such as the disparities between temperate and tropical regions (e.g., Middlebach et al. 2007) and the Neo- and Paleotropics (e.g., Phillips et al. 1994) dominate the scientific literature. There are many potential explanations for differences in these large-scale patterns including, but not limited to, geological and climatic history, area, the extent of biotic interactions, and speciation versus extinction rates. Outside of these large-scale patterns are sharp differences in species diversity within relatively small biogeographic regions and these discrete instances may lead to the understanding of local-scale processes that are also important in shaping diversity patterns.

A unique form of disparity in species diversity, found in southeast Asia, is characterized by high species richness in the eastern and western regions, coupled with remarkably low diversity in Wallacea (Dransfield 1981, 1987). This bimodal pattern has been reported in grasses and palms (Baker et al. 1998), Caesalpinoid legumes, sedges, and diptocarps (van Welzen and Slik 2009) and although not unique to the angiosperms (e.g., hawkmoths, Beck et al. 2006), the pattern has been suggested to be most

pronounced in the palm family Arecaceae (Dransfield 1981, 1987; Baker et al. 1998; Baker and Couvreur in press*).

Understanding the origin of this unusual pattern will shed light on the processes that have generated some of the diversity in Southeast Asia where three biodiversity hotspots are located (Myers et al. 2000). The complex geological history of the region that combines important reorganization of terrestrial habitats with the collision of the Sunda and Sahul shelves leading to volcanic uplifting, and repeated fluctuation of sea levels (Morley 2000; Hall 2009), has engendered many opportunities for habitat fragmentation and allopatric speciation. To understand the origin of the bimodal distribution pattern, we need to evaluate the relative contribution of migration events across Wallacea and diversification within each biogeographic region. At one extreme, the pattern might be caused by numerous instances of migration across Wallacea followed by little *in situ* diversification. At the other extreme, the pattern might reflect few migration events followed by high *in situ* diversification. Furthermore, the timing of these events might also be important to understand the dynamics of diversification: in the event that few migration instances were involved, high diversification rates need to be invoked if these migration events were recent rather than ancient. Finally extinction within Wallacea may have reinforced the role migration and diversification had played in shaping this pattern.

The bimodal species diversity pattern in southeast Asian palms is interesting because of the extreme biogeographical disjunction it forms across a relatively small area (western region: 302 palm species in Borneo, 162 in the Philippines; eastern region: 243 palm species in New Guinea; Wallacea: 62 palm species in Sulawesi, 40 in the Moluccas,

and 6 in the Lesser Sunda Islands (Baker and Couvruer in press*). Within the palms, subtribe Livistoninae (Arecaceae, Coryphoideae, Trachycarpeae) is an ideal group to examine bimodal species richness patterns because it has been the focus of recent phylogenetic studies, though inter-generic relationships have remained tenuous (Bacon et al. in review*). Livistoninae comprise approximately 198 species in six genera - *Johannesteijsmannia* (four species), *Licuala* (144), *Livistona* (27), *Pholidocarpus* (six), *Saribus* (nine), and *Lanonia* (8; Henderson 2009; Henderson and Bacon, in review*). The ancestral stem lineage of this monophyletic subtribe originated in the New World in the Late Oligocene to early Miocene (ca. 18.5 – 34 Ma; Bacon et al. in review*). The extant distribution of Livistoninae is from Bhutan and China into Malesia and crosses Wallace's Line into New Guinea and Australia (Henderson 2009). Within Livistoninae *Licuala*, *Livistona*, and *Saribus* display strong bimodal biogeographic patterns with extremely low diversity in Wallacea (≤ five species each; Dransfield 2008).

To understand the relative importance of migration between biogeographic regions and diversification in shaping the bimodal distribution patterns, we infer the tempo and mode of species diversification in Livistoninae palm lineages. We use a time-calibrated multi-locus phylogeny to test the monophyly of genera and the timing of lineage origination and diversification. Likelihood models of historical biogeography allow us to localize the timed lineages in geographical space and estimate the number of vicariance and dispersal events along phylogenetic branches to test the contribution if migration in patterns of species diversity. We use estimates of net diversification rates to detect whether significant shifts are present, where they occurred on the phylogeny, and whether shift in diversification rates may have contributed to shape the bimodal pattern.

Taken together, these analyses also permit the synthesis of origin, diversification, timing and geography of species diversity patterns into a geological and climatic framework to examine the abiotic processes that may have contributed to disparities in species diversity and the bimodal biogeographic patterns in southeast Asia.

Materials and Methods

STUDY REGION - SOUTHEAST ASIA

The Sunda continental shelf spans southern Indochina, to the Thai-Malay peninsula, and to Sumatra, representing the ancient continental core of the region (Fig. 1; Hall and Morley 2004). To the east is the Sahul shelf, which forms the Australian continent. Between the Sunda and Sahul regions is Wallacea, which is bounded to the west by Wallace's Line, the biogeographic demarcation between Asian and Australian biota. Wallacea is the collision area between the two plates and constitutes the most geologically complex part of southeast Asia (Hall 2009). The sharp differentiation between the biota on either side of Wallacea has been maintained by a deep, cold-water oceanic trench (Nagao and Selya 1995) and in general, areas to the west and east of Wallace's Line are characterized by an ever-wet climate, whereas the intervening area of Wallacea has a dry monsoonal climate (Van Welzen et al. 2005). The strength of the biogeographic barrier differs between species and is dependent on dispersal capability (e.g., Mayr 1944).

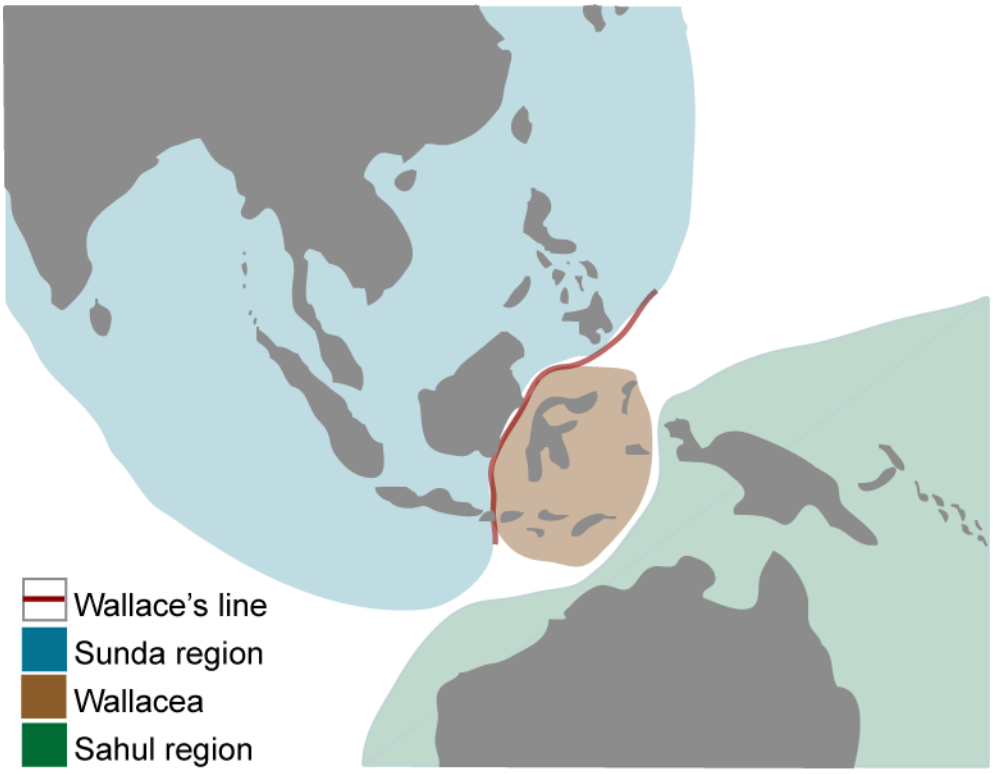


Fig. 1. Map of southeast Asia with the two major tectonic plates, Sahul and Sunda, as well as the biogeographic region Wallacea and the demarcation of Wallace's Line.

TAXON SAMPLING AND DNA SEQUENCING

Dense species-level sampling allowed for accurate assessments of phylogenetic relationships and was based on Bacon et al. (in review*) with the addition of 26 species and DNA sequences for another nuclear gene (MS; Appendix 1). The two outgroups [*Acoelorrhaphe wrightii* H. Wendl. and *Serenoa repens* (W. Bartram) Small] were chosen based on previous analysis (Bacon et al. in review*). Between 31 and 100% of species from each Livistoninae genus were sampled and a total of 98 terminals were included in the simultaneous analysis (Kluge 1989; Nixon and Carpenter 1996). Total genomic DNA was extracted from silica-gel dried leaves following Alexander et al. (2007). Sequences for three plastid (*matK*, *ndhF*, and *trnDT*) and four nuclear loci

(CISP4, CISP5, MS, and RPB2) were generated (Table 1). Single amplifications of the *matK* locus used primers *matK*-19F and *matK*-1862R, with internal sequencing primers *matK*-300F, *matK*-809F, and *matK*-971R to construct contiguous sequences (Steele and Vilgalys 1994; Asmussen et al. 2006). Amplifications of CISPs 4 and 5 followed Bacon et al. (2008), MS followed Crisp et al. (2010), *ndhF* followed Cuenca and Asmussen-Lange (2007), RPB2 followed Roncal et al. (2005), and *trnDT* followed Hahn (2002). Amplified products were purified using Qiagen PCR purification kits and sequenced by the Cancer Research Center DNA Sequencing Facility at the University of Chicago (Illinois, USA). All new sequences generated in this study have been deposited in GenBank under accession numbers HQ720156 to HQ720240 and HQ720962 to HQ721101 (Appendix 1).

PHYLOGENETIC ANALYSIS

Multi-locus phylogenies enabled the testing of monophyly of Livistoninae genera and biogeographic groups. Preliminary nucleotide alignments were obtained independently for each of the seven loci 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). Gap characters, the inclusion of which affects the inferred parsimony tree topology and increases branch-support values (Simmons et al. 2001), were scored using modified complex indel coding (Simmons and Ochoterena 2000; Müller 2006). Only parsimony-informative gap characters were scored from unambiguously aligned regions. A total of 26 gaps were scored (*matK*: 3; *ndhF*: 1;

Table 1. Data matrix and tree statistics of each parsimony analysis, including gap characters. "PI" = parsimony informative; "MPT" = most parsimonious tree; “CI” = ensemble consistency index; and “RI” = ensemble retention index (Farris 1989).

Matrix	# terminals	# chars.	# PI chars.	% miss. / inappl. chars.	MPT length	# of MPTs	# of JK / BS ≥ 50%	Average JK / BS support (%)	CI	RI
CISP4	74	868	105	22	202	9790	30 / 36	77 / 77	0.80	0.96
CISP5	77	614	50	13	122	9760	20 / 50	77 / 75	0.68	0.96
MS	66	795	120	2	318	6360	30 / 35	80 / 79	0.60	0.88
RPB2	74	890	128	20	243	9620	36 / 41	81 / 83	0.84	0.97
nDNA (CISPs 4 and 5, MS, RPB2)	94	3167	403	33	964	2480	48 / 53	80 / 81	0.64	0.91
matK	84	1769	59	8	178	5290	15 / 28	70 / 70	0.69	0.93
ndhF	92	956	31	6	64	5880	18 / 27	72 / 71	0.95	0.99
trnDT	84	963	56	14	152	6040	15 / 23	77 / 76	0.56	0.88
Plastid (*matK*, *ndhF*, *trnDT*)	96	3688	146	18	432	1690	32 / 31	75 / 82	0.58	0.90
Simultaneous	98	6855	549	27	1451	1360	56 / 53	82 / 82	0.59	0.89

trnDT: 6; CISP4: 8; CISP5: 0; MS: 2; RPB2: 6). Parsimony tree searches were conducted using 1000 random addition tree-bisection-reconnection (TBR) searches in PAUP* v4.0b10 (Swofford 2001) with a maximum of ten trees held per replicate. Parsimony jackknife (JK) analyses (Farris et al. 1996) were conducted using PAUP* and 1000 replicates were performed with 100 random addition TBR searches per replicate. jModeltest v0.1.1 (Posada 2008) was used to select the best-fit likelihood model for each data matrix using the Akaike Information Criterion (Akaike 1974) without considering invariant-site models following Yang (2006). Searches for optimal maximum likelihood trees (Felsenstein 1973) and 1000 bootstrap replicates (Felsenstein 1985) in the CIPRES Portal v2.2 used the RAxML-III algorithm (Stamatakis et al. 2005; Stamatakis et al. 2008). The simultaneous analysis was performed using the GTR + Γ model and the data matrix is available from TreeBase (study accession 11108).

BAYESIAN DIVERGENCE TIME ESTIMATION

We estimated divergence times using BEAST v1.5.4 (Drummond et al. 2006; Drummond and Rambaut 2007), which infers the age of all nodes in the tree and allowed for testing whether lineages conformed to a time-to-speciation effect. Because we do not know of any fossils in Livistoninae that have been identified unambiguously, we used a secondary calibration point obtained from a broader study based on primary fossil calibrations (tribe Trachycarpeae, Bacon et al. in review*). A normal distribution for the secondary calibration point at the stem node of Livistoninae was estimated and the bounds on the prior reflect the 95% credible interval of the calibration. The normal distribution has been shown to be most appropriate for modeling secondary calibrations

because it reflects the uncertainty in imported date estimates (Ho 2007; Ho and Phillips 2009).

The data was partitioned by locus to allow for variation in substitution models and the analysis was run using an uncorrelated log-normal molecular clock model, a Yule pure birth speciation model with no starting tree, the GTR+Γ model of nucleotide substitution with four rate categories, and the default operator. The Markov chains were run for 10 million generations and repeated 10 times to test for MCMC chain convergence and to ensure effective sample sizes (ESS) exceeded 200. After removing an *a priori* determined 10% burn-in, BEAST log files were combined in LogCombiner v1.5.4 to determine whether chains had reached stationarity in Tracer v1.5. Tree files were combined to estimate mean node height and the 95% highest posterior density (HPD) in TreeAnnotator v1.5.4.

BIOGEOGRAPHICAL RECONSTRUCTIONS

To test whether disparity in species diversity is due to the history of migration, we estimated the number of dispersal and vicariance events along phylogenetic branches and the historical biogeography of Livistoninae. Ancestral range patterns were inferred using five geographic areas: A) southeastern North America; B) Africa and Arabia; C) eastern Asia (India to Thailand, excluding the peninsular region), China (including Hainan), and Japan; D) Sunda [west of Wallace's Line (peninsular Thailand and the Philippines to Borneo and Java)], and E) Sahul [east of Wallace's Line (New Guinea and Australia to Vanuatu)]. Biogeographic areas were delimited based on areas of endemism in the tribe and to allow for hypothesis testing of dispersal and its effects on diversification rates

where area D is west and area E is east of Wallace's Line. We did not have sampling of any of the Wallacean species in the phylogeny; therefore Wallacea was not coded as a biogeographic area. In applying character-state reconstruction methods to ancestral distributions, we coded geographic ranges as discrete, multistate characters that allowed for ranges spanning more than one of these five geographic areas (Hardy and Linder 2005).

A likelihood framework for examining historical range shifts was implemented using the Dispersal-Extinction-Cladogenesis model (DEC; Ree et al. 2005) in Lagrange (Ree and Smith 2008a). DEC has been shown to be a robust model of inferring historical biogeography because it incorporates parameters such as divergence time estimates, dispersal capacities, extinction rates, and paleogeographic information between regions in geological time (Ree and Smith 2008b). Lagrange estimates the relative likelihood of each possible ancestral range at each node, given a particular probability of dispersal and extinction. The evolution of geographic range was simulated using a Monte Carlo method that estimated branch-specific transition probabilities and enabled the likelihood of the observed species distributions to be evaluated for a given phylogeny. We used the ultrametric tree generated by BEAST to infer ancestral distributions with default parameters for extinction rates and a single dispersal capacity. The statistical support for biogeographic reconstructions is defined by its relative probability (fraction of the global likelihood).

LIKELIHOOD ESTIMATION OF DIVERSIFICATION RATES

To test whether shifts in diversification rates may have contributed to shape the bimodal pattern of species distribution, we fit birth-death models of diversification to the phylogeny of Livistoninae inferred with BEAST using the R package LASER v2.3 (Rabosky 2006). By using species richness values to the tips of the phylogeny, this method allows the estimation of net diversification rates despite incomplete taxon sampling. We assigned missing taxa to the phylogeny based on the best estimate of the total number of species in each group from reviews of morphology, unpublished work, recent field expeditions, and the World Checklist of Palms (http://apps.kew.org/wcsp/home.do). We also reduced the tree to only include one individual per species to help avoid sampling bias (Rabosky 2006).

To test for shifts in diversification rate, we followed the approach outlined by Rabosky et al. (2007). First, we compared the likelihoods of a model with an equal diversification rate for all lineages within Livistoninae, with a model having two diversification rates. The shift in diversification is evaluated on all possible nodes of the tree. If shifts in rate of diversification in Livistoninae contributed to shape the bimodal pattern, we could expect to detect shifts in the vicinity of a reconstructed migration event across Wallace's Line. To ensure that the value of the relative extinction rate *($a = \mu / \lambda$,* where μ is the extinction rate and λ the speciation rate*)* did not affect our results, we repeated the estimation of the shifts for values of *a* ranging from 0 to 0.99. To test the alternative hypothesis that the shifts were not caused by an increase in diversification rate, but alternatively that a decrease in diversification occurred in some other part of the tree, we repeated the two-rate analyses by constraining the highest diversification rate to

include the root of the phylogeny. To determine whether the results of our analyses were sensitive to the placement of missing taxa, we decreased the resolution of the tree by collapsing terminal tips older than 4.17 Ma, 6.25 Ma, and 8.33 Ma, which correspond to 50%, 75%, and the total age of the node where a significant shift in diversification was detected. Finally, to validate the adequacy of the birth-death model, we simulated 2,000 phylogenetic trees using the maximum likelihood parameter estimates from the diversification analysis for the elevated diversification rates. We then used the distribution of species richness obtained to estimate the probability of the observed species richness for all the clades that originated within the credible interval of the age for the stem node of the New Guinean *Licuala*. The source code for these analyses is available in the R package phylothuria (Michonneau 2011).

Results

GENE TREE INCONGRUENCE AND SYSTEMATICS OF LIVISTONINAE

Parsimony and maximum likelihood analyses similarly resolved relationships across loci although incongruence was detected in inter-generic relationships in three of the seven gene trees (Fig. 2). The CISP4, *matK*, and RPB2 gene trees show differences in the position of *Pholidocarpus* and *Livistona* (Fig. 2). In the CISP4 gene tree *Pholidocarpus* is resolved as sister to *Lanonia* and *Pholidocarpus* + *Lanonia* are nested within a polytomy also encompassing *Johannesteijsmannia*, *Saribus*, and *Licuala*. In the *matK* gene tree, *Pholidocarpus* is resolved outside of the subtribe and in contrast to both the CISP4 and *matK* gene trees, the RPB2 gene tree resolved *Pholidocarpus* in a clade with *Licuala* and *Saribus*. Both the *matK* and RPB2 gene trees resolve *Livistona* within

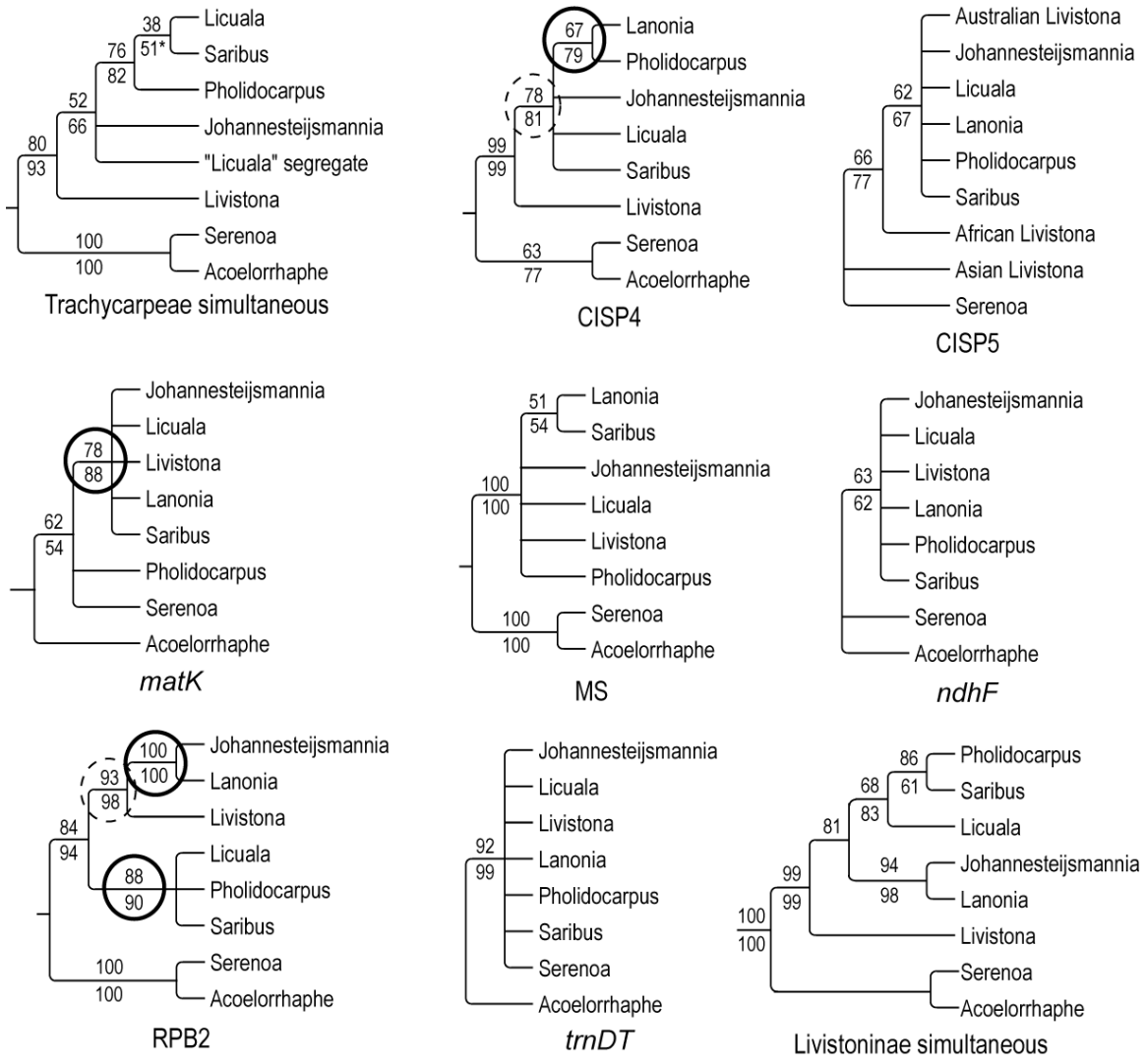


Fig. 2. Simplified inter-generic relationships inferred from previous studies of the tribe Trachycarpeae (Bacon et al., in review), compared to each of the gene tree partitions generated in this study. Bold, solid circles indicate incongruence of *Pholidocarpus* resolution and dashed circles show variation in the position of *Livistona*. *Acoelorrhaphe* was not sampled for CISP5.

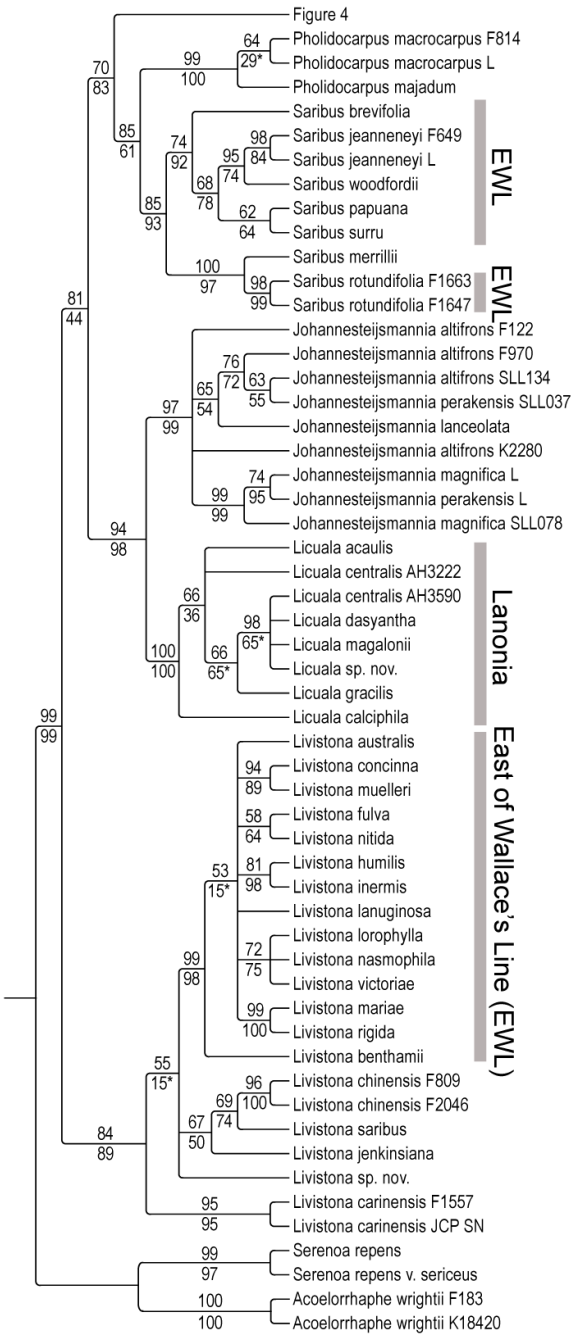


Fig. 3. Basal portion of the simultaneous-analysis maximum parsimony JK tree with parsimony JK values ≥ 50% above and likelihood BS values below each branch. Clades in the parsimony JK tree that were contradicted by clades in the likelihood BS tree are indicated with asterisks, with BS support for the highest contradictory likelihood clade listed.

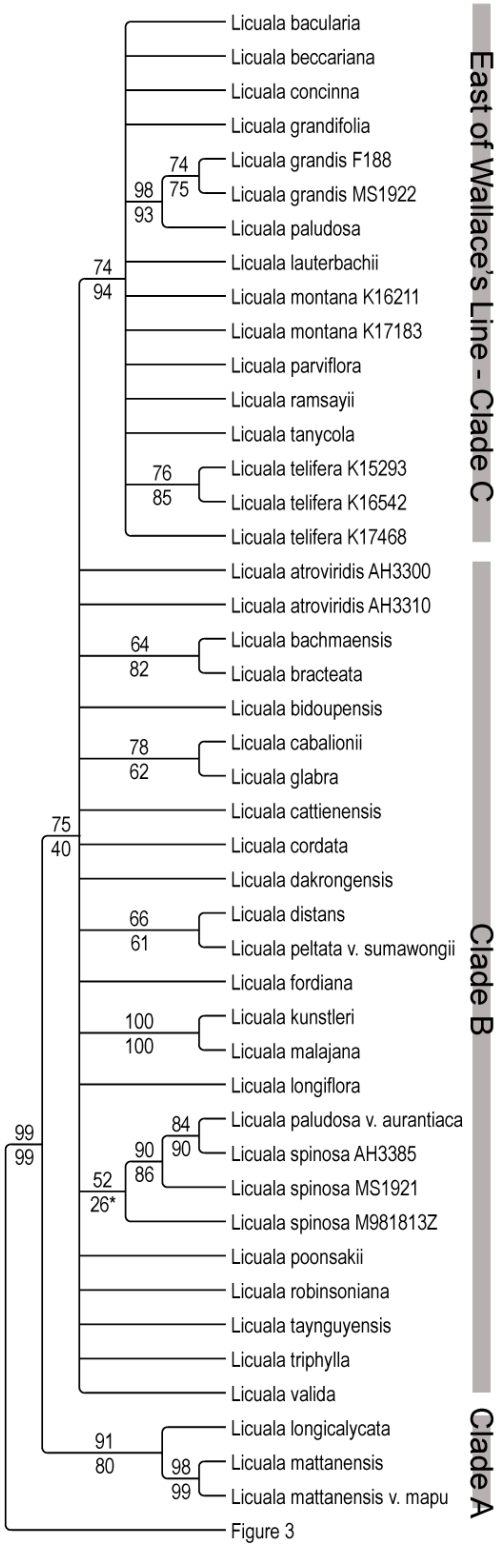


Fig. 4. Distal portion of the maximum parsimony simultaneous-analysis with support values and incongruence indicated as in Fig. 3.

the Livistoninae, whereas the CISP4 gene tree resolves the genus as the early divergent group with high support. In the simultaneous analysis, *Lanonia* is resolved as sister to *Johannesteijsmannia*, which together are sister to *Saribus*, *Licuala*, and *Pholidocarpus* (Figs. 3 and 4). Furthermore, the partitioned Bayesian analysis (BEAST, see below) with unlinked substitution models, resolved the same topology with similar branch-support values as the likelihood and parsimony simultaneous analyses (*Lanonia* and *Johannesteijsmannia* are sister with 1.0 PP). In agreement with previous studies (Asmussen and Chase 2001; Asmussen et al. 2006; Bacon et al. in review*; Baker et al. 2009), Livistoninae was highly supported as monophyletic (Figs. 2-4). Our results support the recognition of a previously resolved segregate *Licuala* group (Bacon et al. in review*), as a new genus of palms, *Lanonia* (Henderson and Bacon in review*). Each of the Livistoninae genera was resolved as monophyletic and highly supported, which created a strong framework with which to address the disparities of species diversity in southeast Asia (Figs. 3 and 4).

DIVERGENCE TIMES IN LIVISTONINAE

Two metrics were used to evaluate the appropriateness of assuming a model of uncorrelated rates of molecular evolution when estimating divergence times. First, the covariance statistic was examined in Tracer v1.5, which provides an approximation of autocorrelation. The distribution for these analyses centers on zero (P = -0.0414, 95% HPD of -0.1713 to $8.4707E^{-2}$], indicating that there is no support for molecular rates to be inherited from parent to child nodes throughout the phylogeny. Second, the coefficient of

variation was also examined in Tracer, which measures the proportion of the variation in rates surrounding the mean. The distribution of possible coefficients of variation is centered far from zero (0.5495 with 95% HPD of 0.4 to 0.7068), suggesting that rates vary more than 55% away from the mean and is indicative of the extreme rate heterogeneity that was specifically accounted for in the model. Our results indicate that the crown group of Livistoninae originated at ca. 24 Ma (Fig. 5; Table 2; 95% HPD of 16.1 to 28.5 Ma, PP=1.0). The three genera with bimodal distributions across Wallace's Line had monophyletic crown groups that originated between ca.12 to 15.5 Ma and are the three oldest crown ages in the phylogeny (Table 2). Despite this, the highest species diversity is in *Licuala*, which did not have the oldest inferred age of the bimodal clades (Table 2).

Table 2. Mean and credible interval (upper and lower) of divergence times for each clade in the Livistoninae with ages in millions of years (Ma). Distributions east of Wallace's Line are abbreviated EWL.

	Stem			**Crown**		
Clade	Mean	Lower	Upper	Mean	Lower	Upper
Acoelorrhaphe	10.49	5.12	16.46	2.28	1.94	9.59
Johannesteijsmannia	16.65	10.89	22.52	4.82	2.46	7.45
Lanonia	16.65	10.89	22.52	8.93	4.90	13.48
Licuala	20.39	14.10	26.38	13.65	9.10	18.58
EWL *Licuala*	6.02	3.75	8.63	5.08	3.14	7.29
Livistona	22.40	16.13	28.48	15.40	9.49	21.90
EWL *Livistona*	12.02	7.59	17.37	5.56	3.20	8.28
Livistoninae	25.14	19.64	30.39	22.40	16.13	28.48
Pholidocarpus	17.74	11.96	23.82	1.82	0.43	3.54
Saribus	17.74	11.96	23.82	11.99	7.22	16.64
EWL *Saribus*	11.99	7.22	16.64	8.00	4.58	11.84
Serenoa	10.49	5.12	16.46	5.42	0.56	4.44

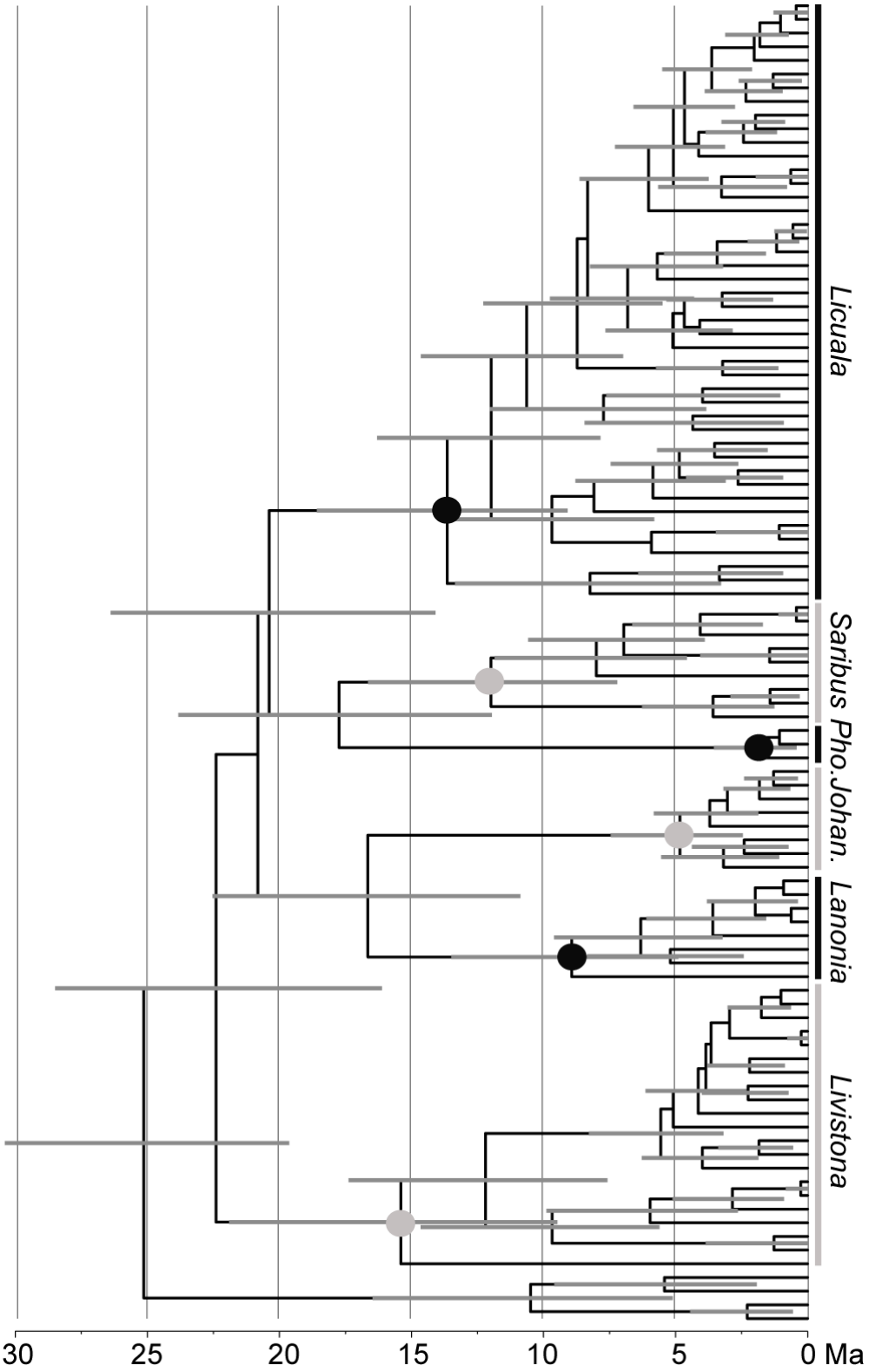


Fig. 5. The maximum clade credibility tree from the Bayesian divergence time analysis. Each of the crown nodes for the genera and the credible sets for each node are shown.

BIOGEOGRAPHICAL RECONSTRUCTIONS

Estimation of historical ranges and biogeographical events (e.g., dispersal, vicariance) allowed for the localization of ancestral lineages in geographical space. Coding of the distributions required scoring the following five species as polymorphic: one (*Saribus rotundifolius*) that is found from Borneo to New Guinea (areas D and E) and four others (*Licuala paludosa*, *L. spinosa*, *Livistona saribus*, and *L. jenkinsiana*) that are found in both eastern Asia and Peninsular Thailand and the Philippines to Borneo and Java (areas C and D). The nodes with likelihood scores that were not significantly different between reconstructions (within -2 lnL; Ree and Smith 2008b) are shown in Table 3. The "widespread ancestor problem" (Ree et al. 2005) was not detected in the Livistoninae biogeographic reconstructions and only five (non-terminal) nodes were reconstructed as ranging across more than one area (Fig. 6). As one might intuitively expect, all five of the widespread nodes spanned across eastern Asia and the Sunda region (areas C and D), which have no extant barriers to gene flow and came into contact well before the Cretaceous (Hall 2009).

The backbone of the tree is inferred to have ancestral distributions in eastern Asia (area C), see nodes 1, 2, and 3 of Livistoninae (Fig. 6). All other Livistoninae genera are inferred to have a Sunda origin (area D). From the consensus scenario of range inheritance in Livistoninae, biogeographical reconstructions resulted in 13 instances of dispersal, ten local extinctions, and one vicariance event. Three instances of dispersal were reconstructed from the Sunda region across Wallace's Line, into the Sahul region in *Licuala*, *Livistona*, and *Saribus*. No biogeographic events were inferred to have occurred in the crown lineages of *Pholidocarpus* and *Johannesteisjmannia*, whereas *Lanonia* had

Table 3. Alternative historical distributions for crown nodes that had more than one likely reconstruction (within 2 log likelihood units of the maximum). The nodes correspond to Fig. 6 and the global likelihoods and relative probabilities are given. The first area is the range inherited by the upper descendant branch, the second is inherited by the lower, and where there is only one area listed both descendant branches inherit the same range. Livistoninae geographic distributions are: A) southeastern North America; B) Africa and Arabia; C) eastern Asia: India to Thailand (excluding the peninsular region), China (including Hainan), and Japan; D) Sunda: west of Wallace's Line, peninsular Thailand and the Philippines to Borneo and Java, and E) Sahul: east of Wallace's Line, New Guinea and Australia to Vanuatu.

Node	Area(s) inferred	-lnL	Rel. Prob.	Node	Area(s) inferred	-lnL	Rel. Prob.
1	C-A	112	0.6	8	E-D	111.9	0.6
	D-A	112.6	0.3		D	112.6	0.3
2	C	112.5	0.4	9	E	111.9	0.6
	D-C	113	0.2		DE-E	112.5	0.4
	CD-C	113	0.2	10	E	111.9	0.3
	D-E	114.1	0.07		DE-E	112.5	0.4
	D	114.2	0.07	11	E	111.9	0.3
3	D-CD	112.4	0.4		E-DE	112.5	0.4
	D	112.5	0.4	12	D	111.7	0.8
	CD-D	113.3	0.2		D-CD	113.3	0.2
4	D	111.7	0.8	13	E-DE	111.7	0.8
	CD-D	113.1	0.2		E-D	113.2	0.2
5	CD-D	112.1	0.5	14	CD-C	111.6	0.9
	D	112.3	0.4		C	113.5	0.1
6	CD-C	111.6	0.8	15	D	112.2	0.5
	C	113.5	0.1		D-CD	112.4	0.4
7	D-CD	111.6	0.8	16	D-C	113.3	0.1
	D	113.6	0.1		C	112.1	0.5

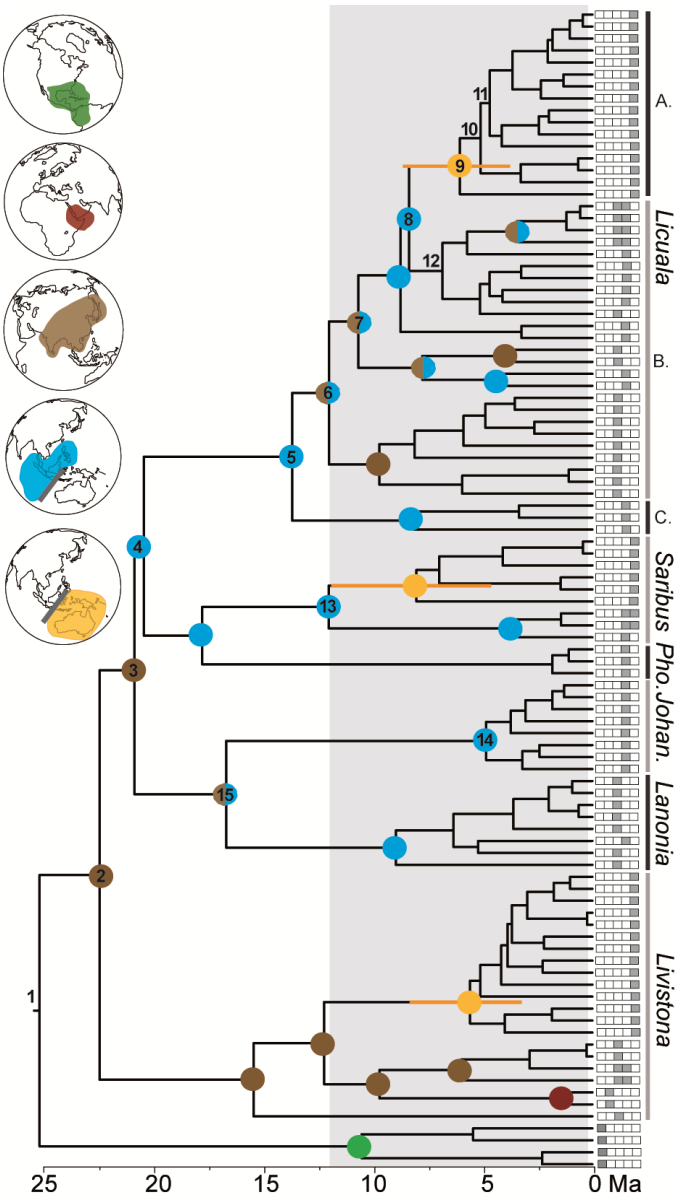


Fig. 6. Biogeographical reconstruction of Livistoninae produced from the dated phylogeny and ancestral range analysis. The consensus topology is shown and uncertainty in reconstructions is described in Table 3. The five biogeographic regions under consideration are color-coded on the tree and mapped to their geographic position. The grey line in the two lower maps represents Wallace's Line. Yellow credible sets from divergence time estimation are shown for the three instances of successful dispersal across Wallace's Line and occur between 1-12 Ma, which is highlighted in gray.

two, *Saribus* three, *Livistona* six, and *Licuala* had eight events inferred. The number of events per genus that display bimodal patterns supports the hypothesis that the history of migration may factor into species richness patterns.

NET DIVERSIFICATION IN LIVISTONINAE

Our data have strong signal supporting a net diversification rate increase at the stem node of the New Guinean *Licuala* clade, which corresponds to the dispersal event reconstructed across Wallace's Line (node 9, Fig. 6; ΔAIC = 47.4 for $a = 0$. Fig. 7; Table 4). The location of the shift was not altered when we varied the values of the relative extinction rate (a) from 0 to 0.99. The approximate maximum likelihood estimate of the relative extinction rate is at 0.46 (95% confidence interval: 0 to 0.77, Fig. 7B). The analyses testing rate decreases in alternative portions of the tree consistently resulted in much lower likelihoods, indicating that an increase in diversification was the more likely scenario (ΔAIC = 39.9 for $a = 0$, Table 4). Furthermore, when we decreased the resolution of the tree by collapsing terminal tips to various degrees, the analyses consistently recovered a shift that occurred at the stem node of the New Guinean *Licuala*. The results of the simulations show that it is unlikely that the other clades that originated in the credible interval of the stem node of the New Guinean *Licuala* could be the result of the same regime of diversification.

Table 4. Results of the maximum-likelihood estimation of net diversification rates in Livistoninae for 1-rate model (constant diversification throughout the phylogeny) and the 2-rate model (estimation of diversification rates in all possible bipartitions of the tree; results are given for the bipartition with the highest log-likelihood score). *a* is the relative extinction rate, *r* is the background diversification rate, r_L is the rate of diversification for the bipartition including the stem node of the New Guinean *Licuala* clade.

	***a* = 0**			***a* = 0.99**		
Models	Log-likelihood	AIC	Parameters	Log-likelihood	AIC	Parameters
1-rate model	-295.6	593.2	$r = 0.274$	-296.4	594.7	$r = 0.007$
2-rate model	-269.9	545.8	$r = 0.178$, $r_L = 0.554$	-278.3	562.5	$r = 0.003$, $r_L = 0.021$
2-rate-decrease model	-289.8	585.6	$r_L = 0.283$, $r = 0.001$	-293.5	593.1	$r = 0.001$, $r_L = 0.007$

Discussion

The potential explanations for broad-scale patterns in species richness may apply generally to disparities across small spatial scales. But explicit hypothesis testing to understand sharp differences in species diversity at a local-scale may lead to innovative insights that can be applied to global patterns. In this study we focused on southeast Asia and specifically the bimodal pattern in species richness between the Sunda and Sahul regions versus Wallacea. Based on the evidence from *Licuala*, *Livistona*, and *Saribus*, the bimodal distributions result from a few migration events across Wallace's Line followed by *in situ* diversification within the Sahul region. Furthermore, the bimodal pattern is accentuated by the rapid diversification of *Licuala* in New Guinea and in Sunda. Although there are limitations to the method used (e.g., minimum age constraints,

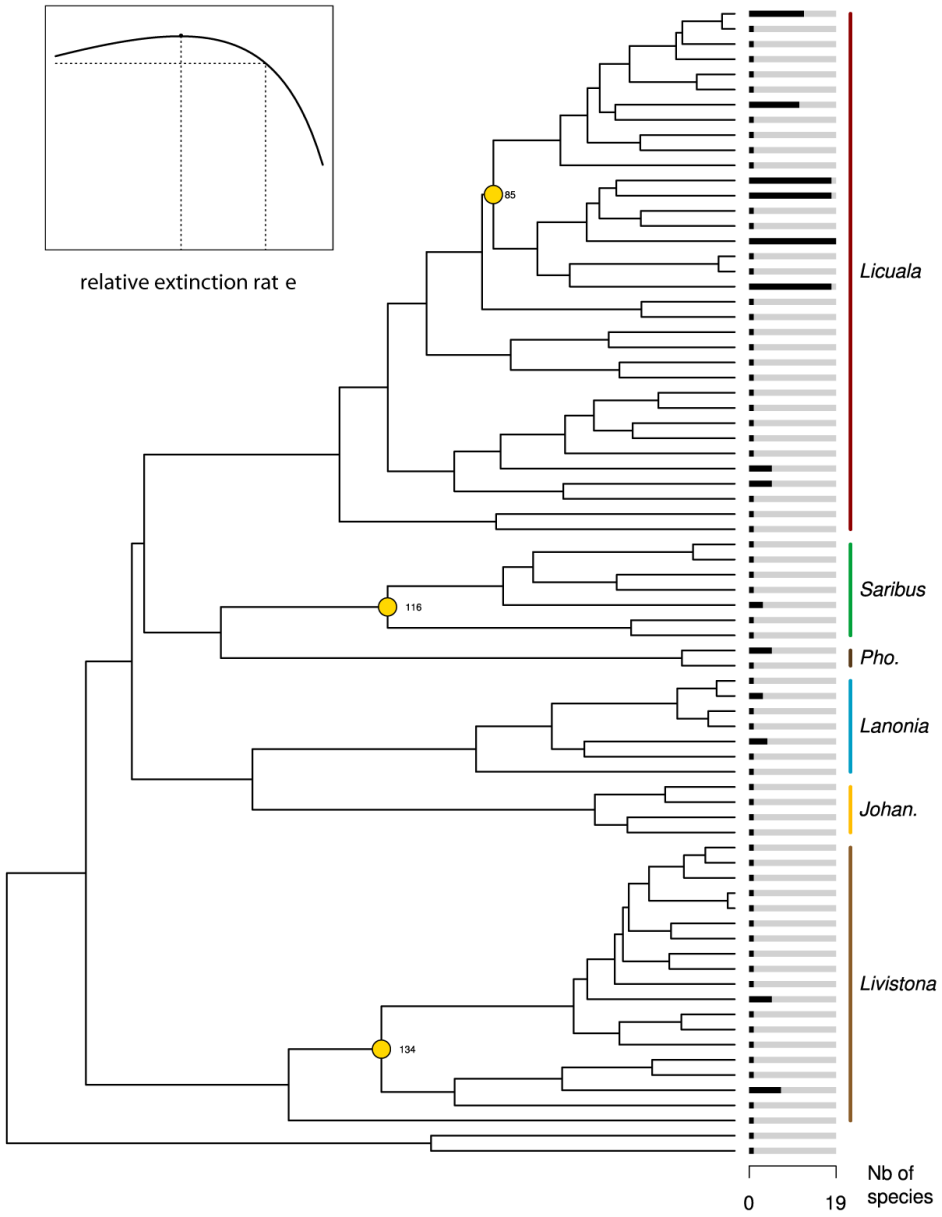


Fig. 7. Analysis of diversification rates in Livistoninae. (A) Dated phylogeny (from Fig. 5) showing the number of unsampled species assigned to the tips of the tree. Yellow dots on the nodes, represent dispersal events across Wallace's line reconstructed by Lagrange (Fig. 6). (B) Approximate likelihood profile for the relative extinction rate with 95% confidence interval for the 2-rate diversification model. Regardless of the value of the relative extinction rate, the shift in diversification rate was always associated with node 85 with the maximum-likelihood value.

error in fossil age determinations, difficulties with diversification rate inference), our estimates, in concert, detect mechanisms of species diversification that correspond to the geological and climatic history of the region.

TAXONOMIC HYPOTHESES

The monophyly of Livistoninae has been previously recognized, although intergeneric relationships within Livistoninae were poorly understood due to weak branch support (Asmussen and Chase 2001; Asmussen et al. 2006; Baker et al. 2009; Bacon et al. in review*). Our data indicate that *Livistona* is the earliest divergent genus in the tribe (Fig. 3) corroborating our previous results (Bacon et al. in review*). The CISP 5 gene tree resolved a non-monophyletic *Livistona*, with *L. carinensis* separated from the rest of the genus by at least one branch. In this study, the other six gene trees, each genome partition, the combined analysis, and the partitioned Bayesian analysis resolved a monophyletic *Livistona*, including *L. carinensis* (Fig. 3). Non-monophyly of *Livistona* had been reported before (Crisp et al. 2010) and *L. carinensis* has been previously recognized as the separate genus *Wissmannia* until 1983 (Dransfield and Uhl 1983). The distribution of *Livistona* is considered relictual due to past climate changes and shifts in boreotropical forest distribution (Dransfield 1987; Bacon et al., in review*).

Sister to the rest of the Livistoninae, we resolved a sister relationship between *Johannesteijsmannia* and a new genus, *Lanonia* (Fig. 3; Henderson and Bacon in review*). Inter-specific relationships of *Johannesteijsmannia* were poorly resolved in our analysis, with two non-exclusive species, potentially reflecting misidentifications in the field or with botanical-garden material. The clade of *Saribus* + *Pholidocarpus* was

resolved as sister to *Licuala* (Figs. 3 and 4). *Saribus* has recently been resurrected as a genus based on molecular and morphological data (Bacon et al. in review*) and is further supported in this study with the addition of three other species (Fig. 3). *Licuala* is highly supported as monophyletic, although interspecific relationships are poorly resolved (Fig. 4). The following three major groups within *Licuala* were reconstructed: *L. longicalycata* + *L. mattanensis*, an Indochina grade, and an east-of-Wallace's-Line clade (clades A, B, and C; Fig. 4).

TEMPORAL AND SPATIAL PATTERNS OF DIVERSIFICATION

Although secondary calibration can be a potential source of error due to estimation errors (e.g., Graur and Martin 2004), our estimate was derived from a broader study based on robust fossil data and the uncertainty therein was incorporated in the credible interval at the stem node of Livistoninae (Bacon et al. in review*). Our results show that the dates estimated for Livistoninae correlate to the fossil history of the group, for example, the Australian Oligocene (26.5–28 Ma) trunk fossil *Palmoxylon queenslandicum* is suggested to resemble *Livistona* and *Licuala* (Conran and Rozefelds 2003). The divergence times estimated for Livistoninae diversification overlap with the estimated age of the *Palmoxylon* fossil substrate formation and our results on the position of *Livistona* as the earliest divergent genus also substantiates our divergence-time results.

The mean age estimated for the crown node of the tribe was approximately 25 Ma (95% HPD: 19.64 – 30.39 Ma) and was reconstructed in eastern Asia (area C; Figs. 5 and 6). The origin of the tribe corresponds to the most important period of plate-boundary reorganization within southeast Asia (20-30 Ma; Hall 1998). Our biogeographical

reconstruction analysis suggests that the ancestors of modern Livistoninae did not disperse into islands of the Sunda region for five million years (~16-21 Ma; Miocene; node 6 in Fig. 6). Dispersal from eastern Asia to insular areas in southeast Asia coincides with the timing of major tectonic activity and the collision between the Sunda and Sahul plates that caused continental fragments to be split off and rearranged throughout the region (Hall 2002). After the Early Miocene rejuxtaposition of land and changes in sea levels facilitated the dispersal of the terrestrial flora from Sunda (area D; Fig. 6) into Sahul regions (area E; Fig. 5). During this time period the former oceanic barrier between the two shelves in Wallacea had been reduced and included several small islands that could serve as stepping-stones for dispersal across Wallace's Line (Hall 2009).

NET DIVERSIFICATION IN LIVISTONINAE

To test our hypothesis that increased diversification rates in species that dispersed across Wallace's Line contributed to shaping the bimodal distribution pattern in Livistoninae, a rate increase would need to be detected in the vicinity of at least one of the three instances of dispersal to the Sahul region (Fig. 6). Based on our diversification rate analysis, a significant increase in net diversification rate was detected at the stem node of the New Guinean *Licuala* and the crown node led to the colonization of the island (Fig. 7). This increase in diversification rate therefore accentuated the bimodal pattern by elevating the number of species found on either side of Wallacea. In addition, our results show no evidence for dispersal between major geographic areas in *Lanonia*, *Johannesteijsmannia*, and *Pholidocarpus*, while *Licuala*, *Livistona*, and *Saribus*

experienced range expansions into the Sahul regions of New Guinea and Australia to Vanuatu (area E; Fig. 6).

The Livistoninae lineages that crossed Wallace's Line all share similar dispersal-related morphological characteristics: fruits that are small in size (less than 1.5 cm; Henderson 2009), are brightly colored (red in *Licuala*, blue to purple in *Livistona*, orange to red in *Saribus*) and are inferred to be bird-dispersed and have high dispersal capability (Dowe 2009). In contrast, those Livistoninae lineages that remained in eastern Asia or in the Sunda region have low dispersal ability (e.g., *Johannesteijsmannia, Pholidocarpus*) with large, green to brown fruits that are likely mammal-dispersed (3.5-12; cm Zona & Henderson 1989).

The possible causes of shifts in rate diversification are debated as both intrinsic (i.e., morphological innovations) and extrinsic correlates (i.e., biotic and abiotic factors) have been hypothesized to play a role (e.g., Forest et al. 2007; Moore and Donoghue 2007; Rabosky 2009). In particular, the recent recognition that diversity does not grow unbounded, but is limited by ecological interactions is reshaping the interpretation and nature of diversification analyses (Raboksy 2009; Rabosky and Glor 2010). However, in Livistoninae, as in other studies of diversification in southeast Asia (e.g, shrews, Esselstyn et al. 2009), it appears that the ecological limit has not been reached as the number of lineages increases exponentially. The highly dynamic nature of terrestrial habitats in southeast Asia over the last 10 Ma, and in particular the uplift of mountains at present day heights in the last 5 Ma has most likely generated multiple opportunities for speciation (Hall 2009). However, understanding why New Guinea *Licuala* exhibit

elevated diversification would require a detailed analysis including fine-scale distributional data.

WALLACE'S LINE AND BIMODAL PALM DISTRIBUTIONS

Dransfield (1981) first observed the unusual patterns of species distributions in southeast Asian Livistoninae and hypothesized that the bimodal pattern of species diversity was due to a combination of post-Miocene migration from the west and possibly the east (but see Dransfield 1987), and Pleistocene climatic changes that increased extinction rates in Wallacea. Furthermore, he rejected the Gondwanan origin of the Livistoninae genera found in the Sahul region given the paucity of widespread genera in South America. Three instances of dispersal were reconstructed from the Sunda region across Wallace's Line into the Sahul region in *Licuala, Livistona, and Saribus* (area E; Fig. 6) indicating that *Licuala, Livistona, and Saribus* ancestors most likely colonized the Malesian region of southeast Asia from the west (Fig. 6) and refutes the idea that the group colonized the region on two fronts. No dispersals out of the Sahul region were inferred in Livistoninae, which may reflect the inability for long-distance dispersal further east to the smaller island chains such as Fiji, French Polynesia, and Hawaii.

Recent stable isotope data have shown that islands in Wallacea experienced a severe dry period in the Pleistocene that caused major forest contractions (~125 Ka; Bird et al. 2005, Wurster et al. 2010). These dry conditions might have been unfavorable for palm lineages in Wallacea (Bjorholm et al. 2006), leading to their extinction and therefore exacerbating the bimodal biogeographic pattern in the Livistoninae. Despite this, the tests of diversification rate decrease did not detect any significant declines that

could be attributed to extinctions due to climatic affects. Other ecological factors may also contribute to the low species richness observed in Wallacea, such as species-area relationships and/or competition from ecologically similar species. Species-area relationships in geologically complex systems such as Wallacea are difficult to parse, but low species richness in the region could also simply be due to island area (e.g., MacArthur and Wilson 1967) and the fragmented nature of the island habitats (e.g., the Celebes). Southeast Asia, specifically Malesia, harbors the highest percent of global palm diversity with 50 genera and 992 species in comparison to 65 and 16 genera and 730 and 65 species in South America and Africa, respectively (Baker and Couvreur, in press*). From this striking diversity (Baker et al. 2009), Livistoninae lineages may have encountered ecologically similar species (e.g., *Areca*, *Calyptroclayx*, *Iguanura*, *Nenga*, *Pinanga*, *Sommieria*) that impeded establishment due to resource limitation or led to competitive exclusion.

Conclusions

On a general scale, our divergence time and historical biogeography results show a close correlation with geological events and climatic oscillations that have shaped current distributions. The fossil history and estimated divergence times for early divergent Livistoninae show the influence of tectonic activity at the Sunda and Sahul plate boundary, the dispersal of *Licuala* to New Guinea corresponds to the timing of island formation and mountain uplift, and forest contraction due to climate changes caused palm extinctions in the Early Pleistocene. Plant lineages such as palms, legumes, and Annonaceae have been suggested to be excellent systems to understand the evolution

of tropical forests because their physiological requirements largely restrict them to these biomes (Morley 2000) and have been fossilized in the earliest records of rainforests (e.g. Wing et al. 2009). Recent studies in *Pseudovaria* closely mirror the biogeographic movements (Annonaceae; Su and Saunders 2010) of Livistoninae and are likely concordant with the evolutionary change of southeast Asian rainforests as a whole. Although Wallace's Line may be more strongly correlated with extant mammal diversity, we have shown here that it and net diversification rates played an important role in shaping bimodal palm distributions. We suggest that the dynamic history of southeast Asia has generated innumerous opportunities for allopatric speciation and that comparisons with other southeast Asian lineages should provide general understanding of these spectacular biogeographical patterns. Furthermore, to understand broader scale species diversity disparities, groups like palms may be an important element to reveal general patterns.

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Appendix 1.

List of taxa sampled with taxonomic authorities, voucher or DNA source information and GenBank accession numbers for new sequences generated for this study.

Acoelorrhaphe wrightii H. Wendl.— Fairchild Tropical Garden Live Collection P.2313 (DNA Bank 183); MS HQ720963. ***Acoelorrhaphe wrightii*** H. Wendl.—Kew DNA Bank 18420; MS HQ720962. ***Johannesteijsmannia altifrons*** (Rchb.f. & Zoll.) H.E. Moore— Fairchild Tropical Garden DNA Bank 970; CISP4 HQ721027. ***Johannesteijsmannia altifrons*** (Rchb.f. & Zoll.) H.E. Moore— Fairchild Tropical Garden Live Collection 86547E (DNA Bank 122); MS HQ720964. ***Johannesteijsmannia altifrons*** (Rchb.f. & Zoll.) H.E. Moore—Lyon Arboretum Live Collection; CISP5 HQ721050. ***Johannesteijsmannia altifrons*** (Rchb.f. & Zoll.) H.E. Moore—*S.L. Look 134* (K); MS HQ720965. ***Johannesteijsmannia lanceolata*** J. Dransf.—*S.L. Look 061* (K); MS HQ720966. ***Johannesteijsmannia magnifica*** J. Dransf.—Lyon Live Collection 90.0308; CISP4, MS HQ720967. ***Johannesteijsmannia magnifica*** J. Dransf.—*S.L. Look 078* (K); MS HQ720968. ***Johannesteijsmannia perakensis*** J. Dransf.—Lyon Live Collection 2006.0062; CISP4 HQ721029, CISP5 HQ721051, MS HQ720969. ***Johannesteijsmannia perakensis*** J. Dransf.—*S.L. Look 037* (K); MS HQ720970. ***Lanonia acaulis*** A.J. Henderson ined.—*A.J. Henderson 3309* (NY); CISP4 HQ721030, CISP5 HQ721052, *matK* HQ720156, *ndhF* HQ721078. ***Lanonia calciphila*** A.J. Henderson ined.—*A.J. Henderson 3328* (NY); *matK* HQ720163, MS HQ720976, RPB2 HQ720202, *trnDT* HQ720219. ***Lanonia centralis*** A.J. Henderson ined.—*A.J. Henderson 3222* (NY); *matK* HQ720165, MS HQ720978, *trnDT* HQ720220. ***Lanonia centralis*** A.J. Henderson ined.—*A.J. Henderson 3590* (NY); CISP4 HQ721035, CISP5 HQ721059, *matK* HQ720166, MS HQ720979, *ndhF* HQ721080, RPB2

HQ720203, *trnDT* HQ720221. ***Lanonia dasyantha*** A.J. Henderson ined.—*A.J. Henderson 3363* (NY); CISP4 HQ721037, *matK* HQ720170. ***Lanonia gracilis*** A.J. Henderson ined.—*W.J. Baker 1353* (K); CISP4 HQ721039, *matK* HQ720173, MS HQ720986, *ndhF* HQ721085, *trnDT* HQ720226. ***Lanonia magolonii*** A.J. Henderson ined.—*A.J. Henderson 3268*, Vietnam (NY); CISP4 HQ721040, CISP5 HQ721065, *matK* HQ720177. ***Lanoina sp.*** A.J. Henderson ined.— *A.J. Henderson 3643* (NY); *matK* HQ720186, *ndhF* HQ721094, *trnDT* HQ720234. ***Licuala atroviridis*** A.J. Henderson, N.K. Ban, & N.Q. Dung—*A.J. Henderson 3300* (NY); CISP4 HQ721031, CISP5 HQ721053, *matK* HQ720157, MS HQ720971, RPB2 HQ720196, *trnDT* HQ720217. ***Licuala atroviridis*** A.J. Henderson, N.K. Ban, & N.Q. Dung—*A.J. Henderson 3310* (NY); *matK* HQ720158, RPB2 HQ720197. ***Licuala bachmaensis*** A.J. Henderson, N.K. Ban, & N.Q. Dung—*A.J. Henderson 3254* (NY); CISP4 HQ721032, CISP5 HQ721054, *matK* HQ720159, MS HQ720972, RPB2 HQ720198. ***Licuala bidoupensis*** A.J. Henderson, N.K. Ban, & N.Q. Dung—*A.J. Henderson 3419* (NY); CISP4 HQ721033, CISP5 HQ721055, *matK* HQ720160, MS HQ720973, RPB2 HQ720199. ***Licuala bracteata*** Gagnep.—*A.J. Henderson 3456* (NY); CISP5 HQ721056, *matK* HQ720161, MS HQ720974, RPB2 HQ720200. ***Licuala cabalionii*** Dowe—Lyon Arboretum Live Collection; CISP4 HQ721034, CISP5 HQ721057, *matK* HQ720162, MS HQ720975, *ndhF* HQ721079, RPB2 HQ720201, *trnDT* HQ720218. ***Licuala cattienensis*** A.J. Henderson, N.K. Ban, & N.Q. Dung—*A.J. Henderson 3407* (NY); CISP5 HQ721058, *matK* HQ720164, MS HQ720977. ***Licuala concinna*** Burret— Montgomery Botanical Center Live Collection 2000524.V; *matK* HQ720167, MS HQ720980. ***Licuala cordata*** A.J. Henderson, N.K. Ban, & N.Q. Dung—Lyon Arboretum Live Collection; CISP4 HQ721036, CISP5 HQ721060, *matK* HQ720168, MS HQ720981, *ndhF* HQ721081, *trnDT* HQ720222. ***Licuala dakrongensis*** A.J. Henderson ined.— *A.J. Henderson 3498* (NY); CISP5 HQ721061, *matK* HQ720169, MS HQ720982, *ndhF* HQ721082, RPB2 HQ720204, *trnDT* HQ720223.

Licuala distans Ridl.— Montgomery Botanical Center Live Collection 99669.BB; MS HQ720983. ***Licuala fordiana*** Becc.—Floribunda Live Collection; CISP4 HQ721038, CISP5 HQ721062, *matK* HQ720171, MS HQ720984, *ndhF* HQ721083, RPB2 HQ720205, *trnDT* HQ720224. ***Licuala glabra*** Griff.—Lyon Arboretum Live Collection; CISP5 HQ721063, *matK* HQ720172, MS HQ720985, *ndhF* HQ721084, RPB2 HQ720206, *trnDT* HQ720225. ***Licuala grandis*** H. Wendl.— *M.P. Simmons 1922* (MO); *matK* HQ720174, MS HQ720987. ***Licuala lauterbachii*** Dammer & K. Schum.—*C.D. Heatubun 187* (K); *matK* HQ720175. ***Licuala longicalycata*** Furtado—*Ayau FRI 34631* (K); CISP5 HQ721064, RPB2 HQ720207. ***Licuala longiflora*** A.J. Henderson, N.K. Ban, & N.Q. Dung—*A.J. Henderson 3641* (NY); *matK* HQ720176, MS HQ720988, *ndhF* HQ721086, *trnDT* HQ720227. ***Licuala malajana*** Becc.—Lyon Arboretum Live Collection; CISP4 HQ721041, CISP5 HQ721066, *matK* HQ720178, MS HQ720989, *ndhF* HQ721087, RPB2 HQ720208, *trnDT* HQ720228. ***Licuala mattanensis*** Becc.—Lyon Arboretum Live Collection; CISP4 HQ721043, CISP5 HQ721067, *matK* HQ720180, MS HQ720990, *ndhF* HQ721088, *trnDT* HQ720229. ***Licuala mattanensis*** Becc.—Floribunda Live Collection; CISP4 HQ721042, CISP5 HQ721068, *matK* HQ720179, MS HQ720991, *ndhF* HQ721089, RPB2 HQ720209, *trnDT* HQ720230. ***Licuala montana*** Dammer & K. Schum.—*W.J. Baker 576* (K); CISP5 HQ721069. ***Licuala paludosa*** Griff.—Floribunda Live Collection; CISP4 HQ721044, CISP5 HQ721070, *matK* HQ720181, MS HQ720993, *ndhF*, *trnDT* HQ720231. ***Licuala paludosa*** Griff.—Montgomery Botanical Center Live Collection; *matK* HQ720182, MS HQ720992. ***Licuala parviflora*** Dammer ex Becc.—Floribunda Live Collection; CISP4 HQ721045, CISP5 HQ721071, *matK* HQ720183, MS HQ720994, *ndhF* HQ721091, RPB2 HQ720210, *trnDT* HQ720232. ***Licuala peltata*** v. sumawongii Saw— Fairchild Tropical Garden Live Collection 70320G (DNA Bank 207); MS HQ720995. ***Licuala poonsakii*** Hodel—Floribunda Live Collection; CISP5 HQ721072, *matK* HQ720184, MS HQ720996, *ndhF* HQ721092,

RPB2 HQ720211, *trnDT* HQ720233. ***Licuala ramsayi*** (F. Muell.) Domin.—*J.W. Horn 4930* (PTBG); MS HQ720997, *ndhF* HQ721093. ***Licuala robinsoniana*** Becc.—*A.J. Henderson 3457* (NY); CISP4 HQ721046, CISP5 HQ721073, *matK* HQ720185, RPB2 HQ720212. ***Licuala spinosa*** Wurmb.—*A. J. Henderson 3385* (NY); MS HQ720998. ***Licuala spinosa*** Wurmb.— Montgomery Botanical Center Live Collection 981813.Z; MS HQ720999. ***Licuala spinosa*** Wurmb.—*M.P. Simmons 1921* (MO); *matK* HQ720187, MS HQ721000. ***Licuala tanycola*** H.E. Moore—*Baker 1139* (K); RPB2 HQ720213. ***Licuala tayguyensus*** Barford & Borchs.— *A.S. Barford et al. 102* (AAU); *matK* HQ720188, MS HQ721001, *ndhF* HQ721095, RPB2 HQ720214, *trnDT* HQ720235. ***Licuala telifera*** Becc.—*Dransfield 7686* (K); RPB2 HQ720215. ***Licuala triphylla*** Griff.—*A.S. Barford 43819* (AAU); *ndhF* HQ721096, *trnDT* HQ720236. ***Licuala valida*** Becc.—Floridbunda Live Collection; CISP4 HQ721047, CISP5 HQ721074, *matK* HQ720189, MS HQ721002, *ndhF* HQ721097, RPB2 HQ720216, *trnDT* HQ720237. ***Livistona australis*** (R. Br.) Mart.—*J.L. Dowe 313* (FTG); MS HQ721003. ***Livistona benthamii*** F.M. Bailey—Montgomery Botanical Center Live Collection 69691.G; CISP4 HQ721048, MS HQ721004. ***Livistona carinensis*** (Chiov.) J. Dranf.—Fairchild Tropical Garden DNA Bank 1557; MS HQ721005. ***Livistona chinensis*** (Jacq.) R. Br. ex Mart.—Fairchild Tropical Garden DNA Bank 2046; MS HQ721006. ***Livistona concinna*** Dowe & Barford—Montgomery Botanical Center Live Collection 9659.H; CISP5 HQ721075, MS HQ721007. ***Livistona fulva*** Rodd—Montgomery Botanical Center Live Collection 96212; MS HQ721008. ***Livistona humilis*** R. Br.—Fairchild Tropical Garden Live Collection 84202F (DNA Bank 33); MS HQ721009. ***Livistona inermis*** R. Br.— Montgomery Botanical Center Live Collection 97973.G; MS HQ721010. ***Livistona jenkinsiana*** Griff.— *A.J. Henderson 3232* (NY); *matK* HQ720190. ***Livistona lanuginosa*** Rodd—Montgomery Botanical Center Live Collection 9670.B; CISP4 HQ721049, MS HQ721011. ***Livistona mariae*** F. Muell.—*J. Doupe 353* (FTG); MS HQ721012.

Livistona muelleri F.M. Bailey—Montgomery Botanical Center Live Collection 9619.P; MS HQ721013. ***Livistona nasmophila*** Dowe & D.L. Jones—Montgomery Botanical Center Live Collection 20011342.A; MS HQ721014. ***Livistona nitida*** Rodd—Fairchild Tropical Garden DNA Bank 1646; MS HQ721015. ***Livistona saribus*** (Lour.) Merr. ex A. Chev.—Fairchild Tropical Garden DNA Bank 1648 ; MS HQ721016. ***Livistona sp.*** A.J. Henderson ined.—*N.Q. Dung 2024* (NY); *matK* HQ720191, MS HQ721017, *ndhF* HQ721098, *trnDT* HQ720238. ***Livistona victoriae*** Rodd—Montgomery Botanical Center Live Collection 96265.H; CISP5 HQ721076, *ndhF* HQ721099. ***Pholidocarpus macrocarpus*** Becc.—Fairchild Tropical Garden Live Collection 2002-0584A; MS HQ721018. ***Pholidocarpus macrocarpus*** Becc.—Lyon Live Collection 2000.0369; MS HQ721019, *ndhF* ***Saribus brevifolius*** (Dowe & Mogea) C.D. Bacon & W.J. Baker—*C. Heatabun S.N.* (K); CISP5 HQ721077, *matK* HQ720192, MS HQ721020, *ndhF* HQ721100, *trnDT* HQ720239. ***Saribus jeanneneyi*** Becc.—Lyon Live Collection 2000.0182; *matK* HQ720193, MS HQ721021. ***Saribus merrillii*** Becc.—*J.W. Horn 4925* (FTG); MS HQ721022. ***Saribus papuanus*** (Becc.)—*W.J. Baker 851* (K); *matK* HQ720194. ***Saribus rotundifolius*** (Lam.) Mart.—Fairchild Tropical Garden DNA Bank 1663; MS HQ721024. ***Saribus rotundifolius*** (Lam.) Mart.—Fairchild Tropical Garden DNA Bank 1647; MS HQ721023. ***Saribus surru*** (Dowe & Barford) C.D. Bacon & W.J. Baker—*J. Dowe S.N.* (K); *matK* HQ720195, MS HQ721025, *ndhF* HQ721101, *trnDT* HQ720240. ***Serenoa repens*** (W. Bartram) Small—Fairchild Tropical Garden Live Collection 71522C (DNA Bank 350); MS HQ721026. ***Serenoa repens*** (W. Bartram) Small—New York Botanical Garden Live Collection 4131/95D; MS HQ721027.

Chapter 4: Evaluating multiple criteria for species delimitation: an empirical example using Hawaiian palms (Arecaceae: *Pritchardia*)

Species are a fundamental unit in biological studies and their robust delimitation is essential to many fields of evolutionary biology, particularly systematics, biogeography, and conservation biology. Lineage separation and divergence form a temporal process that may render populations reciprocally monophyletic, reproductively isolated, ecologically divergent, and/or morphologically distinctive. These properties serve as operational criteria for systematists to delimit species and they can occur at different times or orders during speciation. de Queiroz (1998, 2007) proposed that at the root of all modern species concepts is the general agreement on the fundamental nature of species: species are separately evolving metapopulation lineages. The perspective that species are lineages, and that multiple criteria should be used to identify them, has been termed the general lineage species concept (de Queiroz 1998). Applying this lineage-based framework to species delimitation shifts the focus from a single operational criterion and increases the importance of sampling multiple lines of evidence. Species delimitation is notoriously difficult when alternative criteria delimit incongruent species boundaries, but this is to be expected in recent radiations (e.g., Belfiore et al. 2008; Leaché et al. 2009; Willyard et al. in press). Evaluating multiple criteria not only

increases our ability to detect recently separated lineages, but also can provide stronger support for lineage separation when they are in agreement (de Quieroz 2007; Reeves and Richards 2011).

The difficulty in recognizing species and their limits (the "species problem"; de Querioz 2005) is particularly compounded on islands. Because most islands are considerably younger terrestrial systems than continental areas (Carlquist 1974), there has generally been less time for the completion of speciation processes. Time is an important factor for incomplete lineage sorting because the existence of ancestral polymorphism and differential extinction thereof can cause bias in phylogenetic inference (e.g., Doyle 1992) and the identification of distinct lineages (e.g., Knowles and Carstens 2007). Furthermore, the tendency for island colonizers to quickly fill available habitat often leads to species that are ecologically isolated but not considerably diverged genetically, potentially leading to hybridization if mating barriers are broken down due to secondary contact (e.g., Givnish 2010). The evolutionary processes of incomplete lineage sorting and hybridization cause the "species problem" to be compounded on young volcanic islands. Hawaii is the longest archipelago on earth and has developed linearly in a chronological fashion from a volcanic hotspot (Carson and Clague 1995) over the last 23-29 Ma (Clague et al. 2010). The islands have the highest degree of endemism of any known flora (Sakai et al. 2002) and are part of the Polynesian/Micronesia biodiversity hotspot (Myers et al. 2004). Difficulty in delimiting species is not restricted to angiosperms on the Hawaiian archipelago (e.g., *Hylaeus* bees, Magnacca and Danforth 2007; spoon tarsus *Drosophila*, LaPoint et al. 2011), but studies on Hawaiian

angiosperms have dominated the literature (e.g., Gemmill et al. 2002; Harbaugh and Baldwin 2007; Clark et al. 2009; Harbaugh et al. 2009a, 2009b; Bacon et al. 2011a).

An excellent group within which to address the evaluation of species boundaries based on various delimitation criteria is the Hawaiian *Pritchardia* (Arecaceae: Palmae) radiation. *Pritchardia* is economically important as a widely cultivated ornamental (Maunder et al. 2001), displays high endemism, and is a conservation priority for the State of Hawaii (15 threatened or endangered species; IUCN 2010). *Pritchardia* is one of the most species-rich plant genera in Hawaii (Wagner et al. 1999) and contains 27 currently recognized, primarily single-island endemic species (Fig. 1; Hodel 2007, 2009). The genus also occurs on small islands in the eastern Pacific (Cook, Fiji, Niue, Samoa, Solomons, Tonga). Based on the most recent phylogenetic results *Pritchardia* is monophyletic and sister to *Copernicia*, although generic relationships among *Copernicia*, *Pritchardia*, and *Washingtonia* were ambiguous due to gene-tree incongruence (Bacon et al. in review). Previous work has also shown that the North American and Caribbean lineage leading to *Pritchardia* colonized the eastern Pacific and then dispersed to Hawaii between 3.5-8 million years ago (MA; mean stem-crown ages; Bacon et al. in review). Although no explicit species concept was applied, Hodel (2007) recently revised *Pritchardia* using morphological data. Hodel (2007) noted that character states were often difficult to define because *Pritchardia* morphology is highly labile based on environmental conditions (see also St. John 1932; Wagner et al. 1999). Accurate estimation of species limits is important to understanding the evolution and radiation of *Pritchardia* species and is essential to conservation efforts on the Hawaiian Islands.

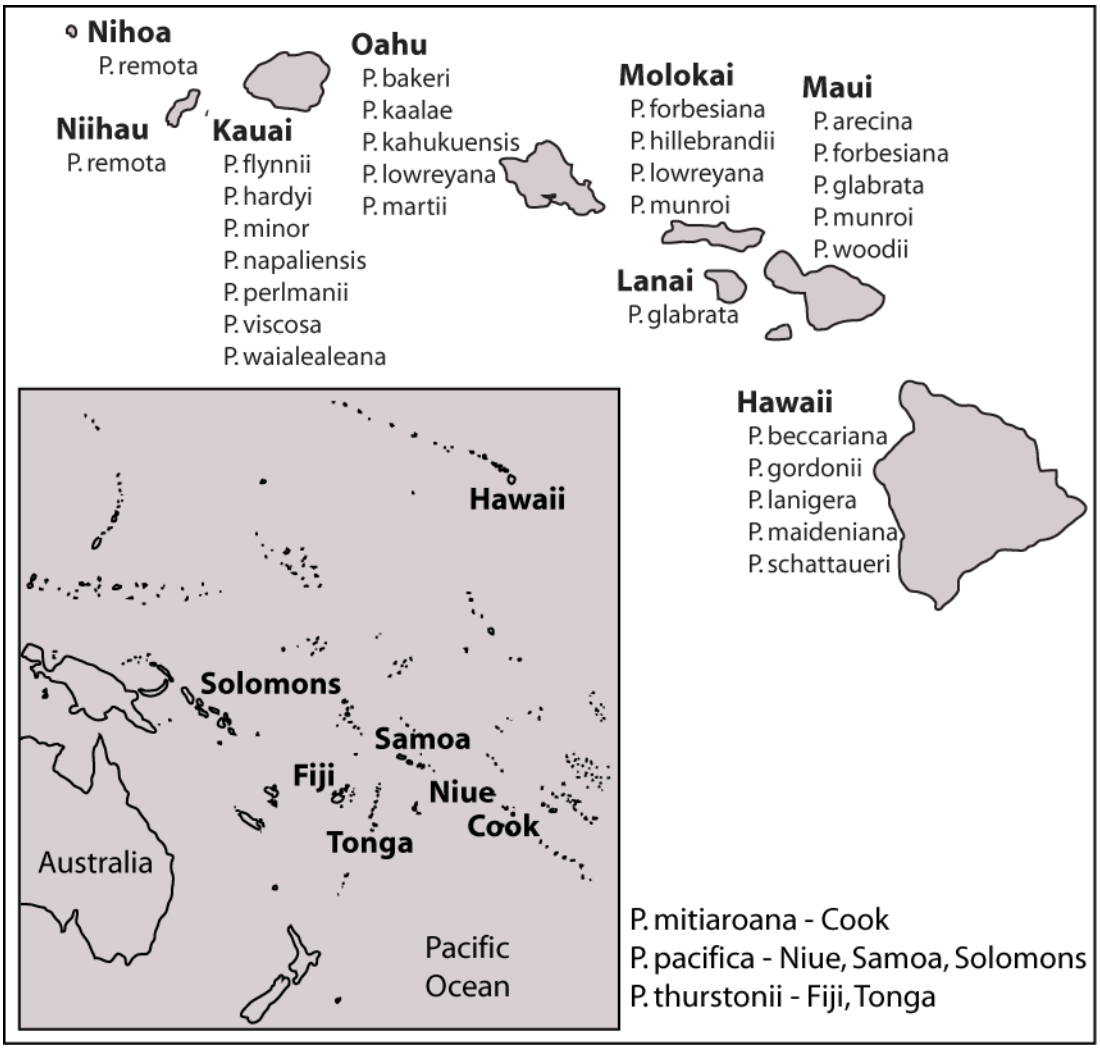

Figure 1. Geographic distribution of Hawaiian *Pritchardia* species according to the most recent morphological classification (Hodel 2007) and inset are the distributions of the eastern Pacific species.

Species concepts can address both the evolutionary patterns consistent with evolution along lineages and the evolutionary processes that are fundamental in maintaining distinct evolutionary lineages (e.g., Reeves and Richards 2011). Under the

phylogenetic species concept I (PSCI; Cracraft 1983), species are defined as “the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals" (Nixon and Wheeler 1990, p. 211). To apply PSCI, fixed (or mutually exclusive) character-state differences are used as evidence to infer that gene flow has ceased between the sampled populations in Population Aggregation Analysis (Davis and Nixon 1992). An alternate version of the phylogenetic species concept (PSCII) requires exclusivity to recognize a species and differs from PSCI by basing species recognition strictly on monophyletic groups (sensu de Queiroz and Donoghue 1988; properly exclusive lineages sensu Freudenstein 1998). A third alternative is the genotypic cluster species concept (GSC; Mallet 1995), which defines species as genetic groups with few or no intermediates between them. The GSC can be implemented using a variety of clustering algorithms or assignment tests. Looking across species delimitation criteria allows for the implementation of the general-lineage species concept where the greater the number of criteria satisfied by a putative lineage, the more likely it is to represent an independent evolutionary trajectory (de Queiroz 2007).

Adaptive radiations are difficult evolutionary scenarios because gene lineages may be so recently separated that they do not coalesce before the time of species divergence (Edwards et al. 2007). Among recently diverged species, genealogies inferred from independent genomic regions are likely to disagree due to the differential sorting of ancestral polymorphism into daughter lineages such that each inferred gene tree might differ from the species tree (e.g., Degnan and Rosenberg 2006). Because estimation of a coalescent species tree explicitly models incomplete lineage sorting, comparison with the

simultaneous-analysis (Kluge 1989; Nixon and Carpenter 1996) allows for the inference of hybridization from any incongruence between the two topologies when only orthologous alleles are sampled.

In this study we aim to provide a comprehensive assessment of species diversity in *Pritchardia* using a multifaceted approach and independent sources of plastid, nuclear, and morphological data to assess three species-delimitation criteria - monophyly, the absence of genotypic intermediates, and diagnosability using mutually exclusive character states. We test whether currently recognized *Pritchardia* species merit taxonomic recognition as distinct evolutionary lineages, particularly with respect to the accumulation of evidence in favor of their delimitation. We also take advantage of the power of the coalescent to infer the species tree to understand potential conflicts in our results that can be introduced by incomplete lineage sorting and/or hybridization.

Materials and Methods

PHYLOGENETIC ANALYSES

Two phylogenetic analyses were conducted within *Pritchardia* (Trachycarpeae, Coryphoideae, Arecaceae). Analysis 1 (A1) included sequence data generated from seven loci and microsatellite data (see below) coded as multistate characters with heterozygous individuals coded as polymorphic. Sampling for A1 included all previously recognized *Pritchardia* species except for *P. gordonii* and *P. woodii*, which are both recently described species with highly restricted distributions and are considered endangered (Hodel 2007). Based on a recent tribal-level analysis (Bacon et al. in review) two species of each of the most closely related genera to *Pritchardia* (*Copernicia* and *Washingtonia*)

and three other Coryphoideae species (*Cryosophila*, *Phoenix*, and *Sabal*) were sampled as outgroups for a total of 105 terminals in the initial A1 simultaneous analysis.

Total genomic DNA was extracted from silica-gel dried leaves following Alexander et al. (2007). Sequences for three plastid (*matK*, *ndhF*, and *trnD-trnT*) and four nuclear loci (CISP4, CISP5, MS, and RPB2) were generated. Single amplifications of the *matK* locus used primers *matK*-19F and *matK*-1862R, and internal sequencing using *matK*-300F, *matK*-809F, and *matK*-971R allowed for the construction of contiguous sequences (Steele and Vilgalys 1994; Asmussen et al. 2006). Amplifications of CISPs 4 and 5 followed Bacon et al. (2008), MS followed Crisp et al. (2010), *ndhF* followed Cuenca and Asmussen-Lange (2007), RPB2 followed Roncal et al. (2005), and *trnD-trnT* followed Hahn (2002). Amplified products were purified using Qiagen PCR purification kits and sequenced by the Cancer Research Center DNA Sequencing Facility at the University of Chicago (Illinois, USA) or at Macrogen (Seoul, Korea). All 502 new sequences generated in this study have been deposited in GenBank under accession numbers JF904936 to JF905438 (Appendix 1).

Preliminary nucleotide alignments were obtained independently for each of the seven loci 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). Each parsimony-informative character was confirmed by rechecking chromatograms in Aligner (CodonCode Corp., MA). Maximum parsimony (MP) tree searches were conducted using 1000 random addition tree-bisection-reconnection (TBR) searches in PAUP* v4.0b10 (Swofford 2001) with a maximum of ten trees held per replicate. MP jackknife (JK) analyses (Farris et al. 1996) were

conducted using PAUP* and 1000 replicates were performed with 100 random addition TBR searches per replicate. Maximum likelihood (ML; Felsenstein 1973) analyses of nucleotide characters from each of the molecular data matrices were performed. jModeltest v0.1.1 (Posada 2008) was used to select the best-fit likelihood model for each data matrix using the Akaike Information Criterion (Akaike 1974) without considering invariant-site models following Yang (2006). Searches for optimal ML trees and 1000 bootstrap replicates (BS; Felsenstein 1985) in the CIPRES Portal v2.2 used the RAxML-HPC2 algorithm (Stamatakis et al. 2005, 2008). MP Adams consensus trees (Adams 1972) were examined for wildcard terminals (potential hybrids; Nixon and Wheeler 1991) of uncertain phylogenetic position that were then omitted. Eleven iterations were conducted until a trade-off was reached between sacrificing taxonomically important terminals and gaining resolution in the strict consensus tree. A total of 72 of the original 105 terminals were included in the final A1 matrix.

Analysis 2 (A2) incorporated the A1, morphological, and isozyme data and was reduced to 35 composite terminals (Nixon and Davis 1991) representing all putative *Pritchardia* species. Nine discrete morphological characters of flower and fruit morphology were measured from specimens at BISH, NY, PTBG, and US and ten morphological characters were derived from species descriptions (Hodel 2007, 2009; Appendix 2). To include lineages that are not currently recognized as species according to Hodel (2007, 2009) morphological character states were extrapolated from recognized species to now synonymous entities. None of the synonymous taxa were described originally as differing in any of the character states from the taxa in which they are now included. We did not incorporate the preliminary morphological matrix from Gemmill

(1996) because of inconsistencies. A matrix of seven variable isozymes was derived from Gemmill (1996). Three terminals (*Pritchardia gordonii*, cultivated 'elliptica' from Lanai City, Lanai, and *P. minor*) were omitted from the A2 matrix following the procedure outlined above in which Adams consensus were constructed. The two simultaneous analyses (A1 and A2; TreeBase study accession 11604) were estimated and subsequently examined to determine the degree of support for monophyletic species (A1; PSCII) and for inferring robust inter-specific relationships due to decreased missing data and the use of all available characters (A2).

COALESCENT-SPECIES-TREE ANALYSIS

The coalescent species tree was inferred using *BEAST in the BEAST v1.6.1 package (Drummond and Rambaut 2007; Heled and Drummond 2010). *BEAST infers coalescent species trees from multilocus data and has been shown to have advantages in computational speed and accuracy over similar methods when applied to rapid radiations (Heled and Drummond 2010; but see Leaché and Rannala 2011). Coalescent-species-tree methods estimate each gene genealogy independently and assume that conflict between gene trees is due exclusively to incomplete lineage sorting. The sequence data from the A1 matrix was analyzed to avoid the inclusion of any potential hybrids. Each of the seven sequenced loci was unlinked to allow for variation in substitution models and the clock models for the chloroplast loci were linked to account for its single genetic history. The analysis was run using a Yule species tree prior and the GTR+Γ model of nucleotide substitution with four rate categories. The Markov chains were run for 50 million generations and repeated 10 times to test for MCMC chain convergence and to ensure

effective sample sizes (ESS) exceeded 200. Burn-in was determined in Tracer v1.5 based on ESSs and parameter trajectories and was removed in LogCombiner v1.6.1. Tree files were summarized in biopy v0.1.2 (Heled 2011), the posterior was resampled, and the variance among 100 random resampled species trees was visualized in DensiTree (Bouckaert 2010). We also estimated a single coalescent species tree in FigTree v1.3.1 by combining all tree files in LogCombiner v.1.6.1 (Drummond and Rambaut 2007). We compared the coalescent species tree with the simultaneous analysis to determine whether accounting for incomplete lineage sorting resulted in a different topology. The coalescent species tree and the A1 and A2 topologies also allowed for the examination of recent synonymy of species by Hodel (2007; *Pritchardia affinis* into *P. maideniana*, *P. aylmer-robinsonii* into *P. remota*, *P. elliptica* and *P. lanaiensis* into *P. glabrata*, *P. limahuliensis* into *P. napaliensis,* and both *P. pericularum* and *P. vuylstekeana* into *P. mitiaroana*).

POPULATION STRUCTURE ANALYSES

To test for the presence of intermediates between Hawaiian *Pritchardia* species, five microsatellite markers (Bacon et al. 2011b) were amplified in 197 individuals representing all 28 of the previously recognized species. PeakScanner software (ABI) was used for allele calling and FlexiBin v2 was used to bin alleles (Amos et al. 2007). GenoDive v20b19 (Meirmans et al. 2004) was used to test for Hardy-Weinberg equilibrium within populations with the default settings. Using the default settings, Microchecker v.2.2.3 (Oosterhout et al. 2004) was used to check for stutter, large-allele dropout, or evidence for null alleles based on a 99% confidence interval. A Bayesian procedure (Structure; Pritchard 2000) was used that minimizes the deviation from Hardy-

Weinberg and linkage equilibrium within each putative cluster by the fractional assignment of individual genomes to *K* populations. The admixture model was implemented with correlated allele frequencies and without the use of a priori information from populations of origin. Simulations included 10 iterations for each *K* value from *K*=1 to 30, with a 100,000-generation burn-in and 100,000 chain length. The most probable number of genetically homogeneous groups (*K*) was determined by the Δ*K* statistical procedure (Evanno et al. 2005) as implemented in Structure Harvester v0.6 (Earl 2011). Multimodality across the 10 replicate iterations of the Structure analysis was addressed by permuting 1,000 times using the greedy algorithm and averaging across membership coefficients in CLUMPP (Jakobsson and Rosenberg 2007); the results were graphically displayed using Distruct v1.1 (Rosenberg 2004).

POPULATION AGGREGATION ANALYSIS

Mutually exclusive microsatellite character-states were used to infer that gene flow had ceased between the sampled populations (Nixon and Wheeler 1990). To test whether previously recognized species were diagnosable and satisfy the PSCI, character-state differences were identified using population aggregation analysis (PAA) following Davis and Nixon (1992). As more populations are incorporated into PAA, each is compared to all species previously delimited. Each time a species profile is aggregated due to the inclusion of another population, the new profile is compared to all other species profiles to check if further aggregation is needed. We used PAA for the microsatellite, morphological, and sequence data independently of each other (because of differences in which terminals were sampled), and then performed PAA for all three data

types to detect diagnosable groups. Missing and ambiguous data were treated as polymorphic for all states present, but these entries were not used to collapse otherwise diagnosable groups in PAA as suggested by J. I. Davis (pers. comm. 2011).

Results

PHYLOGENETIC ANALYSES

Gene tree incongruence was detected among five of the seven loci for the resolution of the sister group of *Pritchardia* and among two of the seven loci for the sister group of Hawaiian *Pritchardia* (Fig. 2). The A1 dataset comprised seven genes and five microsatellite loci for 72 individuals; 134 characters were variable and 81 were parsimony-informative within *Pritchardia* (CI 0.62, RI 0.71; Fig. 3). Application of PSCII to the *Pritchardia* relationships in our A1 matrix indicated that the three currently recognized species of eastern Pacific *Pritchardia* [*P. thurstonii*, *P. pacifica*, and *P. mitiaroana* (including *P. pericularum* and *P. vuylstekeana* sensu Hodel 2007); Fig. 3], are each distinct evolutionary lineages. Despite low branch support, Hawaiian *P. affinis, P. kaalae*, and *P. remota* were resolved as unique monophyletic groups and satisfy the PSCII criterion (Fig. 3). A monophyletic group of *P. bakeri* from Pupukea, Oahu was also resolved and likely represents population structure within the Koolau mountain range. A clade of that included a subset of *Pritchardia glabrata* individuals and a clade of that included a subset of *P. perlmanii* individuals were resolved (Fig. 3), consistent with being distinct evolutionary lineages according to the PSCII criterion.

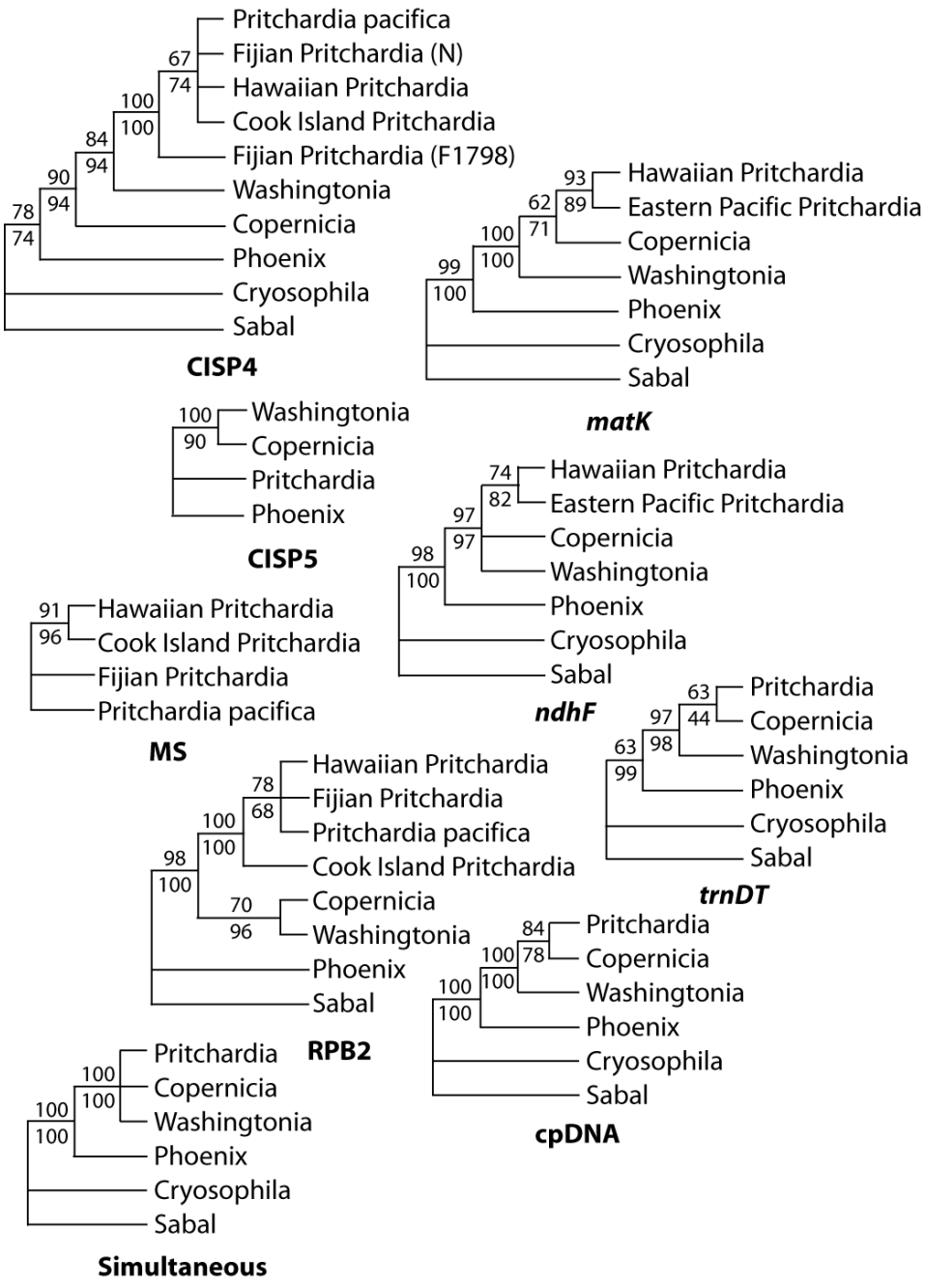

Figure 2. Parsimony strict consensus trees of all the sequence data with parsimony jackknife support values above, and likelihood bootstrap values below each branch of each gene individually, the plastid partition, and the simultaneous analysis. Trees are summarized to show only the inter-generic relationships and *Pritchardia* from different island chains.

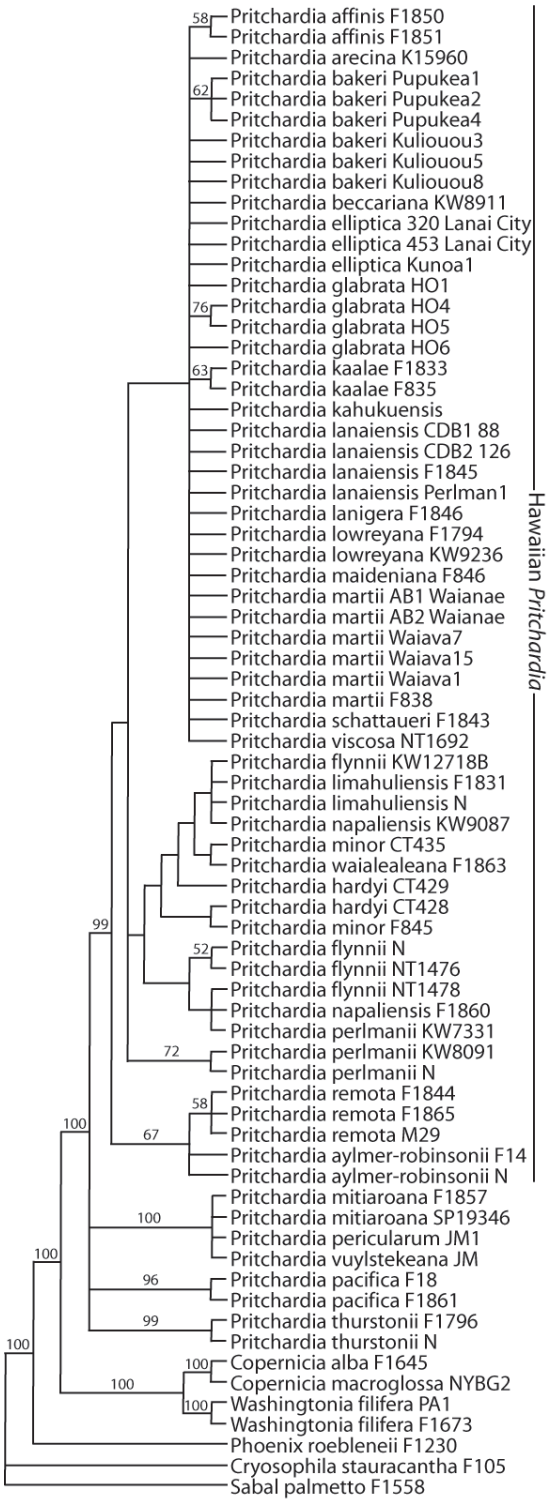

Figure 3. Analysis 1 (A1) parsimony tree inferred from DNA sequence and nuclear microsatellite data.

The 35 species sampled in the A2 matrix was reduced to 33 by deleting wildcard taxa identified from comparisons of the Adams and strict consensus trees. The reduced A2 matrix has 79 parsimony informative characters (CI 0.72, RI 0.75; Fig. 4). The eastern Pacific *Pritchardia* species *P. pacifica* and *P. mitiaroana* (including *P. pericularum* and *P. vuylstekeana*) were resolved as part of a basal polytomy within *Pritchardia*, but there was strong support for monophyly of the *P. mitiaroana* group (100% JK; Fig. 4), which is consistent with Hodel's (2007) recent synonymy of those species. *Pritchardia thurstonii* was well supported (81% JK) as the sister species to the Hawaiian clade, which was well supported (97% JK) as a monophyletic group. *Pritchardia aylmer-robinsonii* and *P. remota* were strongly supported as sister species (98% JK), consistent with their synonymy (Hodel 2007). *Pritchardia affinis* and *P. maideniana* were well-supported (89% JK) as sister taxa, also consistent with recent synonymy (Hodel 2007), and *P. hillebrandii* was weakly supported (54% JK) as its sister species. *Pritchardia hardyi* and *P. viscosa* were also weakly supported (53% JK) as sister species.

COALESCENT-SPECIES-TREE ANALYSES

We explicitly modeled incomplete lineage sorting through the use of a multispecies coalescent tree (Fig. 5). The topology did not have any well-supported (≥75% branch support) conflicts with the A1 or A2 trees. The congruence between methods indicates that the trees used for species delimitation (A1) and for inference of inter-specific relationships (A2) may not be overwhelmed by patterns of lineage sorting. The *BEAST species tree resolved four moderately supported groupings of Hawaiian

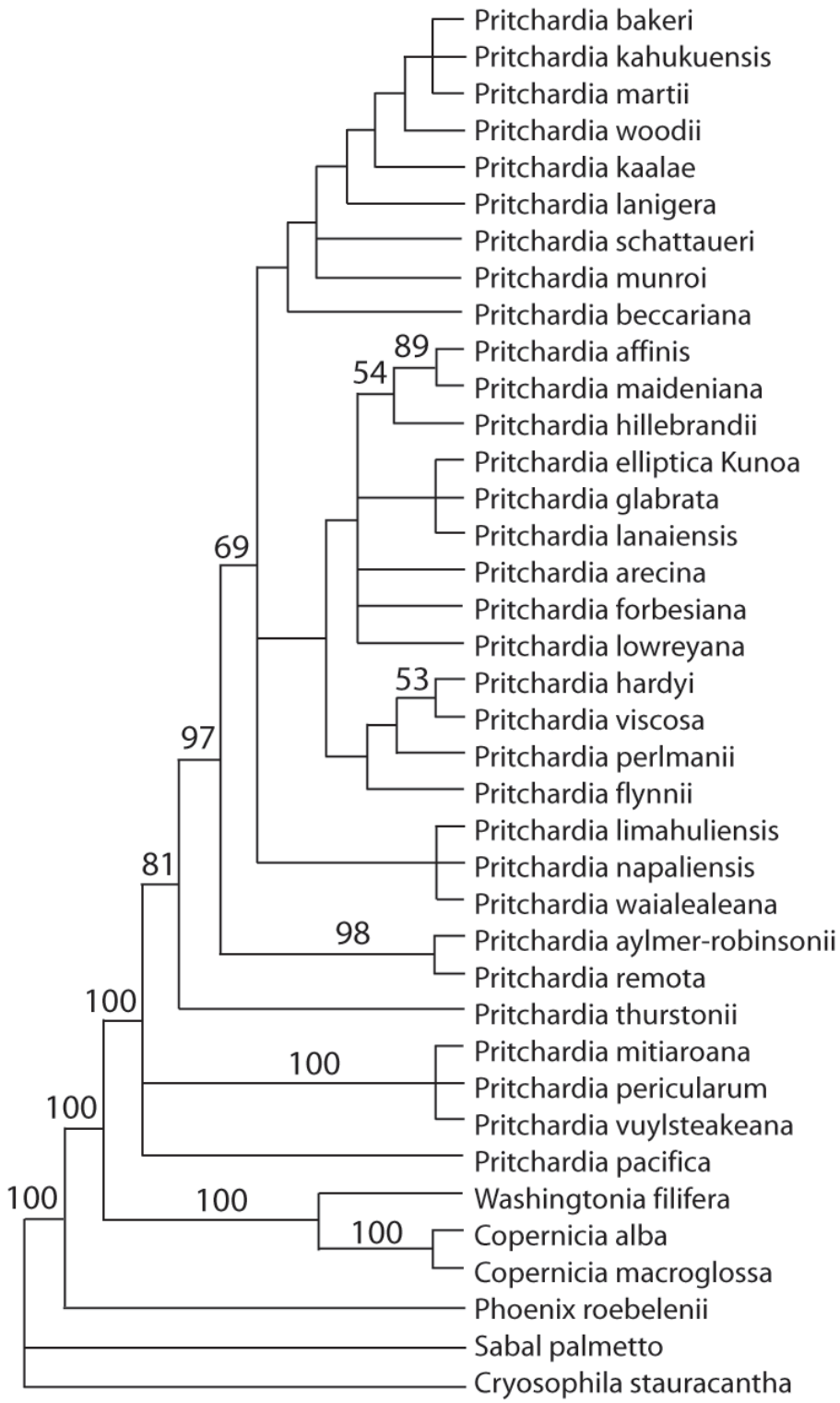

Figure 4. Analysis 2 (A2) parsimony tree inferred from the data in A1 and isozyme and morphological data showing inter-specific relationships.

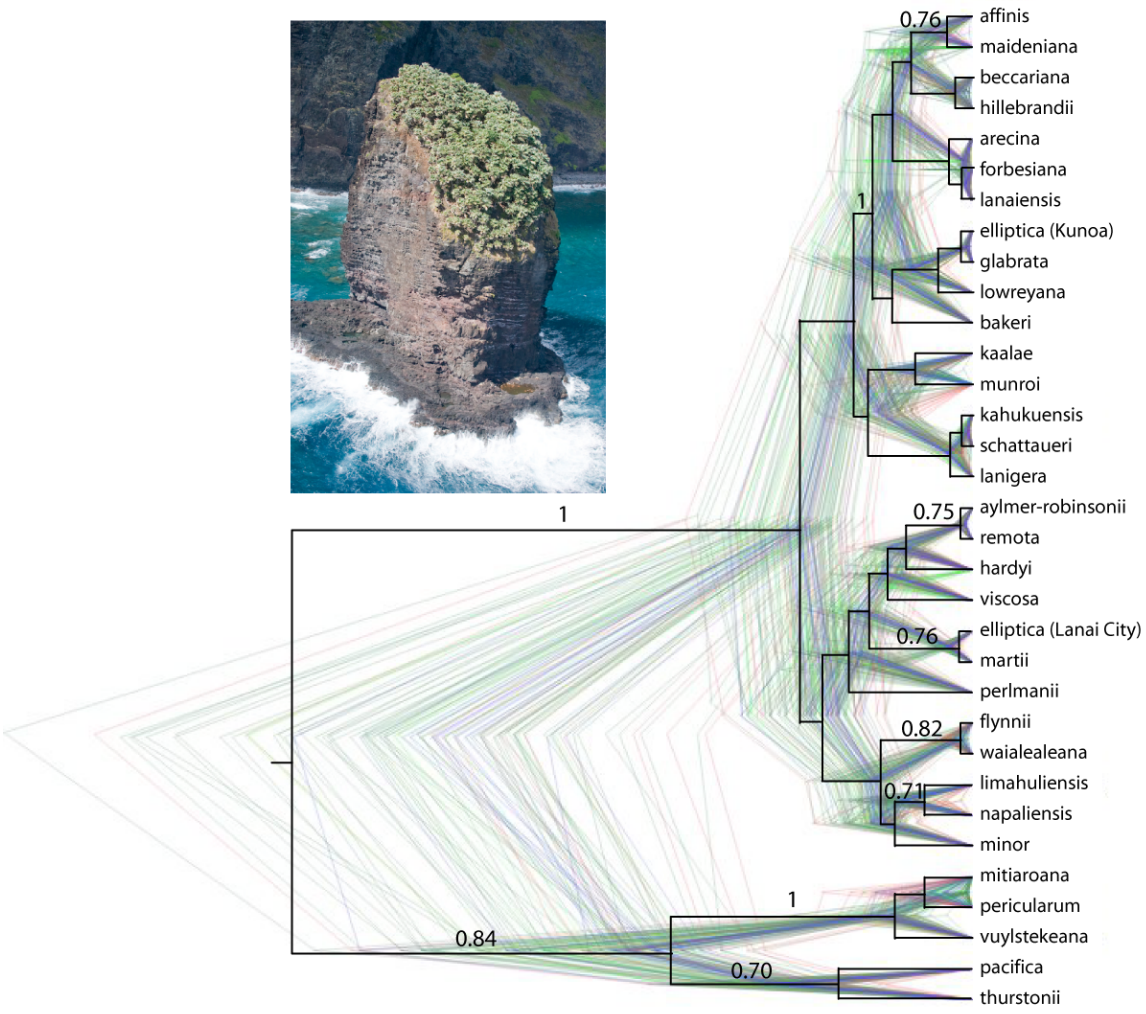

Figure 5. Resampled posterior species trees as inferred from *BEAST are in color and posterior probabilities based on the single combined tree are overlaid in black. *Pritchardia hillebrandii*, which has one of the most restricted distributions in the genus, is pictured on Huelo Islet (photo and copyright D.R. Hodel).

individuals not seen in the comparable A2 analysis (Fig. 4), although this may be due to differences between parsimony and Bayesian tree reconstruction and branch support methods. The recently synonymized *P. napaliensis* including *P. limahuliensis, P. maideniana* including *P. affinis*, and *P. remota* including *P. aylmer-robinsonii* (Hodel 2007) were each resolved within monophyletic groups. Although the posterior probabilities for these cases of synonymy were modest (between 0.71 and 0.76 PP), it is an indication that these three taxonomic changes based on Hodel's (2007) morphological revision are consistent with our molecular results.

POPULATION STRUCTURE ANALYSES

Significant p-values indicating disequilibrium were detected in the '90' locus for two populations (martii Waianae and lanigera 2) and no evidence for stutter, large allele dropout, or null alleles was detected at any of the loci based on 99% confidence intervals. Structure analyses resulted in mean LnP(K) values that appeared to plateau when graphed in Structure Harvester, making it difficult to identify the most likely K value for the number of genetic groups present in the data. Therefore the ΔK method was applied and the highest probability for the number of groups that individuals were assigned to (K) was 21 (Mean LnP(K) = -2802, ΔK = 3.84). Upon visualization of population assignments from across the Structure iterations, the presence of genetic intermediates between *Pritchardia* species was evident (Fig. 6). Levels of admixture were particularly high in areas of sympatry such as in the Makaleha and Namolokama ranges in Kauai where up to five species overlap in geographic distribution [*P. flynii*, *P. hardyi*, *P. perlmanii* (albeit to a lesser extent), *P. viscosa*, and *P. waialealeana*] and in the Koolau Mountains of Oahu

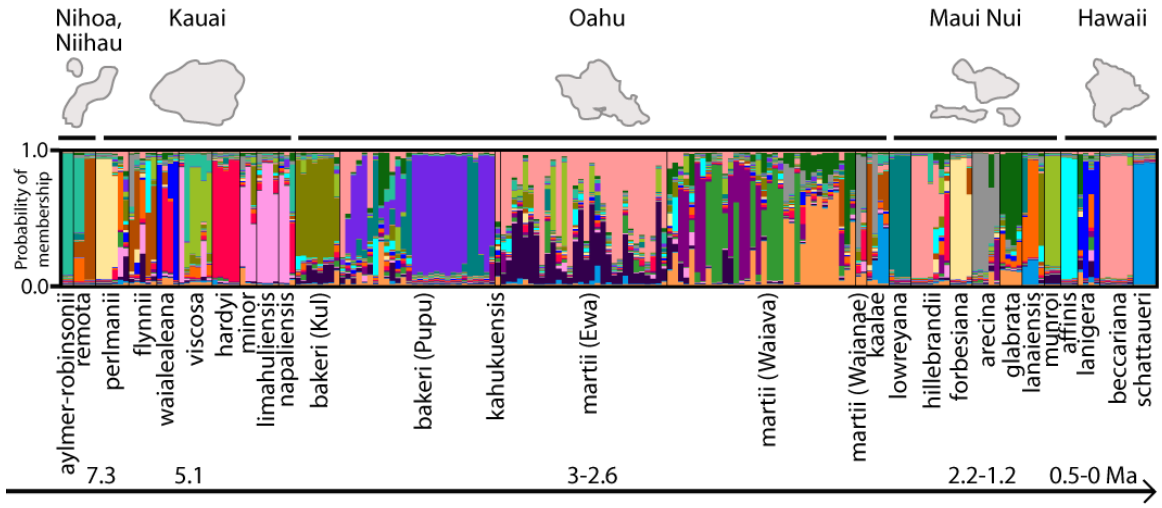

Figure 6. The *K* = 21 bar plot estimated across 197 individuals and five microsatellite loci. Evidence for distinct evolutionary lineages without significant admixture or the presence of intermediates supports *Pritchardia affinis, P. aylmer-robinsonii*, *P. hardyi, P. munroi,* and *P. schattaueri* as independent lineages. Putative species are labeled below and Hawaiian distributions from the oldest to the youngest island are indicated above the bar plot.

where three species are sympatric (*P. bakeri*, *P. kahukuensis*, and *P. martii*). Genetic subdivision and little admixture between species were detected among *P. affinis, P. aylmer-robinsonii*, *P. beccariana*, *P. forbesiana*, *P. hardyi, P. lowreyana, P. munroi,* and *P. scahttaeuri* and these eight groups meet the necessary criterion of high probability of assignment to their respective genetic groups (>0.8 membership coefficient). However, when taking the individual Q matrix of assignment to groups into consideration, *P. beccariana, P. forbesiana,* and *P. lowreyana* do not represent distinct evolutionary lineages according to the GSC because they do not group as *unique* clusters; with other individuals in the Q matrix having >0.8 posterior probability of falling within those

groups. Although the 0.8 cut-off is arbitrarily defined, the maximum values from the Q matrices show a discontinuous distribution where individuals have a membership coefficient of >0.8, while the remaining have <0.5 with few in between. Therefore, only *P. affinis, P. aylmer-robinsonii*, *P. hardyi, P. munroi,* and *P. schattaueri* meet the necessary and sufficient criteria as distinct evolutionary lineages without intermediates according to the GSC (Table 1).

POPULATION AGGREGATION ANALYSIS

Four distinct lineages within *Pritchardia* for the microsatellite data using PAA, 33 for the sequence data, and 12 for the morphology, although individuals with missing data for diagnostic characters were left out of aggregations to avoid collapsing otherwise distinct groups. For example, in the sequence data, seven terminals had missing data for diagnostic characters and were arbitrarily assigned to a single group rather than collapsing the otherwise diagnosable groups. Due to uneven sampling between data types, only the individuals sampled for the sequence dataset were used to perform PAA across the microsatellite and morphological data. In the three datasets we generated for this study, 43 lineages were indentified that are diagnosable and satisfy the PSCI. Of the 43 PSCI species, unique combinations of character states support 18 currently recognized *Pritchardia* species (Table 1).

Discussion

Hawaii is an unparalleled example of insular evolution because of its ecological heterogeneity, volcanic origin, and isolation from the nearest continental land mass

Table 1. Conformance of currently recognized Hawaiian *Pritchardia* with three distinct criteria for species delimitation. Monophyly, as required by the phylogenetic species concept II, is shown as parsimony jackknife branch support. Genotypic clusters are labeled with their inferred genetic group and their estimated membership coefficient. Diagnosability to satisfy the phylogenetic species concept I was determined by PAA.

Hawaiian *Pritchardia* species	Monophyletic	Genotypic cluster	Diagnosable
affinis	**58%**	**12; 0.91**	No
arecina	No	19; 0.71	**Yes**
aylmer-robinsonii	No	**18; 0.91**	**Yes**
bakeri Kuliouou	No	13; 0.67	No
bakeri Pupukea	**62%**	17; 0.51	**Yes**
beccariana	No	14; 0.90	No
elliptica Kunoa	No	4; 0.48	No
elliptica Lanai City	No	-	No
flynii	No	11; 0.40	No
forbesiana	No	10; 0.83	**Yes**
glabrata	**76%**	20; 0.58	**Yes**
gordonii	-	**-**	**Yes**
hardyi	No	**7; 0.86**	**Yes**
hillebrandii	No	14; 0.59	**Yes**
kaalae	**63%**	11; 0.31	**Yes**
kahukuensis	No	21; 0.52	No
lanaiensis	No	8; 0.46	No
lanigera	No	9; 0.55	No
limahuliensis	No	4; 0.78	No
lowreyana	No	15; 0.89	**Yes**
maideniana	No	-	**Yes**
martii Ewa	No	21; 0.44	No
martii Waiawa	No	19; 0.54	**Yes**
martii Waianae	No	11; 0.31	No
minor	No	4; 0.62	No
munroi	No	**16; 0.83**	**Yes**
napaliensis	No	4; 0.52	No
perlmanii	**72%**	10; 0.57	No
remota	**58%**	11; 0.51	**Yes**
schattaueri	No	**2; 0.91**	**Yes**
viscosa	No	16; 0.40	**Yes**
waialealeana	No	9; 0.50	**Yes**
woodii	-	-	**Yes**

(Carlqist 1980). It is the longest archipelago on earth and developed linearly in a chronological fashion (Carson and Clague 1995). Despite the limited time available for diversification in comparison to ancient landmasses (Price and Clague 2002; Clague et al. 2010), Hawaii has the highest degree of endemism for any known flora (Sakai et al. 2002). Within Hawaii, many angiosperms show evidence for recent and rapid radiations, which frequently make species delimitation difficult (e.g., Clark et al. 2009; Harbaugh et al. 2009b; Bacon et al. 2011a). We applied three species-delimitation criteria- phylogenetic species concepts I and II and genotypic species cluster concept- to identify evolutionary lineages using dense genetic and geographic sampling in Hawaiian *Pritchardia*. Robust species delimitations are important for *Pritchardia* because many of the currently recognized species are of conservation concern and threats continue to increase due habitat degradation and invasive herbivores and competitors (Chapin et al. 2004).

We applied the criterion of monophyly to test whether currently recognized *Pritchardia* species were distinct evolutionary lineages using PSCII. MP analysis of the A1 matrix revealed support for *P. affinis, P. glabrata, P. kaalae*, *P. perlmanii* and *P. remota* as clades (Fig. 3). Although these are weakly supported lineages, they satisfy the monophyly requirement of the PSCII (e.g., de Queiroz and Donoghue 1988). Despite its popularity, monophyly as inferred from a phylogenetic tree may be a poor indicator of whether evolutionary lineages are distinct in the presence of gene flow (Huson and Bryant 2006; Reeves and Richards 2007) or due to the error associated with randomly sampling few individuals from a complex underlying genealogy (Rosenberg 2007).

Furthermore, decoupling hybridization from incomplete lineage sorting on a phylogeny is difficult in recently diverged species because both produce the same pattern of shared polymorphisms between morphologically identifiable species (e.g., Wendel and Doyle 1998; Holder et al. 2001; Mallet 2005).

The genotypic cluster criterion defines species as "distinguishable groups of individuals that have few or no intermediates when in contact" (Mallet 1995, p. 296). A Bayesian assignment test, as implemented in Structure, was used to quantify the degree of admixture (essentially the absence of intermediates) between species. Although issues can arise with imperfect geographical sampling, especially in cases of isolation by distance or environmental gradients (e.g., Schwartz and McKelvey 2009), strong signal for the delimitation of *P. affinis, P. aylmer-robinsonii*, *P. hardyi, P. munroi,* and *P. schattaueri* was detected with high probability of assignment to unique populations (> 0.8 proportion of membership). A lack of intermediates satisfies this species criterion and these five groups are distinct evolutionary lineages according to the GSC. On the other end of the speciation spectrum, sympatric species appear to have ongoing gene flow among lineages where the probabilities of membership among some heterogeneous individuals and populations were shared (Fig. 6), particularly in Kauai (*P. flynnii, P. limahuliensis, P. napaliensis, P. minor, P. perlmanii, P. waialealeana,* and *P. viscose*) and Oahu (*P. bakeri, P. kahukuensis,* and *P. martii*).

Under the criterion of diagnosability, species are identified as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals" (Nixon and Wheeler 1990, p. 211). Using PAA, 43 lineages were identified as diagnosable, and although they conform

to PSCI as independent lineages, we do not advocate their formal recognition as species. Rather, our goal was to implement the general lineage species concept and infer across species delimiting criteria to reach a more stable taxonomic solution for the Hawaiian *Pritchardia*. Furthermore, PAA can be highly sensitive to sampling error (Davis and Nixon 1992), where incomplete sampling of characters, individuals within populations, or populations can each lead to incorrect assessment of species. In our Hawaiian *Pritchardia* data, the nucleotide sequence matrix had 24% percent missing or ambiguous data, which was mostly due to a lack of sampling in the MS gene (Suppl. Fig. 1). Both the microsatellite and morphological matrices had 0.05% missing data. Between one and six individuals were sampled per population with an average of 1.5 individuals and 1.7 populations per species in the nucleotide sequences of the A1 matrix. Between one and 34 individuals were sampled per population with an average of 7 individuals and two populations per species for the microsatellite matrix. The morphological matrix comprised character states that were fixed within currently recognized species and were not typically scored from the actual specimens used in the sequence-based and microsatellite analyses. Additionally, ten of the morphological characters were derived from species descriptions (Hodel 2007, 2009) rather than herbarium material. Certainly no study is immune to these types of error, but we recognize that undersampling of individuals within populations and populations within species have affected the PAA results in this study by over-splitting.

DISTINCT EVOLUTIONARY LINEAGES OF PRITCHARDIA

As currently defined, *Pritchardia* species are recognized by a suite of morphological characters and their geographic distributions (Hodel 2007, 2009). Yet when considering distinct evolutionary lineages identified in this study, none of the *Pritchardia* species satisfy all the three of the species-delimitation criteria that we applied. Species are generally recognizable, but some species-delimiting criteria recognize more lineages than others because criteria are met at different times during cladogenesis (de Querioz 2007). Furthermore, when considering the amount of data used by each criterion to infer species delimitations in Hawaiian *Pritchardia* we found the method that uses the most data, PAA, was the most powerful because it recognized the greatest number of splits.

Seven *Pritchardia* lineages satisfy two species-delimitation criteria (*P. affinis*, *P. glabrata, P. hardyi*, *P. kaalae*, *P. munroi*, *P. remota,* and *P. schattaueri*). The taxonomic status of *P. affinis* and *P. remota* are discussed in the interpretation of the A2 and coalescent species tree (see below). *Pritchardia lanaiensis* and *P. elliptica* were recently synonymized into *P. glabrata* (Hodel 2007), yet our results are inconsistent with this designation because a lack of intermediates between them (Fig. 6) and because of the diagnostic grouping of all *P. glabrata* sensu stricto individuals in PAA. *Pritchardia hardyi*, *P. munroi*, and *P. schattaueri* are all distinct lineages based on the species-delimitation criteria of a lack of intermediates and the presence of diagnostic character states. These results are consistent with Hodel's (2007) description of morphological autapomorphies that define each of these independent lineages. *Pritchardia kaalae* is identified as an independent lineage based on the formation of a monophyletic group and

the presence of diagnostic character states. Despite its distinction as an independent lineage, *P. kaalae* appears to have significant levels of admixture based on the Structure results, particularly with Waianae and central Koolau (Waiava) populations of *P. martii* (Fig. 6). Admixture may be indicative of the *Pritchardia*-dominated ancestral forest between the Waianae and Koolau mountains of Oahu that may have facilitated gene flow (Carlquist 1980; Cuddihy and Stone 1990). The once-contiguous palm forest likely formed an isolation-by-distance-based cline of gene flow, and extinction of the intervening lowland populations may have subsequently formed reproductively isolated lineages.

Eleven *Pritchardia* lineages satisfy one species-delimitation criterion (*P. arecina, P. forbesiana, P. gordonii, P. hillebrandii, P. lowreyana, P. maideniana, P. perlmanii, P. viscosa, P. waialealeana,* and *P woodii*). Some of these *Pritchardia* lineages may be recognized as independent due to the sampling artifacts described above. This is particularly a concern with *P. gordonii* and *P. woodii*, which were only sampled for morphology, and *P. hillebrandii*, which was not sampled for the sequence data. Future efforts to tease apart distinct evolutionary lineages in *Pritchardia* should focus on these particular groups, as well as areas of sympatry, with increased sampling of both individuals within populations and of populations within species.

SISTER-GROUP AND INTER-SPECIFIC RELATIONSHIPS OF PRITCHARDIA

In previous studies the sister group of *Pritchardia* has been inferred to be either *Copernicia* (53% BS in maximum representation with parsimony analysis, Baker et al. 2009; <50% JK and BS, Bacon et al. in review) or *Washingtonia* (52% BS; Asmussen et

al. 2006). Our study is consistent with previous work showing the close relationships among the three genera (*Copernicia*, *Pritchardia*, and *Washingtonia*). In the A1 and A2 matrices, *Copernicia* and *Washingtonia* together are inferred to be the sister group to *Pritchardia* with strong support (100% JK in both analyses; Figs. 3 and 4). The strong support for sister relationships is essential for future inference of biogeography in *Pritchardia* and will help elucidate the patterns of colonization to the islands of the Caribbean and Hawaii.

We formed composite terminals from the A1 matrix to construct the A2 matrix for simultaneous analysis of inter-specific relationships (Fig. 4). The A2 matrix did not incorporate divergent lineages into composite taxa based on the A1 terminal omission iterations and can be compared to the coalescent species tree to assess effects of incomplete lineage sorting. In the A2 tree, *P. thurstonii* is sister to the Hawaiian clade, which is well-supported as monophyletic (97% JK) and consistent with Bacon et al. (64% BS / 65% JK; in review). Zielger (2002) proposed the relationship between Fijian and Hawaiian *Pritcharida* based on his hypothesis of an adaptive shift in fruit size upon colonization of the Hawaiian archipelago. The sister relationship between Fijian and Hawaiian angiosperms has also been noted in *Cyrtandra* (Clark et al. 2009) and *Pittosporum* (Gemmill et al. 2002), but not in taxa that ultimately descended from American ancestors, such as *Pritchardia* (Baldwin and Wagner 2010). The synonymy of *P. remota* with *P. aylmer-robinsonii* (Hodel 2007) is consistent with the strongly supported sister relationship (98% JK). The backbone of the Hawaiian clade is an unresolved trichotomy. Weak support was provided for a sister relationship between *P. hardyi* and *P. viscosa* (53% JK), which had been previously suggested based on their flat

leaf blades, the density of lepidia on the abaxial surface of the leaf, and their stiff leaf tips (Hodel 2007). Hodel (2007) also identified a close relationship between *P. maideniana* (including *P. affinis*) and *P. hillebrandii* based on morphological aspects of the lepidia and inflorescences, for which we inferred a well-supported *P. maideniana* sensu lato (89% JK) that was weakly supported as sister to *P. hillbrandii* (54% JK).

The coalescent-species-tree approach has been suggested to be a more accurate estimation of lineage splitting than concatenation because it can model the stochastic forces that drive population divergence (Maddison and Knowles 2006; Edwards et al. 2007; Kubatko and Degnan 2007; Heled and Drummond 2010). Missing data and other issues with species-tree estimation such as mutational and coalescent variance can have detrimental effects on modeling incomplete lineage sorting (e.g., Huang et al. 2010). Another important consideration with species-tree estimation is that species are defined a priori and the coalescent model assumes species are reciprocally monophyletic. This can be highly unlikely in recent radiations where ancestral species are still extant. Despite these issues, the advantage of directly modeling intraspecies polymorphism and incomplete lineage sorting makes species-tree estimation an important approach to data exploration in the identification of evolutionary lineages, especially in rapid species radiations (Heled and Drummond 2010).

The species tree topology provided moderate branch support for three clades that are consistent with synonymy [*P. aylmer-robinsonii* into *P. remota* (0.75 PP), *P. affinis* into *P. maideniana* (0.76 PP), and *P. limahuliensis* into *P. napaliensis* (0.71 PP); Fig. 5]. The coalescent species tree identified *P. flynnii* and *P. waialealeana* as sister taxa, which together are sister to *P. minor* (Fig. 5). Lastly, individuals planted by early Hawaiian

naturalist George Munro in Lanai City, Lanai had been hypothesized to represent the extinct *P. elliptica* lineage (R.W. Hobdy, pers. comm. 2008), but are here shown to be consistent with a *P. marti* source from Oahu (0.76 PP; see also Suppl. Fig. 3) and separated from *P.* cf. *elliptica* individuals collected from natural populations in Kunoa Valley by eight branches, one of which is moderately well-supported (Fig. 5). Secondly, the species tree was used to test for congruence with the simultaneous-analysis A2 topology. Because the two distinct methods generally resolved the same well-supported clades, we can infer that the extrapolation from the gene trees to the phylogenetic tree is likely accurate. This is not to say that the process of lineage sorting has not occurred, but rather we have no evidence that it has confounded the species-level relationships as estimated from the simultaneous-analysis tree.

INCOMPLETE LINEAGE SORTING, THE TEMPO OF RADIATION, AND HYBRIDIZATION IN PRITCHARDIA

The identification of distinct evolutionary lineages is a necessary precursor to the delimitation of species (Sites and Marshall 2003; de Quieroz 2007). Satisfaction of multiple species criteria can ensure accurate, stable, and uncontroversial species delimitations (e.g., Leaché et al. 2009; Reeves and Richards 2011). For taxa of conservation concern, accurate identification of lineages may facilitate management efforts by focusing on distinct species, rather than ambiguous groups. Our results, which are based on data from both the plastid and nuclear genomes, show little sequence differentiation among most *Pritchardia* species. The lack of differentiation may be due to

incomplete lineage sorting, the tempo of the *Pritchardia* radiation, and/or hybridization between sympatric species, and distinguishing between these factors can be difficult.

Incomplete lineage sorting is one hypothesis for gene-tree incongruence and a lack of resolution within island radiations. Differential lineage sorting can bias species inference and may be further compounded by the estimated long generation time for other tropical understory palms that have undergone island colonization (e.g., 68 year mean in the Fijian endemic *Balaka microcarpa*; Ash 1998). Large ancestral effective population sizes have been hypothesized from fossil evidence and *Pritchardia* has been shown to be the dominant component of pre-human Quaternary forests on the Hawaiian archipelago (2.6 Ma-822 yrs before present; Burney et al. 2001; Burney and Kikuchi 2006). Despite this, coalescence times for Hawaiian *Pritchardia* species are likely to be shorter than their continental tribal counterparts. Congruence between the simultaneous and species tree analysis together with information on coalescence times suggests that differential lineage sorting does not drive current diversity patterns within *Pritchardia*.

A general trend emerging from this and other phylogenetic studies on the Hawaiian flora is the difficulty in estimating relationships among woody and long-lived groups [e.g., *Cyrtandra* (Clark et al. 2009), lobeliads (e.g., Givnish et al. 2009), *Melicope* (Harbaugh et al. 2009a); *Metrosideros* (Percy et al. 2008; Harbaugh et al. 2009b); *Pittosporum* (Gemmill et al. 2006; Bacon et al. 2011a); *Pyschotria* (Nepokroeff et al. 2003); *Santalum* (Harbaugh and Baldwin 2007), *Schiedea* (Willyard et al. in press), and the silversword alliance (e.g., Baldwin and Sanderson 1998)]. Another example is Hawaiian *Pritchardia*. Aside from the sympatric species, the lack of resolution may be caused by the insufficient time for divergence between lineages. Because of the age of

the oldest extant Hawaiian Island (Nihoa; 7.3 Ma; Price and Clague 2002; Clague et al. 2010) and because the *Pritchardia* colonization of Hawaii was estimated to occur between 3.5-8 Ma (mean stem to crown-stem ages; Bacon et al. in review), an average of three new species would have had to form every million years to account for the 24 species in the radiation. Clearly this rapid rate of anagenesis and cladogenesis has not allowed for much divergence within the Hawaiian *Pritchardia* radiation.

We also suggest that hybridization has played a key role in the diversification of Hawaiian *Pritchardia* lineages from geographic regions of sympatry of Kauai (*P. flynnii, P. limahuliensis, P. napaliensis, P. minor, P. waialealeana,* and *P. viscosa*) and Oahu (*P. bakeri, P. kahukuensis,* and *P. martii*). Removing wildcard terminals through the use of Adams consensus trees may be biased towards deletion of hybrids given that they are expected to be resolved as basal lineages (McDade 1992) and our iterative exclusion process is consistent with the exclusion of hybrids because 66% (22 of the 33) of the excluded terminals were from areas of high sympatry such as in the Makaleha and Namolokamain ranges in Kauai and in the Koolau Mountains of Oahu. Examination of the character conflict present in the *Pritchardia* sequence was hampered by a general lack of resolution in the gene trees (each nDNA versus the single cpDNA tree; Fig. 2, Suppl. Figs. 1 and 2). Despite this, review of the parsimony-informative sequence characters revealed six polymorphisms found on both forward and reverse sequence reads that suggest introgression in two genes given how different the alleles are (nuclear MS and plastid *trnD-trnT*). Although widespread hybridization has been observed in cultivation (Hodel 1980; Ellison and Ellison 2001), it has been difficult to detect in the field due to

the high phenotypic plasticity that characterizes the genus (Wagner et al. 1999; Hodel 2007).

The ability to hybridize is common among island species (e.g., Carlquist 1974) and has likely been a major force in shaping other Hawaiian angiosperm lineages such as *Metrosideros* (Percy et al. 2008; Harbaugh et al. 2009), *Pittosporum* (Wagner et al. 1999; Bacon et al. 2011a), and silverswords (e.g. Friar et al. 2008). Outside of the lack of reproductive barriers or incompatibility mechanisms, anthropogenic change on the archipelago may have caused a breakdown of species boundaries. For example, native Hawaiians cultivated *Pritchardia* species in coastal settlements and although they had a variety of ethnobotanical uses (reviewed in Gemmill 1996), the leaves and fibers were primarily used for thatching. The movement of plants by humans could have introduced new genotypes into existing coastal native species and admixed with other cultivated species. Also, the likely extinction of natural pollinators and dispersers and the introduction of invasives that generally have higher mobility and efficiency (Aizen et al. 2008) may also facilitate gene flow between populations and species.

Research at the interface of population genetics and phylogenetics is greatly expanding, as seen in the increasing numbers of publications on coalescent methods to infer species trees (e.g., Maddison and Knowles 2006; Edwards et al. 2007; Kubatko and Degnan 2007; Heled and Drummond 2010). A limitation to the current implementations of species-tree methods is the assumption of lack of gene flow among lineages, yet in empirical studies this assumption is often violated, especially at the taxonomic level these methods are designed for. Although there are methods that model gene flow as well as the coalescent (i.e., the isolation-with-migration model of Hey and Nielsen 2004 or the

hierarchical approximate Bayesian computation approach of Huang et al. 2011), these approaches do not provide an estimate of a species tree under a model of divergence with gene flow and may be less powerful than species tree estimates because they require such strong priors (e.g., on migration rates; Heled and Drummond 2010). To best address species delimitation in rapid radiations, especially in island groups like *Pritchardia* palms, methods that allow for simultaneously capturing vertical and horizontal inheritance of genetic information are needed, but are not yet available (Yu et al. 2011; but see Chung and Ané 2011).

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Appendix 1.

List of taxa sampled with taxonomic authorities, voucher information, and GenBank accession numbers for new sequences generated for this study. Fairchild Tropical Botanical Garden and National Tropical Botanic Garden are abbreviated as FTBG and NTBG respectively.

Pritchardia affinis Becc.-FTBG DNA Bank 1850; CISP4 JF904936, CISP5 JF905062, *matK* JF905351, *ndhF* JF905121, RPB2 JF905197, *trnDT* JF905269. ***P. affinis*** Becc.-FTBG DNA Bank 1851; CISP4 JF904937, CISP5 JF905023, *matK* JF905352, *ndhF* JF905122, RPB2 JF905198, *trnDT* JF905270. ***P. arecina*** Becc.-FTBG DNA Bank 1853; CISP4 JF904938, *matK* JF905353, *ndhF* JF905123, RPB2 JF905199, *trnDT* JF905271. ***P. arecina*** Becc.-*Baker 1183* (K), Royal Botanic Gardens, Kew DNA Bank 15960; CISP4 JF904939, CISP5 JF905024, *matK* JF905354, *ndhF* JF905124, RPB2 JF905200, *trnDT* JF905272. ***P. aylmer-robinsonii*** H.St.John- FTBG DNA Bank 14; CISP4 JF904940, CISP5 JF905025, *matK* JF905355, *ndhF* JF905125, RPB2 JF905201, *trnDT* JF905273. ***P. aylmer-robinsonii*** H.St.John-NTBG Live Collection; CISP4 JF904941, CISP5 JF905026, *matK* JF905356, *ndhF* JF905126, RPB2 JF905202, *trnDT* JF905274. ***P. bakeri*** Hodel-Bacon Pupukea1 SN; CISP4 JF904942, RPB2 JF905203. ***P. bakeri*** Hodel-Bacon Pupukea2 SN; CISP4 JF904943, CISP5 JF905027, RPB2 JF905204. ***P. bakeri*** Hodel-Bacon Pupukea3 SN; CISP4 JF904944. ***P. bakeri*** Hodel-Bacon Pupukea4 SN; CISP4 JF904945. ***P. bakeri*** Hodel-Bacon Kuliouou3 SN; CISP4 JF904989, *matK*

JF905402, MS JF905094, *ndhF* JF905164, *trnDT* JF905316. ***P. bakeri*** Hodel-Bacon Kuliouou5 SN; CISP4 JF904990, *matK* JF905403, MS JF905095, *ndhF* JF905165, *trnDT* JF905317. ***P. bakeri*** Hodel-Bacon Kuliouou8 SN; CISP4 JF904991, *matK* JF905404, MS JF905096, *ndhF* JF905166, RPB2 JF905244, *trnDT* JF905318. ***P. beccariana*** Rock-FTBG DNA Bank 1862; CISP4 JF904946, CISP5 JF905063, *matK* JF905357, *ndhF* JF905127, RPB2 JF905205, *trnDT* JF905275. ***P. beccariana*** Rock-*Wood 8911* (PTBG); CISP4 JF904947, CISP5 JF905028, *matK* JF905358, RPB2 JF905206, *trnDT* JF905276. ***P. elliptica*** Rock & Caum-cultivated 320 Mahana St. Lanai City, Lanai, HI, USA; CISP4 JF904948, *matK* JF905361. ***P. elliptica*** Rock & Caum-cultivated 452 Lanai St. Lanai City, Lanai, HI, USA; CISP4 JF904949, CISP5 JF905029, *matK* JF905362, *ndhF* JF905128, RPB2 JF905207, *trnDT* JF905277. ***P. elliptica*** Rock & Caum-cultivated 712 Puulani St. Lanai City, Lanai, HI, USA; CISP4 JF904950. ***P. elliptica*** Rock & Caum-Oppenheimer SN1, Kunoa Valley; CISP4 JF904951, CISP5 JF905030, *matK* JF905363, *ndhF* JF905129, RPB2 JF905208, *trnDT* JF905278. ***P. elliptica*** Rock & Caum-Oppenheimer SN6, Kunoa Valley; CISP5 JF905031, *matK* JF905359, *ndhF* JF905130, *trnDT* JF905279. ***P. elliptica*** Rock & Caum-Oppenheimer SN7, Kunoa Valley; CISP4 JF904952, CISP5 JF905032, *matK* JF905364, *ndhF* JF905131, *trnDT* JF905280. ***P. elliptica*** Rock & Caum-Oppenheimer SN8, Kunoa Valley; CISP4 JF904953, CISP5 JF905033, *matK* JF905360, RPB2 JF905209. ***P. flynnii*** Lorence & Gemmill-*Wood 12718B* (PTBG); CISP4 JF904954, *matK* JF905366, MS JF905087, RPB2 JF905210. ***P. flynnii*** Lorence & Gemmill-*Wood 12718C* (PTBG); CISP4 JF904955, *matK* JF905365. ***P. flynnii*** Lorence & Gemmill-NTBG Live Collection; CISP4 JF904956, CISP5 JF905034, *matK* JF905367, *ndhF* JF905132, RPB2 JF905211, *trnDT* JF905281. ***P.***

flynnii Lorence & Gemmill-*Tangalin 1476* (PTBG); CISP4 JF904957, *matK* JF905368, MS JF905097, RPB2 JF905212, *trnDT* JF905282. ***P. flynnii*** Lorence & Gemmill-*Tangalin 1478* (PTBG); CISP4 JF904958, CISP5 JF905035, *matK* JF905369, *ndhF* JF905133, RPB2 JF905213, *trnDT* JF905283. ***P. flynnii*** Lorence & Gemmill-*Tangalin 1480* (PTBG); *trnDT* JF905284. ***P. forbesiana*** Rock- FTBG DNA Bank 1798; *matK* JF905370, *ndhF* JF905134, RPB2 JF905214, *trnDT* JF905285. ***P. forbesiana*** Rock-NTBG Live Collection; CISP4 JF904959, CISP5 JF905036, *matK* JF905371, *ndhF* JF905135, RPB2 JF905215, *trnDT* JF905286. ***P. glabrata*** Becc. & Rock-FTBG DNA Bank 824; CISP4 JF904960, CISP5 JF905037, *matK* JF905372, *ndhF* JF905136, RPB2 JF905216. ***P. glabrata*** Becc. & Rock-Oppenheimer SN1; CISP4 JF904961, CISP5 JF905038, *matK* JF905373, RPB2 JF905217, *trnDT* JF905287. ***P. glabrata*** Becc. & Rock-Oppenheimer SN4; CISP4 JF904962, CISP5 JF905039, *matK* JF905374, MS JF905098, *ndhF* JF905137, RPB2 JF905218, *trnDT* JF905288. ***P. glabrata*** Becc. & Rock-Oppenheimer SN5; CISP4 JF904963, CISP5 JF905040, *matK* JF905375, MS JF905099, *ndhF* JF905138, RPB2 JF905219, *trnDT* JF905289. ***P glabrata*** Becc. & Rock-Oppenheimer SN6; CISP4 JF904964, *matK* JF905376, *ndhF* JF905139, RPB2 JF905220, *trnDT* JF905290. ***P. hardyi*** Rock-*Trauernicht 428* (PTBG); CISP4 JF904965, *matK* JF905377, RPB2 JF905221, *trnDT* JF905291. ***P. hardyi*** Rock-*Trauernicht 429* (PTBG); *matK* JF905378, *ndhF* JF905140. ***P. hardyi*** Rock-*Trauernicht 430* (PTBG); CISP4 JF904966, *matK* JF905379, *ndhF* JF905141. ***P. hardyi*** Rock-FTBG DNA Bank 1848; CISP4 JF904967, CISP5 JF905064, *matK* JF905380, MS JF905088, *ndhF* JF905142, RPB2 JF905222, *trnDT* JF905292. ***P. hardyi*** Rock-FTBG DNA Bank 1858; CISP4 JF904968, CISP5 JF905065, *matK* JF905381, MS JF905089, *ndhF* JF905143,

RPB2 JF905223, *trnDT* JF905293. ***P. hardyi*** Rock-*Tangalin 1705* (PTBG); *trnDT* JF905294. ***P. hillebrandii*** Becc.-FTBG DNA Bank 646; CISP4 JF904969, CISP5 JF905041, *matK* JF905382, *ndhF* JF905144, RPB2 JF905224, *trnDT* JF905295. ***P. hillebrandii*** Becc.-FTBG DNA Bank 834; CISP4 JF904970, CISP5 JF905042, *matK* JF905383, *ndhF* JF905145, RPB2 JF905225, *trnDT* JF905296. ***P. kaalae*** Rock-FTBG DNA Bank 835; CISP4 JF904973, CISP5 JF905043, *matK* JF905386, *ndhF* JF905148, RPB2 JF905228, *trnDT* JF905299. ***P. kaalae*** Rock-FTBG DNA Bank 1833; CISP4 JF904971, CISP5 JF905066, *matK* JF905384, *ndhF* JF905146, RPB2 JF905226, *trnDT* JF905297. ***P. kaalae*** Rock-FTBG DNA Bank 1847; CISP4 JF904972, CISP5 JF905067, *matK* JF905385, *ndhF* JF905147, RPB2 JF905227, *trnDT* JF905298. ***P. kahukuensis*** Caum- *Kawelo SN* (BISH); CISP4 JF904974, CISP5 JF905044, *matK* JF905387, *ndhF* JF905149, RPB2 JF905229, *trnDT* JF905300. ***P. lanaiensis*** Becc. & Rock-Bacon 88; CISP4 JF904975, CISP5 JF905045, *matK* JF905388, *ndhF* JF905150, RPB2 JF905230, *trnDT* JF905301. ***P. lanaiensis*** Becc. & Rock-Bacon 126; CISP4 JF904976, CISP5 JF905068, *matK* JF905389, *ndhF* JF905151, RPB2 JF905231, *trnDT* JF905302. ***P. lanaiensis*** Becc. & Rock-FTBG DNA Bank 1845; CISP4 JF904977, CISP5 JF905069, *matK* JF905390, MS JF905100, *ndhF* JF905152, RPB2 JF905232, *trnDT* JF905303. ***P. lanaiensis*** Becc. & Rock-*Perlman 19968* (PTBG); CISP4 JF904978, CISP5 JF905046, *matK* JF905391, *ndhF* JF905153, RPB2 JF905233, *trnDT* JF905304. ***P. lanigera*** Becc.-FTBG DNA Bank 1846; CISP4 JF904979, CISP5 JF905070, *matK* JF905392, MS JF905101, *ndhF* JF905154, RPB2 JF905234, *trnDT* JF905305. ***P. limahuliensis*** H.St.John-FTBG DNA Bank 1831; CISP4 JF904980, *matK* JF905393, MS JF905102, *ndhF* JF905155, RPB2 JF905236, *trnDT* JF905307. ***P. limahuliensis*** H.St.John-NTBG

Live Collection; CISP4 JF904981, CISP5 JF905071, *matK* JF905394, MS JF905103, *ndhF* JF905156, RPB2 JF905235, *trnDT* JF905308. ***P. lowreyana*** Rock ex Becc.-FTBG DNA Bank 1794; CISP4 JF904982, CISP5 JF905072, *matK* JF905395, *ndhF* JF905157, RPB2 JF905237, *trnDT* JF905309. ***P. lowreyana*** Rock ex Becc.-*Wood 9236* (PTBG); CISP4 JF904983, CISP5 JF905047, *matK* JF905396, *ndhF* JF905158, RPB2 JF905238, *trnDT* JF905310. ***P. martii*** (Gaudich.) H.Wendl.- Bakutis Waianae SN1; CISP4 JF904984, CISP5 JF905048, *matK* JF905397, *ndhF* JF905159, RPB2 JF905239, *trnDT* JF905311. ***P. martii*** (Gaudich.) H.Wendl.- Bakutis Waianae SN2; CISP4 JF904985, CISP5 JF905049, *matK* JF905398, MS JF905090, *ndhF* JF905160, RPB2 JF905240, *trnDT* JF905312. ***P. martii*** (Gaudich.) H.Wendl.- Bacon Waiava1; CISP4 JF904988, CISP5 JF905052, *matK* JF905401, *ndhF* JF905163, RPB2 JF905243, *trnDT* JF905315. ***P. martii*** (Gaudich.) H.Wendl.- Bacon Waiava7; CISP4 JF904986, CISP5 JF905050, *matK* JF905399, MS JF905104, *ndhF* JF905161, RPB2 JF905241, *trnDT* JF905313. ***P. martii*** (Gaudich.) H.Wendl.- Bacon Waiava15; CISP4 JF904987, CISP5 JF905051, *matK* JF905400, *ndhF* JF905162, RPB2 JF905242, *trnDT* JF905314. ***P. martii*** (Gaudich.) H.Wendl.- FTBG DNA Bank 1855; CISP4 JF904992, CISP5 JF905073, *matK* JF905405, *ndhF* JF905167, RPB2 JF905245, *trnDT* JF905319. ***P. martii*** (Gaudich.) H.Wendl.- FTBG DNA Bank 1859; CISP4 JF904993, CISP5 JF905074, *matK* JF905406, *ndhF* JF905168, RPB2 JF905246, *trnDT* JF905320. ***P. martii*** (Gaudich.) H.Wendl.-National Tropical Botanical Garden Live Collection; CISP4 JF904994, CISP5 JF905053, *matK* JF905406, *ndhF* JF905169. ***P. minor*** Becc.-*Trauernicht 432* (PTBG); *matK* JF905408. ***P. minor*** Becc.-*Trauernicht 434* (PTBG); CISP4 JF904995, *matK* JF905409, *ndhF* JF905170. ***P. minor*** Becc.-*Trauernicht 435* (PTBG); CISP4 JF904996, *matK* JF905410,

MS JF905105, *ndhF* JF905171, *trnDT* JF905321. ***P. minor*** Becc.-FTBG DNA Bank 1797; CISP4 JF904997, CISP5 JF905075, *matK* JF905411, *ndhF* JF905172, RPB2 JF905247, *trnDT* JF905322. ***P. minor*** Becc.-FTBG DNA Bank 845; CISP4 JF904998, CISP5 JF905054, *matK* JF905412, *ndhF* JF905173, RPB2 JF905248, *trnDT* JF905323. ***P. minor*** Becc.- -*Tangalin 1708* (PTBG); *trnDT* JF905324. ***P. mitiaroana*** J.Drans. & Y.Ehrh.-FTBG DNA Bank 1857; CISP4 JF904999, CISP5 JF905076, *matK* JF905413, MS JF905091, *ndhF* JF905174, RPB2 JF905249, *trnDT* JF905325. ***P. mitiaroana*** J.Drans. & Y.Ehrh.-*Perlman 19346* (PTBG); CISP4 JF905000. ***P. munroi*** Rock-FTBG DNA Bank 1832; CISP4 JF905001, CISP5 JF905077, *matK* JF905414, *ndhF* JF905175, RPB2 JF905250, *trnDT* JF905326. ***P. munroi*** Rock-FTBG DNA Bank 841; CISP4 JF905002, CISP5 JF905055, *matK* JF905415, *ndhF* JF905176, RPB2 JF905251, *trnDT* JF905327. ***P. napaliensis*** H.St.John-FTBG DNA Bank 1860; CISP4 JF905003, CISP5 JF905078, *matK* JF905416, MS JF905106, *ndhF* JF905177, RPB2 JF905268, *trnDT* JF905328. ***P. napaliensis*** H.St.John-*Wood 9087* (PTBG); CISP4 JF905004, CISP5 JF905056, *matK* JF905417, MS JF905092, *ndhF* JF905178, *trnDT* JF905329. ***P. pacifica*** Seem. & H.Wendl.-FTBG DNA Bank 18; CISP4 JF905005, CISP5 JF905079, *ndhF* JF905179, RPB2 JF905252, *trnDT* JF905330. ***P. pacifica*** Seem. & H.Wendl.-FTBG DNA Bank 1861; CISP5 JF905080, *matK* JF905418, MS JF905107, *ndhF* JF905180, RPB2 JF905253, *trnDT* JF905331. ***P. pericularum*** H.Wendl. ex Becc.-Meyer SN; CISP4 JF905006, CISP5 JF905057, *matK* JF905419, MS JF905108, *ndhF* JF905181, RPB2 JF905254, *trnDT* JF905332. ***P. perlmanii*** Gemmill-*Wood 7331* (PTBG); CISP4 JF905007, *matK* JF905421, MS JF905109, *ndhF* JF905183, *trnDT* JF905333. ***P. perlmanii*** Gemmill-*Wood 8091* (PTBG); CISP4 JF905008, CISP5 JF905058, *matK*

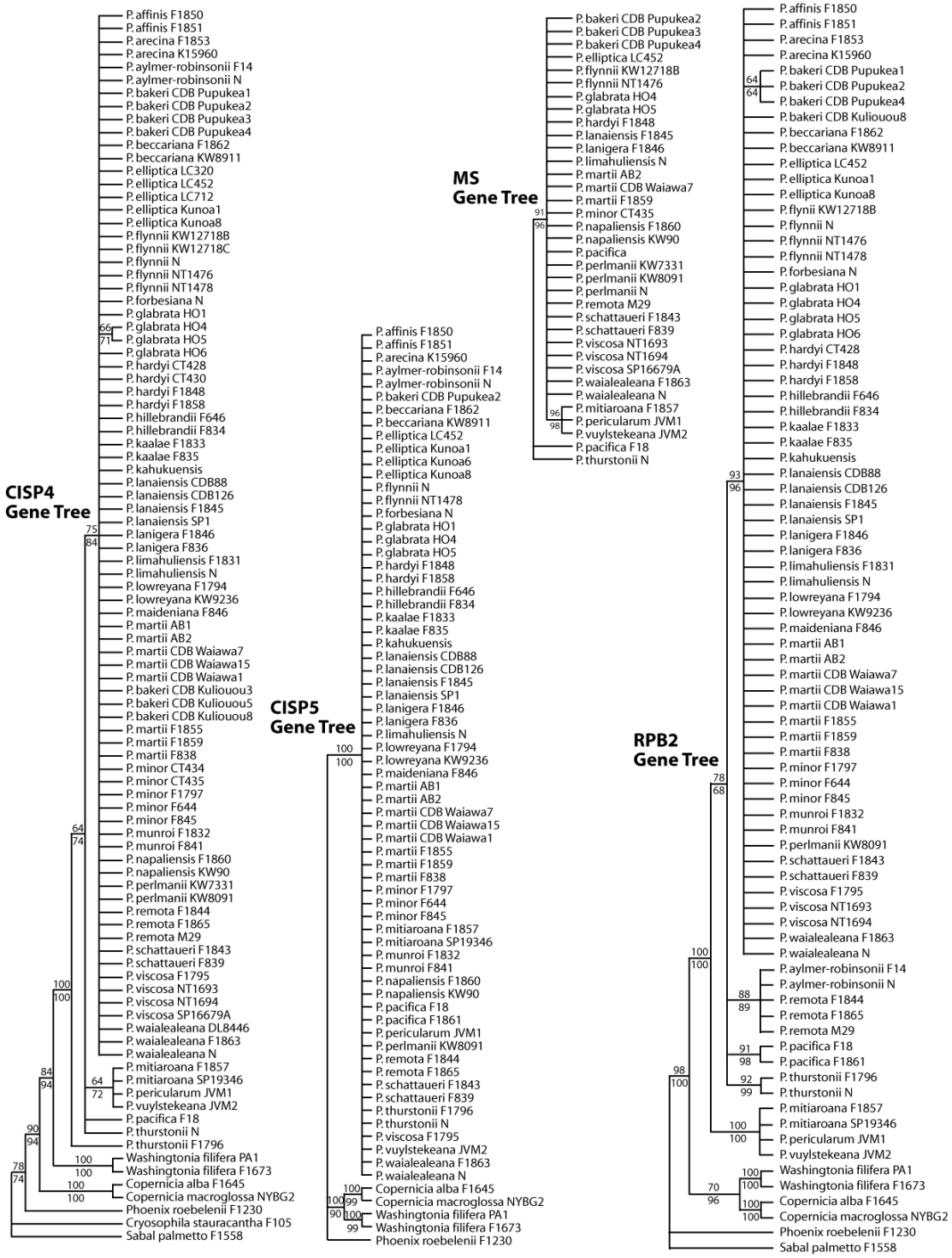
JF905422, MS JF905110, *ndhF* JF905184, RPB2 JF905255, *trnDT* JF905334. ***P. perlmanii*** Gemmill-NTBG Live Collection; *matK* JF905420, MS JF905111, *ndhF* JF905182, *trnDT* JF905335. ***P. remota*** (Kuntze) Becc.-FTBG DNA Bank 1844; CISP4 JF905009, CISP5 JF905081, *matK* JF905423, *ndhF* JF905185, RPB2 JF905256, *trnDT* JF905336. ***P. remota*** (Kuntze) Becc.-FTBG DNA Bank 1865; CISP4 JF905010, CISP5 JF905082, *matK* JF905424, *ndhF* JF905186, RPB2 JF905257, *trnDT* JF905337. ***P. remota*** (Kuntze) Becc.-Montgomery Botanical Center Live Collection 29; CISP4 JF905011, *matK* JF905425, MS JF905112, RPB2 JF905258, *trnDT* JF905338. ***P. schattaueri*** Hodel-FTBG DNA Bank 1843; CISP4 JF905012, CISP5 JF905083, *matK* JF905426, MS JF905113, *ndhF* JF905187, RPB2 JF905259, *trnDT* JF905339. ***P. schattaueri*** Hodel-FTBG DNA Bank 839; CISP4 JF905013, CISP5 JF905059, *matK* JF905427, MS JF905114, *ndhF* JF905188, RPB2 JF905260, *trnDT* JF905340. ***P. thurstonii*** F.Muell. & Drude-NTBG Live Collection; CISP4 JF905014, CISP5 JF905060, *matK* JF905428, MS JF905115, *ndhF* JF905189, RPB2 JF905261, *trnDT* JF905341. ***P. viscosa*** Rock-FTBG DNA Bank 1795; CISP4 JF905015, CISP5 JF905084, *matK* JF905429, *ndhF* JF905190, RPB2 JF905262, *trnDT* JF905342. *matK* JF905430, *ndhF* JF905191. ***P. viscosa*** Rock-*Tangalin 1693* (PTBG); CISP4 JF905016, *matK* JF905431, MS JF905116, RPB2 JF905263, *trnDT* JF905343. ***P. viscosa*** Rock-*Tangalin 1694* (PTBG); CISP4 JF905017, *matK* JF905432, MS JF905117, RPB2 JF905264, *trnDT* JF905344. ***P. viscosa*** Rock-*Perlman 16679A* (PTBG); CISP4 JF905018, *matK* JF905433, MS JF905093, *ndhF* JF905192, *trnDT* JF905345. ***P. vuylstekeana*** H.Wendl.-Meyer SN; CISP4 JF905019, CISP5 JF905085, *matK* JF905434, MS JF905118, *ndhF* JF905193, RPB2 JF905265, *trnDT* JF905346. ***P. waialealeana*** Read-*Trauernicht 423* (PTBG);

matK JF905436, *trnDT* JF905347. ***P. waialealeana*** Read-*Lorence 8446* (PTBG); CISP4 JF905021, *matK* JF905435, *ndhF* JF905194, *trnDT* JF905348. ***P. waialealeana*** Read-FTBG DNA Bank 1863; CISP4 JF905020, CISP5 JF905086, *matK* JF905437, MS JF905119, *ndhF* JF905195, RPB2 JF905266, *trnDT* JF905349. ***P. waialealeana*** Read-NTBG Live Collection; CISP4 JF905022, CISP5 JF905061, *matK* JF905438, MS JF905120, *ndhF* JF905196, RPB2 JF905267, *trnDT* JF905350.

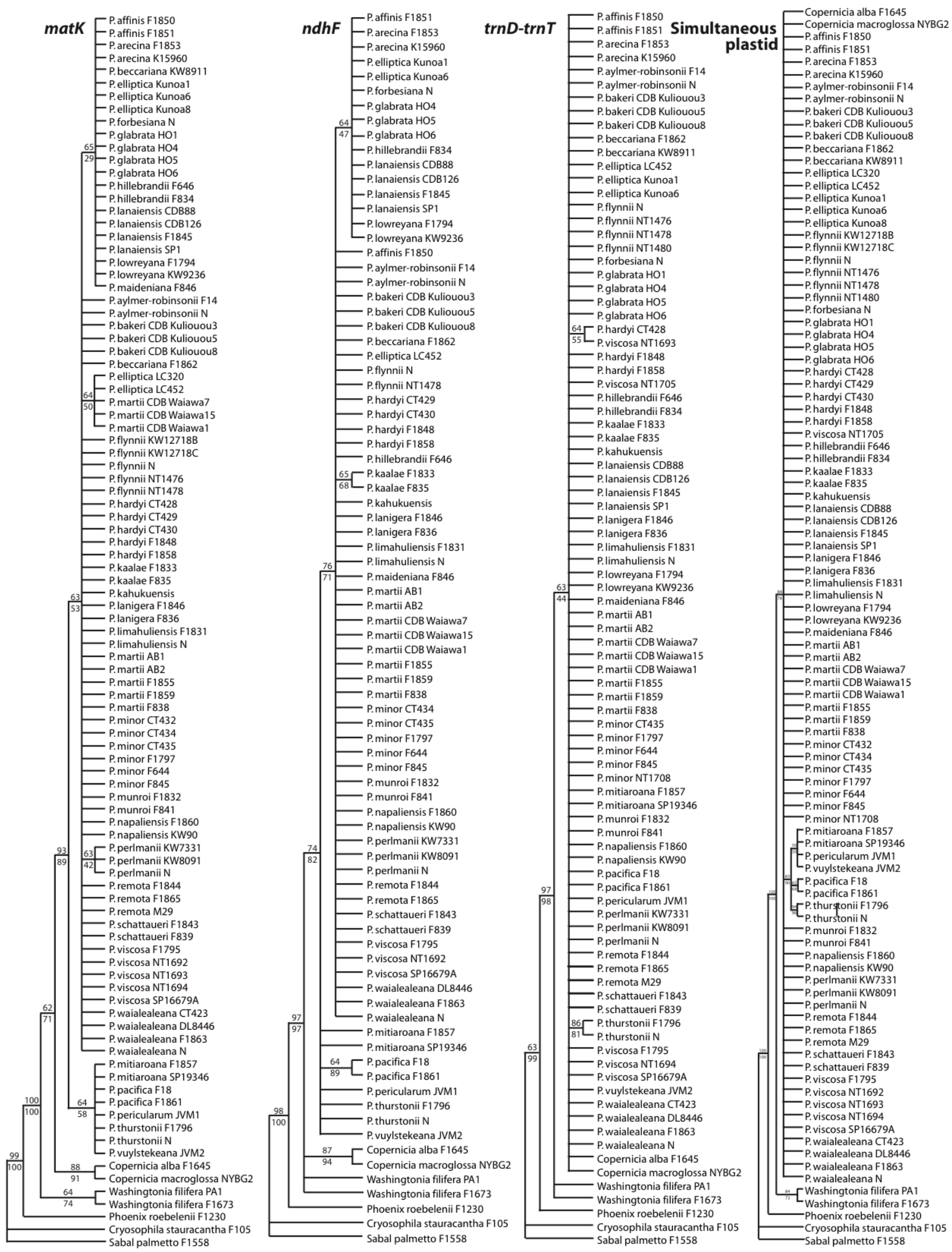
Appendix 2. List of the *Pritchardia* morphological characters that were included in analysis 2. Characters states were identified from herbarium specimens at BISH, NY, PTBG, and US and derived from the most recent review of the genus (Hodel 2007).

Character	Character State
1. Hastula shape	0 = rounded
	1 = triangular, apiculate
2. Degree of panicle branching	0 = two orders
	1 = three orders
3. Inflorescence length	0 = shorter than petioles
	1 = equal
	2 = longer than petioles
4. Petiole fiber density	0 = scare to moderate
	1 = abundant
5. Abaxial leaf blade folds	0 = glaucous
	1 = cottony, mealy indumentum
6. Abaxial leaf blade cover	0 = green
	1 = silvery-gray
7. Leaf blade shape	0 = nearly circular
	1 = diamond
8. Leaf blade with waxy, glaucous bloom	0 = absent
	1 = present
9. Leaf blade surface	0 = flat
	1 = nearly flat, undulate
10. Leaf tips	0 = drooping
	1 = stiff
11. Lepidia density	0 = absent
	1 = incompletely covered
	2 = completely covered
12. Rachillae tomentum	0 = glabrous
	1 = velutinous
	2 = floccose, lanate
13. Rachillae viscosity	0 = absent
	1 = present
14. Style - ovary ratio	0 = equal
	1 = style longer
	2 = style shorter
15. Outer calyx venation	0 = absent
	1 = conspicuous
	2 = present near opening with finer lines
16. Calyx indumentum	0 = glabrous
	1 = tomentose
	2 = viscous

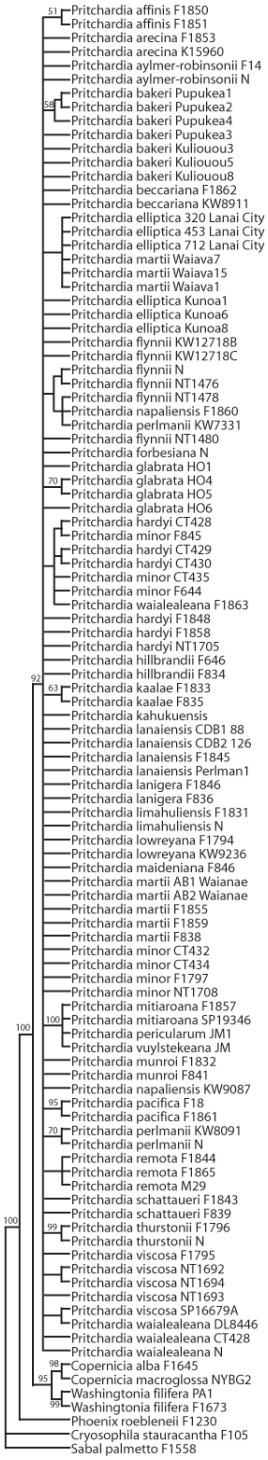
17. Fruit ridges	0 = absent
	1 = present
18. Fruit shape	0 = globose
	1 = ellipsoid
	2 = ovoid
	3 = obovoid
	4 = oblate
19. Fruit length	0 = < 3cm
	1= > 3cm



Supplemental Figure 1. The individual nuclear gene trees estimated for *Pritchardia* species delimitation as shown in the parsimony strict consensus with parsimony jackknife values above and likelihood bootstrap values below each branch.



Supplemental Figure 2. The individual plastid gene trees and the plastid simultaneous-analysis estimated for *Pritchardia* species delimitation as shown in the parsimony strict consensus with jackknife branch support values above and bootstrap values below each branch.



Supplemental Figure 3. Simultaneous analysis parsimony strict consensus tree of all the 105 terminals sampled for nucleotide data with parsimony jackknife values shown.