



Phylogenetics of Iriarteeae (Arecaceae), cross-Andean disjunctions and convergence of clustered infructescence morphology in *Wettinia*

CHRISTINE D. BACON^{1,2,*}, FRANCISCO VELÁSQUEZ-PUENTES², ALEXANDER FLÓREZ-RODRÍGUEZ^{2,3}, HENRIK BALSLEV⁴, GLORIA GALEANO⁵, RODRIGO BERNAL⁵ and ALEXANDRE ANTONELLI^{1,6}

¹Department of Biological and Environmental Sciences, University of Gothenburg, Box 461, SE-405 30 Göteborg, Sweden

²Laboratorio de Biología Molecular CINBIN, Universidad Industrial de Santander, Bucaramanga, Santander, Colombia

³Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

⁴Ecoinformatics and Biodiversity Group, Department of Bioscience, Aarhus University, Ny Munkegade 116, Build 1540, 8000 Aarhus C, Denmark

⁵Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, Colombia

⁶Gothenburg Botanical Garden, Carl Skottsbergs gata 22A, SE-41319 Göteborg, Sweden

Received 23 September 2015; revised 1 February 2016; accepted for publication 28 February 2016

The Neotropical palm tribe Iriarteeae is ubiquitous in several lowland and montane biomes across northern South America, but the phylogenetic relationships among genera and species remain unresolved. A well resolved phylogenetic tree is key to exploring morphological evolution in the tribe, including striking features such as the complex and unique inflorescence structures in *Wettinia*. We generated data from five plastid (*ndhA*, *petD-rpoA*, *psbK-trnS* and *trnG*) and six nuclear (AG1, CISP4 and 5, PRK, RPB2 and WRKY21) molecular loci to infer the phylogeny. We explored the evolutionary patterns of trait evolution using the D statistic and stochastic character mapping. All genera were inferred as monophyletic and their relationships were recovered with strong to moderate support. Based on these results we synonymize the two species of *Iriartella* under *I. setigera* and resurrect *Socratea montana* from *S. rostrata*. Interspecific relationships were mostly consistent with current morphological classification. One exception concerns trait evolution in *Wettinia*, in which the clustered infructescence was found to have evolved at least four times. Phylogenetic signal for this trait was weak and randomly distributed across the tree, probably representing convergence. Our results provide a robust phylogenetic framework for Iriarteeae, largely corroborating current morphological classification and laying the groundwork for macroevolutionary studies in the tribe. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, 182, 272–286

ADDITIONAL KEYWORDS: Andes – character evolution – infructescence – Neotropics – palms – South America.

INTRODUCTION

The Neotropical tribe Iriarteeae (Arecaceae) comprise medium to large palms (up to 25 m) found across northwestern South America and southern Central

America. Species in the tribe are ubiquitous in the rain forests of western Amazonia, the Pacific lowlands of Colombia and Ecuador and the northern Andes and some of its species are dominant elements in these forests (Galeano & Bernal, 2010). *Iriartea deltoidea* Ruiz & Pav. and *Socratea exorrhiza* (Mart.) H.Wendl. have the widest distributions in the tribe

*Corresponding author. E-mail: christinedbacon@gmail.com

and are found from Central America and the Chocó in the west to the Amazon and Guiana Shield in the east. Furthermore, these two species are the fifth and ninth most abundant species in the Amazonian tree flora (ter Steege *et al.*, 2013), suggesting a fundamental importance in forest structure and function. In terms of aboveground woody biomass, *I. deltoidea* is the tenth most dominant species in Amazonia (Fauset *et al.*, 2015). Despite these examples of hyperdominance, the tribe also includes rare and narrowly distributed highland species, particularly in *Wettinia* Poepp. ex Endl., with *W. lanata* R.Bernal and *W. microcarpa* (Burret) R.Bernal, having ranges of < 6000 km² (Galeano & Bernal, 2010).

Iriarteeae are easily recognized based on their distinctive stilt roots and crownshafts (Dransfield *et al.*, 2008). The tribe comprises five genera and has been resolved as monophyletic in all phylogenetic studies to date (Hahn, 2002a, b; Lewis & Doyle, 2002; Baker *et al.*, 2009). Despite the unequivocal support for the Iriarteeae as a natural group, the relationships among the genera remain controversial (Henderson, 1990; Asmussen *et al.*, 2006; Baker *et al.*, 2009). Based on a phylogenetic analysis of 17 morphological characters scored at the generic level, Henderson (1990) proposed *Iriartea* and *Dictyocaryum* H.Wendl. as sister lineages, making up a clade that is sister to *Wettinia* + *Socratea* H.Karst, with *Iriartella* H.Wendl. as the early divergent genus of the tribe. Analyses of morphological and molecular data found either a lack of variation or incongruence among topologies. For example, based on four plastid markers Asmussen *et al.* (2006) resolved only a sister relationship between *Iriartella* and *Wettinia* and with low bootstrap support (77%). The most complete generic palm phylogenetic analysis to date (Baker *et al.*, 2009) also lacked support for intergeneric relationships in the tribe, but resolved *Iriartea* and *Wettinia* as sister genera that together are resolved in a polytomy with *Iriartella* and *Socratea*, with *Dictyocaryum* as the earliest divergent genus in the tribe. Taken together, these previous studies highlight the need for a comprehensive assessment of generic relationships in Iriarteeae. Furthermore, the monophyly of each genus has never been tested and interspecific relationships have not been explored.

Patterns of morphological evolution remain to be explored in Iriarteeae, once a robust phylogenetic framework is established. For example, pistillate inflorescences in some *Wettinia* spp. have short and thick branches, which results in flowers and fruits that are densely packed along the rachillae, with the pistils and fruits variously angled as a result of mutual physical pressure. For inflorescences that are unbranched, as in *W. augusta* Poepp. & Endl., *W. hirsuta* Burret and *W. longipetala* A.H.Gentry, or have

few branches along a short rachis, as in *W. maynensis* Spruce and *W. quinaria* (O.F.Cook & Doyle) Burret, the resulting infructescence consists of one to few long, cylindrical branches densely packed with obpyramidal fruits (Fig. 1). Conversely, for infructescences with many branches along an elongate rachis, as in *W. castanea* H.E.Moore & J.Dransf., *W. fascicularis* (Burret) H.E.Moore & J.Dransf., *W. oxycarpa* Galeano-Garcés & R.Bernal and *W. verruculosa* H.E.Moore, the resulting infructescence is a single large, compact, ellipsoid mass, in which many inner fruits are deeply buried by the outer ones. Both types of infructescences with tightly packed fruits (few branches along a short rachis and many branches along a long rachis) have congeners with loosely arranged fruits and thinner rachillae [*W. aequatorialis* R.Bernal, *W. anomala* (Burret) R.Bernal, *W. disticha* (R.Bernal) R.Bernal, *W. drudei* (O.F.Cook & Doyle) A.J.Hend., *W. aequalis* (O.F.Cook & Doyle), R.Bernal, *W. kalbreyeri* (Burret) R.Bernal, *W. lanata*, *W. microcarpa*, *W. praemorsa* (Willd.) Wess.Boer and *W. radiata* (O.F.Cook & Doyle) R.Bernal].

Despite various alternative explanations for morphological variation (e.g. phylogenetic signal, character displacement, random phenotypic drift, convergence), a recent study in palms (Roncal *et al.*, 2012) showed there is no correlated phylogenetic signal among traits in *Geonoma* Willd., suggesting that character variation is due to random drift or convergence. Iriarteeae and *Geonoma* are in the same subfamily (Arecoideae) and share similar Amazonian and Andean distributions. Therefore we hypothesize that, similar to traits in *Geonoma*, the phylogenetic signal would be weak in infructescence morphology in *Wettinia* and that convergence may drive morphological patterns. Infructescence morphology may also be plastic in that it may undergo rapid shifts depending on ecological requirements. In this study we infer a molecular phylogeny for Iriarteeae based on 11 loci from the plastid and nuclear genomes. We use the phylogenetic framework to explore intergeneric and interspecific relationships and morphological evolution.

MATERIAL AND METHODS

SAMPLING

Eighty-nine individuals were sampled including seven outgroups: *Aphandra natalia* (Balslev & A.J.Hend.) Barfod, *Astrocaryum murumuru* Mart., *Chamaedorea tepejilote* Liebm., *Hyospathe macrorhachis* Burret, *Mauritia flexuosa* L.f., *Nypa fruticans* Wurbm., and *Serenoa repens* (W.Bartram) Small; (Appendix 1). Our outgroup sampling represents all tribes of subfamily Arecoideae and exemplars from

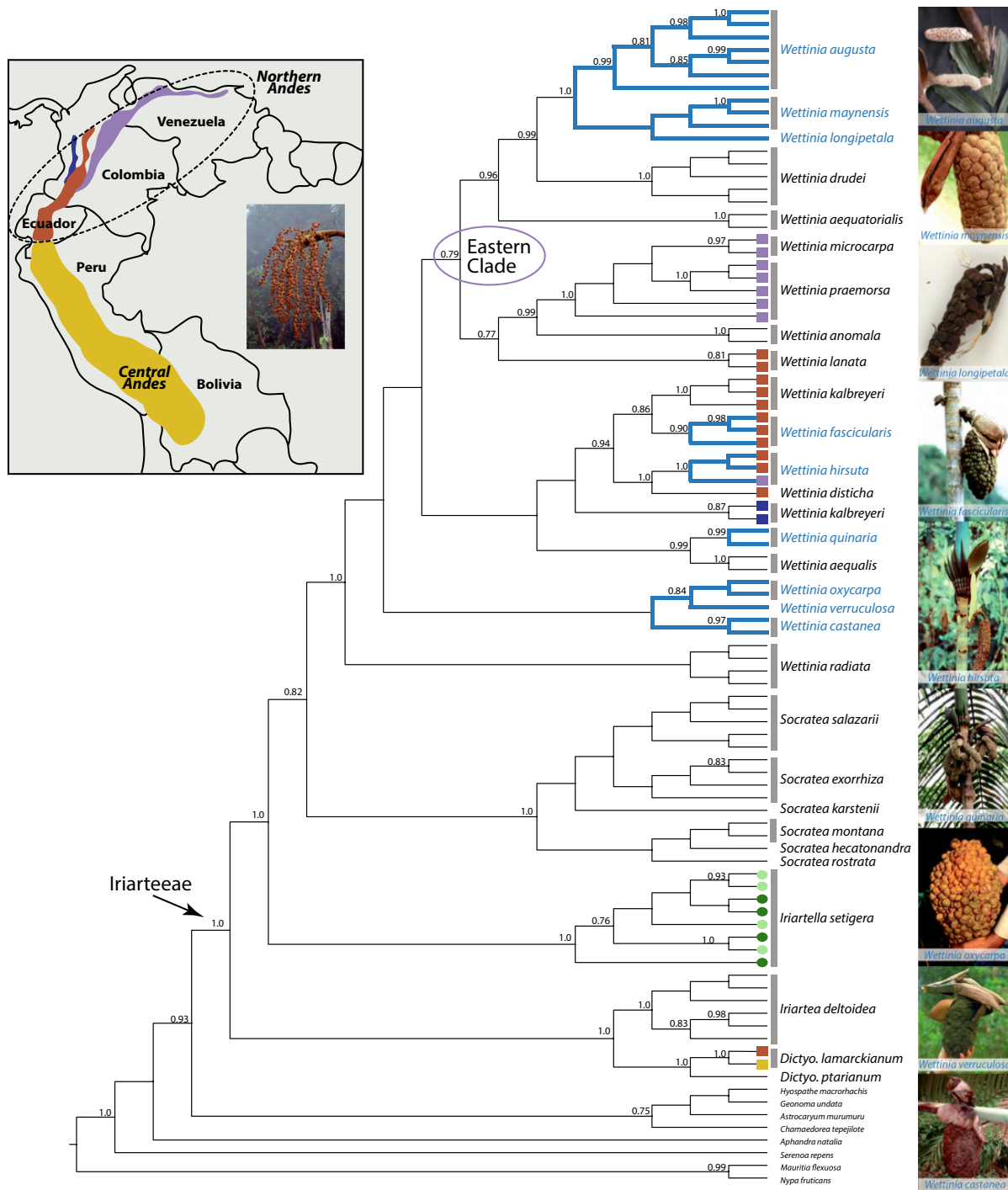


Figure 1. Phylogenetics of the palm tribe Iriarteae estimated using Bayesian inference implemented in BEAST. Clade support > 0.75 (Bayesian posterior probability) is displayed to the upper left of each node. Species are indicated with a grey bar when multiple individuals were sampled and those with a tightly packed infructescence are shown in blue font and branches. The insert map shows the location of the central and northern Andes and the three cordilleras of the northern Andes, in which dark blue is the western, orange is the central and purple is the eastern Cordillera. Andean taxa are indicated with squares at tips with colours reflecting in which Cordillera they occur. A loosely arranged infructescence of *Wettinia disticha* is shown to contrast with the tightly packed morphology, which is shown to the right of the tree. *Dictyocaryum* is abbreviated *Dictyo.* and light and dark green circles represent individuals of *Iriartella setigera* and *I. stenocarpa*, respectively.

the other subfamilies of palms (Dransfield *et al.*, 2005). We sampled *c.* 94% of all described species of Iriarteae (29 out of 31, following the nomenclature of Galeano & Bernal, 2010) and to capture the geographical range and genetic variation within species, more than one individual per species was sampled for all but five species.

Total genomic DNA was extracted from silica-gel-dried leaves following the protocol described by Alexander *et al.* (2006). New sequences for five plastid loci [*ndhA*, *petD-rpoA*, *psbK-trnS* and *trnG* (Scarcelli *et al.*, 2011) and *trnD-trnT* (Hahn, 2002b)] and six nuclear loci [AG1 (Ludena *et al.*, 2011), CISP4 and CISP5 (Bacon *et al.*, 2008), PRK (Lewis & Doyle, 2002), RPB2 (Roncal *et al.*, 2005) and WRKY21 (Mauro-Herrera *et al.*, 2006)] were generated. All 11 loci were amplified following the PCR protocol in the original publications. Amplified products were purified using Qiagen PCR purification kits and sequenced at Macrogen (Korea). The same primers used for PCR were also used for sequencing. All new sequences generated in this study were deposited in GenBank under accession numbers KJ540542 to KJ540615 (Appendix 1).

PHYLOGENETIC ANALYSIS

Nucleotide alignments were obtained independently for each of the 11 loci using default parameters in MUSCLE v3.6 (Edgar, 2004). Manual adjustments to the MUSCLE alignments were performed in Geneious (Biomatters, New Zealand) using the procedure outlined by Simmons (2004), following Zurawski & Clegg (1987). The Akaike information criterion (Akaike, 1974) as implemented in jModeltest v0.1.1 (Posada, 2008) was used to select the best-fit model for each data partition. The nuclear data were partitioned by locus to allow for variation in substitution models and due to the inherent linkage of plastid loci, they were treated as a single locus and analysed as a single partition separate from the nuclear genes in BEAST v. 1.8.1 (Drummond *et al.*, 2012). Effective sample sizes (ESS) values for all parameter values exceeded 200 and most relationships were well supported across the phylogenetic tree. The analysis was run using an uncorrelated lognormal 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 100 million generations and repeated three times to test for Markov chain Monte Carlo chain convergence and to ensure that ESS exceeded 200. After verifying that chains had reached stationarity in Tracer v. 1.5, 50% of the posterior distribution of trees was removed as burn-in and BEAST log files were combined in

LogCombiner v. 1.8.1. The remaining tree files were combined to estimate mean node height and the 95% highest posterior density (HPD) in TreeAnnotator v. 1.8.1. The data matrix is available from TreeBase (study accession 18196).

A coalescent species tree analysis in *BEAST (Heled & Drummond, 2010) was initially attempted on the dataset, but results never converged. There are an accumulating number of studies showing that coalescent methods fail for moderately sized datasets (e.g. Bayzid & Warnow, 2013) and/or for studies at deeper phylogenetic levels (Gatsey & Springer, 2014). Furthermore, despite the recent popularity of species tree analysis, parameter space for 89 individuals across 11 genes in seven partitions scaling > 50 Myr, such as for our data for Iriarteae, is quite large for accurate estimation based on two to three individuals per species (Knowles, 2010). Following these analytical shortcomings and Gatsey & Springer (2014), we therefore considered the concatenation approach as appropriate here, under the expectation that the phylogenetic information in the data should overcome noise associated with incomplete lineage sorting and introgression.

INFRUCTESCENCE EVOLUTION

We investigated the evolution of infructescence types in *Wettinia* by first assessing its phylogenetic signal and then reconstructing ancestral states along the phylogenetic tree. For both analyses, the tree was reduced to one individual per species using a drop random tip function in the R package Phytools v. 0.3-72 (Revell, 2012). To determine the degree of phylogenetic signal we used the D statistic (Fritz & Purvis, 2010), a measure of phylogenetic signal for binary traits based on the sum of sister clade differences in a given phylogenetic tree. The D statistic value will be low (approaching or below 0) for clustered, phylogenetically informative traits and high (approaching or exceeding 1) for phylogenetically labile, strongly overdispersed traits. We computed the distribution of D values for a set of 10 000 *Wettinia* phylogenetic trees from the Bayesian posterior sample and used 1000 permutations to estimate the significance of D on each tree. We then compared this empirical distribution with two alternative distributions: one describing the sister clade differences computed under a random phylogenetic pattern (obtained by shuffling the tips of the tree) and one obtained after simulating traits under a Brownian motion threshold model (keeping the same trait prevalence as seen in the observed data). Trait evolution under Brownian motion will cause related species to have similar trait values, more than expected by chance (e.g. Harvey & Pagel, 1991). We performed

these analyses in the R package *caper* v. 0.5.2 (Orme *et al.*, 2013) using the function ‘*phylo.d*’ to calculate D and test the departure of empirical data from the alternative distributions as described above.

We reconstructed the evolution of infructescence type across the *Wettinia* phylogenetic tree, which was reduced to one individual per species to account for interspecific dynamics and avoid bias from intraspecific sampling. We coded infructescence shape as 1 (tightly packed morphology) and 0 (loosely arranged morphology) from field observations. We used stochastic character mapping (Bollback, 2006) as implemented in Phytools using the function ‘*make.simmap*’. The values for the rate of change matrix (*Q*) were estimated from the data and the most likely values were used in all simulations. We applied an empirical method to estimate ancestral characters and their rate of change across the tree using the ER (equal rates) and the ARD (all rates different) models. To estimate credible intervals for the estimates we performed 1000 stochastic ancestral state reconstructions. A likelihood ratio test and resulting AIC scores were used to find the model (ER or ARD) that best fit the data.

RESULTS

INTERGENERIC RELATIONSHIPS

Our results show strong support for the monophyly of Iriarteeae [1.0 posterior probability (PP)], all intergeneric relationships (> 0.82 PP) and the monophyly of each genus in the tribe (1.0 PP; Fig. 1). The relationships suggested by molecular phylogenetic analyses of Asmussen *et al.* (2006) and Baker *et al.* (2009) were not supported by our data. Phylogenetic relationships among sister genera were consistent with the morphological analysis by Henderson (1990), but clades resolved different deeper relationships (e.g. the topological position of *Iriartella* in the tribe). We reconstructed *Socratea* and *Wettinia* as sister groups (0.82 PP), a relationship that Henderson (1990) also found based on the asymmetrical and triangular staminate flowers and sepals shared by those genera. *Iriartella* was found to be sister to *Socratea* + *Wettinia* with strong support (1.0 PP). Henderson (1990) recognized that *Iriartella* was difficult to place in the tribe, noting its morphological, palynological and anatomical distinctiveness. The early divergent clade (1.0 PP) in our phylogenetic tree is the sister group formed by *Dictyocaryum* + *Iriartea* (1.0 PP). Various morphological characters are shared between these sister genera, including inflorescences branched to two orders, the absence of the prophyll at anthesis, nine to 15 peduncular bracts, gibbous staminate sepals and globose fruits (Henderson, 1990).

EVOLUTION OF INFRACTESCENCE MORPHOLOGY

We found that the tightly packed form of infructescences in *Wettinia* evolved four times across the tree (Fig. 2). The observed D values across the set of trees showed a majority of positive D values (99.98%) with a mean of 0.7, indicating low phylogenetic signal (Fig. 2A). In addition, the departure of D from 1 (random expectation) was non-significant for 100% of the trees ($P > 0.05$), whereas the test of departure of D from 0 (clumping) was significant only for 1.28% of the trees ($P < 0.05$) and non-significant for 98.72% of the trees ($P > 0.05$). Although the ER model of trait evolution had the lowest likelihood (−13.044), it was not significantly better than the fit of the ARD model (−12.843) according to the likelihood ratio test. The AIC test between the models favoured the ER model, which scored lower than the ARD model (28.088 vs. 29.687). Given that the ER model is less parameterized and has lower scores (for likelihood and AIC), we chose this model to best represent the rate of trait evolution (Fig. 2B).

TAXONOMIC TREATMENT

TAXONOMIC TREATMENT OF *IRIARTELLA*

Iriartella setigera (Mart.) H.Wendl., Bonplandia 8: 104. 1860. Basionym: *Iriartea setigera* Mart., Hist. Nat. Palm. 2(2): 39, t. 37. 1824. Lectotype (Moore, 1963). Brazil. Amazonas: Rio Japurá, Feb 1820, Martius s.n. (lectotype, M; syntype, M).

Homotypic synonym

Iriartella setigera var. *pruriens* Barb. Rodr. Sert. Palm. Brasil. 1: 18. 1903. *Iriartella pruriens* (Barb. Rodr.) Barb. Rodr. Sert. Palm. Brasil. 2: 102. 1903.

Heterotypic synonyms

Iriartea spruceana Barb. Rodr., Enum. Palm. Nov. 13. 1875 (‘spruciana’); Type. Brazil. Amazonas: Rio Taruma, nr. Manaus, n.d., Barbosa Rodrigues 346 (destroyed). Lectotype (Henderson, 1990): Barbosa Rodrigues, Sert. Palm. Brasil. 1, t. 7. 1903. *Iriartella spruceana* (Barb. Rodr.) Barb. Rodr., Sert. Palm. Brasil. 1: 18. 1903. *Cuatrecasea spruceana* (Barb. Rodr.) Dugand, Caldasia 2: 72. 1943.

Cuatrecasea vaupesana Dugand, Revista Acad. Colomb. Ci. Exact. 3: 392. 1940. Type. Colombia. Vaupes: Mitú, 200 m, 21 Sep 1939, J. Cuatrecasas 6937 (holotype, COL).

Iriartella stenocarpa Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11: 233.1931. Type. Peru. Loreto: Mouth of Río Napo nr. Río Amazonas, Mar 1931, Hopp 1110 (holotype, B), **Syn. Nov.**

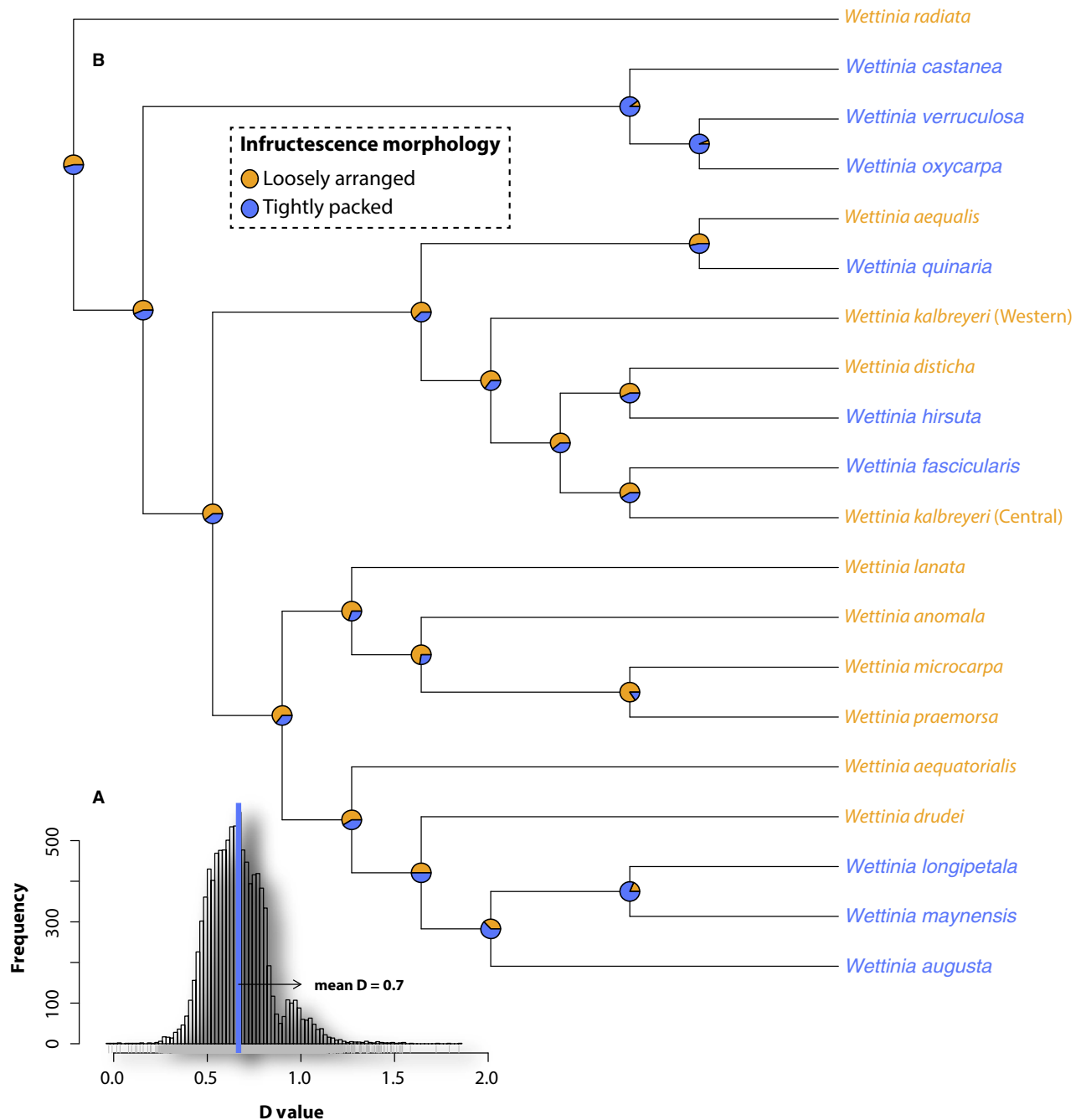


Figure 2. Trait evolution in *Wettinia* infructescences, where pie charts show the probability of each state at ancestral nodes. A, Distribution of the D statistic showing the mean in blue, indicating that infructescence type is not constrained phylogenetically. B, Stochastic mapping showing at least four instances of shifts from loosely arranged to tightly packed infructescence in *Wettinia*.

Iriartella ferreyrae H.E.Moore, Gentes Herb. 9: 278. Fig. 197. 1963. Type. Peru. Ucayali: Province Coronel Portillo, Pampas de Sacramento, a few km Sw of Yurac on road to Boquerón del Padre Abad between Divisoria and Aguaytía, c. 400 m, 28 Apr 1960, Moore *et al.* 8367 (holotype, BH; isotype, USM).

KEY TO THE ROSTRATE-FRUITED *SOCRATEA* SPECIES

- 1 Stilt roots forming a cone to 2 m tall. Pinnae brown abaxially with proximal segments stiff, appearing in four planes. Lowland rainforest of the Chocó region in western Colombia and Ecuador, from sea level to 750 m *S. hecatonandra*

- 2 Stilt roots forming a cone usually more than 2 m tall (up to 5 m tall). Pinnae green abaxially with proximal segments stiff or pendulous 2
- 3 Crownshaft bluish grey. Infructescence with peduncle 2.0–2.5 cm wide at the apex and rachillae 5–8 mm in diam. Eastern slopes of the Andes, from southern Colombia to Peru, between 300 to 1900 m. *S. rostrata*
- 4 Crownshaft grass green. Infructescence with peduncle 4–5 cm wide at the apex and rachillae 15–20 mm in diam. Cloud forests between 800 and 1800 m on the western slopes of the Western Cordillera in Colombia and northern Ecuador *S. montana*

Socratea montana R.Bernal & A.J.Hend., Brittonia 38: 55–56, fig. 1. 1986. Type. Colombia. Antioquia: Mun. Frontino, rd. from Nutibara to La Blanquita, western slope, 1800 m, 2 Jul 1983, Bernal *et al.* 631 (holotype, COL; isotypes, HUA, NY).

Socratea rostrata Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15: 31. 1940. Type. Ecuador. Pastaza: Mera, c. 1000 m, 11 Sep 1938, Schultze-Rhonhof 2805 (holotype, B).

DISCUSSION

Our molecular phylogenetic analysis for Iriarteae inferred robust intergeneric relationships, which are mostly consistent with the previous morphological revision (Henderson, 1990) but also show novel relationships. Strong branch support across the tree allowed for hypothesis testing of the evolution of infructescence types in *Wettinia*. Like previous studies in palms (Roncal *et al.*, 2012), we found that the tightly packed morphology did not have strong phylogenetic signal, leading to convergence across the tree.

DICTYOCARYUM AND IRIARTEA: SISTER TAXA

The sister relationship between *Dictyocaryum* and *Iriartea* (Fig. 1) reflects well their overall morphological similarity, since they mainly differ by the width of their leaf segments and the colour of the undersurfaces (Henderson, 1990). *Dictyocaryum* also occurs at higher elevations than *Iriartea*, with *Dictyocaryum lamarckianum* (Mart.) H.Wendl. replacing *Iriartea deltoidea* in the Andean elevation gradient above 1000–1300 m (Henderson, Galeano & Bernal, 1995; Borchsenius & Skov, 1997; Galeano & Bernal, 2010). Although we could not obtain material for *D. fuscum*, the Venezuelan Andes endemic, we were able to establish monophyly for the other two species recognized, *D. lamarckianum* and *D. ptarianum* (Steierm.) H.E.Moore & Steierm. (1.0 PP). The

monotypic *I. deltoidea* was resolved with strong support (1.0 PP) with six individuals sampled from across its geographical range. Two clades of *I. deltoidea* were found: one from the Putumayo and Caquetá departments of Colombia; and the other comprising two individuals from Loreto, Peru (united by 0.98 PP) clustered with an individual from La Paz, Bolivia (0.83 PP; Fig. 1; Fig. S1).

IRIARTELLA: A MONOTYPIC GENUS

Our results do not support the recognition of two species in *Iriartella*, as delimited by Henderson (1990). In our phylogenetic tree, specimens from AAU, identified as *I. stenocarpa* (light green circles; Fig. 1), are nested in the clade formed by specimens from COL, identified as *I. setigera* (dark green circles; Fig. 1). The monotypic nature of *Iriartella* has been suggested previously (Galeano, 1991; Galeano & Bernal, 2010). The interspecific differences in morphology described by Henderson (1990) are not supported by our study of specimens at COL either. According to Henderson, the taxa differ in the degree of connation of the sepals in staminate and pistillate flowers: connate into a shallow cupule (staminate) and connate basally (pistillate) in *I. setigera* vs. briefly connate below, free and imbricate above (staminate) and distinct and imbricate (pistillate) in *I. stenocarpa*. Moreover, *I. setigera* was considered a larger palm with stems to 12 m × 2–4 cm vs. stems to 3 m × 1–2 cm in *I. stenocarpa*.

Most COL specimens fitting Henderson's description of *I. stenocarpa* (many of them identified by Henderson himself) are indeed slender palms that have staminate and pistillate flowers with free, imbricate sepals. However, some specimens have sepals partially or fully connate, non-imbricate, both in staminate (Galeano *et al.* 8540, *Guataquira et al.* sgg007) and in pistillate flowers (Bernal *et al.* 2570, *Guataquira et al.* sgg007, Galeano 1447, Bernal *et al.* 2611). Likewise, although most specimens fitting *I. setigera* (also mostly determined by Henderson) are larger palms with thicker stems that have staminate and pistillate flowers with connate sepals, there is variation in this character state. Several specimens have staminate flowers with partially free sepals (one sepal free in one side in Galeano *et al.* 8540) and pistillate flowers with sepals ranging from just partially connate with one free sepal (Bernal *et al.* 4462, *García-Barriga* 14270, *Palacios* 2443) to completely free (*Palacios* 2443, Bernal *et al.* 2607, Bernal *et al.* 4462). Finally, soil chemical preferences of nearly 5000 individuals measured across 118 transects in the western Amazon are strongly overlapping, indicating that they occupy similar edaphic niches (H. Balslev & R. Cámara, in review). Based

on our phylogenetic results and the considerations above, we here synonymize *I. stenocarpa* under *I. setigera*.

RESURRECTION OF *SOCRATEA MONTANA* AND VARIATION IN *S. EXORRHIZA*

Socratea was recovered as monophyletic (1.0 PP). Bernal-Gonzalez & Henderson (1986) recognized two groups in *Socratea*: one group comprises species with thick rachillae, larger staminate flowers with numerous stamens (84–145) and rostrate fruits, including *S. hecatonandra* (Dugand) R.Bernal, *S. montana* and *S. rostrata* Burret; the other group comprises species with thinner rachillae, smaller staminate flowers with fewer stamens (27–45) and fruits rounded at the apex, including *S. exorrhiza* and all other species described in the genus up to that time. Our phylogenetic tree (Fig. 1) supports that grouping, adding *S. salazarii* H.E.Moore and *S. karstenii* F.W. Stauffer & Balslev (2012) to the group of *S. exorrhiza*.

Socratea montana was synonymized with *S. rostrata* by Borchsenius, Borgtoft & Balslev (1998), a treatment followed by Galeano & Bernal (2010), although these authors stated that these species should perhaps be regarded as distinct, since *S. montana* has thicker rachillae and pinnae divided into narrower segments than *S. rostrata*. Our phylogenetic tree supports this split, and shows that, as initially proposed by Bernal-Gonzalez & Henderson (1986), *S. montana* is more closely related to *S. hecatonandra* than to *S. rostrata*. Because of this, we resurrect here *S. montana*, which is restricted to the western slopes of the Andes between 900 and 1800 m of elevation.

Four individuals of *S. exorrhiza* were included to represent the geographical and genetic variation of that species. This inclusion was important because this species is the widest spread of all species of Iriarteae and has one of the largest distributions of all American palms (Henderson *et al.*, 1995). Two individuals from the Llanos region of eastern Colombia were strongly supported (0.83 PP) as distinct from individuals sampled from the southern portion of the distribution (Bolivia and Peru), showing population structure across our modest sampling.

INTERSPECIFIC RELATIONSHIPS IN *WETTINIA*

Our phylogenetic analysis supports two separate groups in this genus (0.79 PP), which are consistent with geographical distribution. One (Eastern Clade) is comprised of *W. aequatorialis*, *W. anomala*, *W. augusta*, *W. drudei*, *W. lanata*, *W. longipetala*, *W. maynensis*, *W. microcarpa* and *W. praemorsa*. Except for *W. lanata*, all these species grow on the eastern

slopes of the Andes, from Venezuela to northern Bolivia. The remaining grade comprises *W. castanea*, *W. disticha*, *W. quinaria*, *W. aequalis*, *W. fascicularis*, *W. hirsuta*, *W. kalbreyeri*, *W. oxycarpa*, *W. radiata* and *W. verruculosa*. All of these species grow on the western slopes of the Andes or in the adjacent Pacific lowlands and Panama or, in the case of *W. hirsuta*, in the inter-Andean valley of the Magdalena River, Colombia. This phylogeographic pattern suggests that the Eastern Clade derived from the Western Clade, which fits well with the west-to-east uplift of the northern Andes (e.g. Antonelli *et al.*, 2009; Graham, 2009; Hoorn *et al.*, 2010). A formal biogeographic analysis and divergence time estimation are, however, required to further assess this scenario.

Thirteen of the 20 *Wettinia* spp. were resolved as monophyletic (> 0.81 PP; Fig. 1), but some species, sister relationships and clades in the genus remain unresolved. This lack of phylogenetic resolution in *Wettinia* may partly reflect a rapid diversification during the recently formed northern Cordilleras of the Andes (Hoorn *et al.*, 2010; Bermudez *et al.*, 2015).

A major result in *Wettinia* is the recovery of two distinct clades of *W. kalbreyeri*, each of which are well supported (> 0.87 PP) and are separated by two other well supported branches (> 0.86 PP). Each clade of this species reflects a geographical region, one in the central and one in the western Cordillera of Colombia and may represent a cryptic species with little morphological differentiation or gene flow with other sympatric *Wettinia* spp. *Wettinia kalbreyeri* has the widest distribution in the genus and potential for hybridization may be high with *W. disticha*, which replaces *W. kalbreyeri* above 1700 m elevation in the western Cordillera (Galeano & Bernal, 2010). Without further field and laboratory work and careful revision of specimens we hesitate to make nomenclatural changes at this point.

The phylogenetic position of *Wettinia lanata* is particularly interesting. This species has a narrow distribution in the western slopes of the Andes in Colombia, where it occupies a small range of ca. 3000 km² between 2100 and 2600 m, reaching the highest elevation of any species in the tribe. *Wettinia lanata* resembles the more widely distributed *W. disticha* and abruptly replaces that species above 2100 m; in many respects (including distichous phyllotaxy), these species appear to be sister taxa. Because of this, the position of *W. lanata* in the Eastern Clade is unexpected, more so when one considers that it has homogeneous endosperm, whereas the closest species in its clade (*W. microcarpa*, *W. praemorsa*, *W. anomala*) all have a ruminant endosperm, a character that evolved only once in the tribe.

One result that is more difficult to explain is the position of *W. hirsuta*. This lowland species, endemic to the Magdalena river valley in Colombia, is morphologically similar to *W. augusta* in having undivided pinnae, an unbranched pistillate inflorescence and tightly packed fruits. However, in our phylogenetic analysis it is resolved as sister to the highland *W. disticha*, which has distichous leaves, divided pinnae, inflorescences with a long rachis and many branches and loosely arranged pistillate flowers. Although the recurrent evolution of tightly packed fruits is obvious from our phylogenetic tree, the numerous changes in this taxon in relation to its closest relatives in the clade and its geographical separation from them make this topology unexpected.

INFRUCTESCENCE EVOLUTION

Following our expectations, we found that tightly packed infructescences have evolved several times in *Wettinia*. The underlying cause of these repeated events remain elusive. It is conceivable that the evolution of the compressed fruit is a consequence of a shift in pollinators in those lineages. This hypothesis remains untested as we are unaware of any reports published on the comparative pollination of *Wettinia* spp. with contrasting flower and fruit morphology (but see Nuñez, Bernal & Knudsen, 2005 for data on *W. quinaria*). Preliminary observations suggest that Andean species tend to share pollinators, whereas Amazonian and Chocoan species do not (L. A. Nuñez Avellaneda, pers. comm., April 2015). Shared pollinator assemblages could cause competitive exclusion and speciation (e.g. Van der Niet, Peakall & Johnson, 2014). Our strong phylogenetic framework for Iriarteeae will benefit future studies on the interplay between members of Iriarteeae and their pollinators.

CONCLUSIONS

Our phylogenetic tree, based on 11 gene regions from 89 individuals of 29 species, represents one of the most densely sampled palm phylogenetic analyses to date. This robust topology will be useful for macroevolutionary studies, such as analysis of biogeography and diversification. In particular, the phylogenetic tree lays the groundwork for understanding broad patterns of geographically and geologically driven species diversification in South America (e.g. Bacon, 2013; Hoorn *et al.*, 2013; Roncal *et al.*, 2013) and phylogeographic studies of widespread species, such as *I. deltoidea* and *S. exorrhiza*.

ACKNOWLEDGEMENTS

This publication is dedicated to Dr Jean-Christophe Pintaud, an inspiration for his contributions to the understanding of tropical plants and ecosystems. This research was funded by a Smithsonian Post-Doctoral Fellowship, the Royal Swedish Academy of Sciences (Kungliga Vetenskapsakademien) and International Palm Society grants to C.D.B., the European Commission Framework 7 programme (contract no. 213126 to HB), the Danish Natural Science Research Council (grant no 10-083348 to HB) and by the Swedish Research Council (B0569601), the European Research Council under the European Union's Seventh Framework Programme (FP/2007-2013, ERC Grant Agreement n. 331024) and a Wallenberg Academy Fellowship to A.A. We thank Finn Borchsenius and Mária José Sanín for leaf material, Nery Margarita Franco, Carlos García, and Susana Ortiz for laboratory assistance and Jorge Hernández Torres and Carlos Jaramillo for infrastructure resources.

REFERENCES

- Akaike H.** 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**: 716–723.
- Alexander P, Rajanikanth G, Bacon CD, Bailey CD.** 2006. Recovery of plant DNA using a reciprocating saw and silica-based columns. *Molecular Ecology Notes* **7**: 5–9.
- Antonelli A, Nylander JAA, Persson C, Sanmartín I.** 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences, USA* **106**: 9749–9754.
- Asmussen CB, Dransfield J, Deickman V, Barford AS, Pintaud J-C, Baker WJ.** 2006. A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA phylogeny. *Botanical Journal of the Linnean Society* **151**: 15–38.
- Bacon C, Feltus F, Paterson A, Bailey C.** 2008. Novel nuclear intron-spanning primers for Arecaceae evolutionary biology. *Molecular Ecology Resources* **8**: 211–214.
- Bacon CD.** 2013. Biome evolution and biogeographical change through time. *Frontiers of Biogeography* **5**: 227–231.
- Baker WJ, Savolainen V, Asmussen-Lange CB, Chase MW, Dransfield J, Forest F, Harley MM, Uhl NW, Wilkinson M.** 2009. Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of super-tree and supermatrix approaches. *Systematic Biology* **58**: 240–256.
- Bayzid MS, Warnow T.** 2013. Naive binning improves phylogenomic analyses. *Bioinformatics* **29**: 2277–2284.
- Bermudez MA, Hoorn C, Bernet M, Carrillo E, van der Beek PA, Garver JI, Mora JL, Mehrkian K.** 2015. The detrital record of Late-Miocene to Pliocene surface uplift and exhumation of the Venezuelan Andes in the Maracaibo

- and Barinas foreland basins. *Basin Research*. doi: 10.1111/bre.12154.
- Bernal-Gonzalez R, Henderson AH. 1986.** A new species of *Socratea* (Palmae) from Colombia with notes on the genus. *Brittonia* **38**: 55–59.
- Bollback JP. 2006.** Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics* **7**: e88.
- Borchsenius F, Borgtoft Pederson H, Balslev H. 1998.** Manual to the palms of Ecuador. AAU Reports 37.
- Borchsenius F, Skov F. 1997.** Ecological amplitudes of Ecuadorian palms. *Principes* **41**: 179–183.
- Couvreux TLP, Forest F, Baker WJ. 2011.** Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9**: e44.
- Dransfield J, Uhl N, Asmussen C, Baker W, Harley M, Lewis C. 2005.** A new phylogenetic classification of the palm family, Arecaceae. *Kew Bulletin* **60**: 559–569.
- Dransfield J, Uhl N, Asmussen C, Baker W, Harley M, Lewis C. 2008.** *Genera palmarum: the evolution and classification of palms*. Kew: Kew Publishing.
- Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012.** Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29**: 1969–1973.
- Edgar RC. 2004.** MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**: 1792–1797.
- Fauset S, Johnson MO, Gloor M, Baker TR, Monteagudo MA, Brienens RJW, Feldpausch TR, Lopez-Gonzalez G, Malhi Y, ter Steege H, Pitman NCA, Baraloto C, Engel J, Petronelli P, Andrade A, Camargo JLC, Laurance SGW, Laurance WF, Chave J, Allie E, Nunez Vargas P, Terborgh J, Ruokolainen K, Silveira M, Aymard GA, Arroyo L, Bonal D, Ramirez-Angulo H, Araujo-Murakami A, Neill D, Herault B, Dourdain A, Torres-Lezama A, Marimon BS, Salamao RP, Cominsky JA, Rejou-Mechain M, Toledo M, Licona JC, Alarcon A, Prieto A, Rudas A, van der Meer PJ, Killeen TJ, Marimon B-H Jr, Poorter L, Boot RGA, Stergios B, Vilanova Torre E, Costa FRC, Levis C, Schiatti J, Souza P, Groot N, Arets E, Chama Moscoso V, Castro W, Honorio Coronado EN, Pena-Claros M, Stahl C, Barroso J, Talbot J, Guimaraes Vieira IC, van der Heijden G, Thomas R, Vos VA, Almeida EC, Alvarez Davila E, Aragao LEOC, Erwin TL, Morandi PS, Almeida de Oliveira E, Valadao MBX, Zagt RJ, van der Hout P, Alvarez Loayza P, Pipoly JJ, Wang O, Alexiades MN, Ceron C, Huaman-tupa-Chuquimaco I, Di Fiore A, Peacock J, Pallqui Camacho NC, Umetsu RK, Barbosa de Camargo P, Burnham RJ, Herrera R, Quesada CA, Strupp J, Vieira SA, Steininger M, Reynal Rodriguez C, Restrepo Z, Esquivel Muelbert A, Lewis SL, Pickavance GC, Phillips OL. 2015.** Hyperdominance in Amazonian forest carbon cycling. *Nature Communications* **6**: 6857.
- Fritz SA, Purvis A. 2010.** Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conservation Biology* **24**: 1042–1051.
- Galeano G. 1991.** *Las palmas de la region de Araracuara*. Estudios en la Amazonia Colombiana. Bogota: Tropenbos.
- Galeano G, Bernal R. 2010.** *Palmas de Colombia. Guía de campo*. Bogota: Instituto de Ciencias Naturales, Facultad de Ciencias, Universidad Nacional de Colombia.
- Gatsey J, Springer M. 2014.** Phylogenetic analysis at deep time scales: unreliable gene trees, bypassed hidden support, and the coalescence/concatalescence conundrum. *Molecular Phylogenetics and Evolution* **80**: 231–266.
- Graham A. 2009.** The Andes: a geological overview from a biological perspective. *Annals of the Missouri Botanical Garden* **96**: 371–385.
- Hahn W. 2002a.** A molecular phylogenetic study of the Palmae (Arecaceae) based on *atpB*, *rbcl*, and 18S nrDNA sequences. *Systematic Biology* **51**: 92–112.
- Hahn W. 2002b.** A phylogenetic analysis of the arecoid line of palms based on plastid DNA sequence data. *Molecular Phylogenetics and Evolution* **23**: 189–204.
- Harvey PH, Pagel MD. 1991.** *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Heled J, Drummond AJ. 2010.** Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution* **27**: 570–580.
- Henderson AH. 1990.** Arecaceae. Part I. Introduction and the Iriarteinae. *Flora Neotropica* **53**: 1–100.
- Henderson AH, Galeano G, Bernal R. 1995.** *Field guide to the palms of the Americas*. Princeton: Princeton University Press.
- Horn C, Mosbrugger V, Mulch A, Antonelli A. 2013.** Biodiversity from mountain building. *Nature Geoscience* **6**: 154.
- Horn C, Wesseling FP, ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartin I, Sanchez-Meseguer A, Anderson CL, Figuiereido J, Jaramillo CA, Riff D, Negri FR, Hooghiemstra H, Lundberg J, Stadler T, Sarkinen T, Antonelli A. 2010.** Amazonia through time: Andean uplift, climate change, landscape evolution and biodiversity. *Science* **330**: 927–931.
- Knowles LL. 2010.** Sampling strategies for species tree estimation. In: Knowles LL, Kubatko LS, eds. *Estimating species trees, practical and theoretical aspects*. Hoboken: Wiley-Blackell, 215.
- Lewis C, Doyle J. 2002.** A phylogenetic analysis of tribe Areceae (Arecaceae) using two low-copy nuclear genes. *Plant Systematics and Evolution* **236**: 1–17.
- Ludena B, Chabrilange N, Aberlenc-Bertossi F, Adam H, Tregear J, Pintaud J-C. 2011.** Phylogenetic utility of the nuclear genes AGAMOUS 1 and PHYTOCHROME B in palms (Arecaceae): an example within Bactridinae. *Annals of Botany* **108**: 1433–1444.
- Mauro-Herrera M, Meerow A, Borrone J, Kuhn D, Schnell R. 2006.** Ten informative markers developed from WRKY sequences in coconut (*Cocos nucifera*). *Molecular Ecology Notes* **6**: 904–906.
- Núñez LA, Bernal R, Knudsen J. 2005.** Diurnal palm pollination by mystropine beetles: is it weather-related? *Plant Systematics and Evolution* **254**: 149–171.

- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2013. *caper: comparative analysis of phylogenetics and evolution in R. R package version 0.5.2*. Available at: <https://cran.r-project.org/web/packages/caper/index.html>
- Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* **25**: 1253–1256.
- Revell LJ. 2012. An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- Roncal J, Francisco-Ortega J, Asmussen C, Lewis C. 2005. Molecular phylogenetic of tribe Geonomeae (Arecaceae) using nuclear DNA sequence of phosphoribulokinase and RNA polymerase II. *Systematic Botany* **30**: 275–283.
- Roncal J, Henderson AH, Borchsenius F, Sodre Cardoso SR, Balslev H. 2012. Can phylogenetic signal, character displacement, or random phylogenetic drift explain the morphological variation in the genus *Geonoma* (Arecaceae)? *Biological Journal of the Linnean Society* **106**: 528–539.
- Roncal J, Kahn F, Millan B, Couvreur TLP, Pintaud J-C. 2013. Cenozoic colonization and diversification patterns of tropical American palms: evidence from *Astrocaryum* (Arecaceae). *Botanical Journal of the Linnean Society* **171**: 120–139.
- Scarcelli N, Barnaud A, Eiserhardt W, Treier U, Seveno M, d'Anfray A, Vogouroux Y, Pintaud J-C. 2011. A set of 100 chloroplast DNA primer pairs to study population genetics and phylogeny in monocotyledons. *PLoS ONE* **6**: e19954.
- Simmons MP. 2004. Independence of alignment and tree search. *Molecular Phylogenetics and Evolution* **31**: 874–879.
- Stauffer FW, Balslev H. 2012. *Socratea karstenii* F. W. Stauffer & Balslev (Arecaceae), a new species from Venezuela. *Condollea* **67**: 285–291.
- ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomao RP, Guevara JE, Phillips OL, Castilho CV, Magnusson WE, Molino J-F, Monteagudo A, Nunez Vargas P, Montero JC, Feldpausch TR, Coronado EH, Killeen TJ, Mostacedo B, Vasquez R, Assis RL, Terborgh J, Wittmann F, Andrade A, Laurance WF, Laurance SGW, Marimon BS, Marimon B-H Jr, Guimaraes Vieira IC, Leao Amaral I, Brienen R, Castellanos H, Cardenas Lopez D, Duivenvoorden JF, Mogollon HF, de Almeida Matos FD, Davila N, Garcia-Villacorta R, Stevenson Diaz PR, Costa F, Emilio T, Levis C, Schiatti J, Souza P, Alonso A, Dallmeier F, Duque Montoya AJ, Fernandez Piedade MT, Araujo-Murakami A, Arroyo L, Gribel R, Fine PVA, Peres CA, Toledo M, Aymard CGA, Baker TR, Ceron C, Engel J, Henkel TW, Maas P, Petronelli P, Stropp J, Zartman CE, Daly D, Neill D, Silveira M, Rios Paredes M, Chave J, Lima Filho DdA, Moller Jorgensen P, Fuentes A, Schongart J, Cornejo Valverde F, Di Fiore A, Jimenez EM, Penuela Mora MC, Phillips JF, Rivas G, van Andel TR, von Hildebrand P, Hoffman B, Zent EL, Malhi Y, Prieto A, Rudas A, Ruschell AR, Silva N, Vos V, Zent S, Oliveira AA, Cano Schutz A, Gonzales T, Trinidad Nascimento M, Ramirez-Angulo H, Sierra R, Tirado M, Umana Medina MN, van der Heijden G, Vela CIA, Vilanova Torre E, Vriesendorp C, Wang O, Young KR, Baider C, Balslev H, Ferreira C, Mesones I, Torres-Lezama A, Urrego Giraldo LE, Zagt R, Alexiades MN, Hernandez L, Huamantupa-Chuquimaco I, Milliken W, Palacios Cuenca W, Pauletto D, Valderrama Sandoval G, Silman MR. 2013. Hyperdominance in the Amazonian tree flora. *Science* **342**: 325–326.
- Van der Niet T, Peakall R, Johnson SD. 2014. Pollinator-driven ecological speciation in plants: new evidence and future perspectives. *Annals of Botany* **113**: 199–211.
- Zurawski G, Clegg MT. 1987. Evolution of higher-plant chloroplast DNA-encoded genes: implications for structure-function and phylogenetic studies. *Annual Review of Plant Physiology* **38**: 391–418.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Complete phylogeny of the Iriarteeae with posterior probabilities listed at each node. This topology was randomly reduced to one individual per species to produce results presented in Figure 2.

Appendix 1 Table of sequences generated for this study with taxonomic authorities, voucher or DNA source information, and GenBank accession numbers. Cells containing the * symbol correspond to sequences that were not amplified. There are two sequences shorter than 200 bps denoted with the # symbol that could not be submitted to GenBank because of policies regarding sequence length, therefore we do not report a GenBank accession number for these samples. DNA sources are abbreviated: Museo de Historia Natural, Universidad Nacional de Colombia (COL), herbarium of Aarhus University (AAU), and Herbario San Marcos, Universidad Mayor de San Marcos (USM).

| Species | Taxonomic authority | DNA source | AG1 | CISP4 | CISP5 | ndhA | petD-rpoA | PRK | psbK-trnS | RBP2 | trnDT | trnG | WRKY21 |
|---------------------------|--------------------------------|------------------------|----------|----------|----------|----------|-----------|----------|-----------|----------|----------|----------|----------|
| Dictyocaryum lamarckianum | (Mart.) H.Wendl. | H. Balslev 8319 (AAU) | KF776099 | KF776077 | KF776035 | KF775961 | KF775906 | * | KF775810 | KF775749 | KF775743 | KF775694 | KF775599 |
| Dictyocaryum lamarckianum | (Mart.) H.Wendl. | R. Bernal 4757 (COL) | * | KF776076 | KF776034 | KF775967 | KF775904 | KF775845 | KF775801 | * | KF775697 | KF775692 | * |
| Dictyocaryum pitrianum | (Steyerm.) H.E.Moore & Steyerm | J.-C. Pintaud ENV 1185 | KF776100 | KF776078 | KF776036 | * | KF775905 | KF775846 | KF775796 | KF775755 | KF775744 | KF775693 | KF775600 |
| Iriartea deltoidea | Ruiz & Pav. | H. Balslev 6733 (AAU) | KF776090 | KF776084 | KF776031 | * | KF775931 | * | KF775816 | KF775757 | KF775741 | KF775690 | KF775596 |
| Iriartea deltoidea | Ruiz & Pav. | R. Bernal 2197 (COL) | * | KF776079 | * | KF775974 | KF775930 | * | KF775818 | * | KF775740 | KF775686 | KF775598 |
| Iriartea deltoidea | Ruiz & Pav. | R. Bernal 2200 (COL) | * | KF776081 | KF776029 | KF775966 | KF775929 | * | KF775819 | * | KF775738 | KF775688 | * |
| Iriartea deltoidea | Ruiz & Pav. | R. Bernal 4803 (COL) | KF776092 | KF776083 | KF776032 | * | KF775933 | * | KF775821 | KF775756 | KF775739 | KF775689 | KF775594 |
| Iriartea deltoidea | Ruiz & Pav. | H. Balslev 7965 (AAU) | KF776091 | KF776082 | KF776033 | * | KF775896 | KF775847 | KF775820 | * | KF775737 | KF775691 | KF775595 |
| Iriartea deltoidea | Ruiz & Pav. | H. Balslev 8081 (AAU) | KF776093 | KF776080 | KF776030 | * | KF775932 | * | KF775817 | KF775758 | KF775742 | KF775687 | KF775597 |
| Iriartella setigera | (Mart.) H.Wendl. | R. Bernal 2607 (COL) | * | KF776085 | * | * | KF775897 | * | KF775806 | * | * | KF775685 | * |
| Iriartella setigera | (Mart.) H.Wendl. | R. Bernal 4367 (COL) | KF776088 | * | KF776023 | KF775962 | KF775898 | KF775848 | KF775804 | KF775750 | KF775695 | KF775683 | KF775592 |
| Iriartella stenocarpa | Burret | R. Bernal 7412 (AAU) | KJ540605 | * | * | * | * | * | * | * | * | * | * |
| Iriartella stenocarpa | Burret | H. Balslev 7593 (AAU) | KF776089 | KF776086 | * | KF775963 | KF775899 | KF775849 | KF775805 | KF775751 | KF775696 | KF775684 | KF775593 |
| Iriartella stenocarpa | Burret | H. Balslev 7688 (AAU) | KJ540603 | * | * | * | * | * | * | * | KJ540548 | * | * |
| Iriartella stenocarpa | Burret | H. Balslev 7794 (AAU) | KJ540606 | KJ540589 | KJ540577 | * | * | KJ540575 | * | KJ540557 | * | * | * |
| Iriartella stenocarpa | Burret | H. Balslev 7794 (AAU) | KJ540604 | KJ540589 | KJ540577 | * | * | KJ540575 | * | KJ540557 | * | * | * |
| Iriartella stenocarpa | Burret | H. Balslev 7807 (AAU) | KJ540604 | KJ540590 | * | * | * | KJ540576 | * | * | * | * | * |
| Socratea exorrhiza | (Mart.) H.Wendl. | H. Balslev 6739 (AAU) | KF776097 | KF776037 | KF776026 | KF775970 | KF775909 | KF775852 | KF775787 | KF775753 | KF775746 | KF775680 | KF775632 |
| Socratea exorrhiza | (Mart.) H.Wendl. | C. Bacon 1 (COL) | * | KF776040 | KF776027 | * | KF775907 | KF775850 | * | * | * | * | * |
| Socratea exorrhiza | (Mart.) H.Wendl. | R. Bernal 4442 (COL) | * | * | KF776028 | * | KF775911 | KF775851 | KF775799 | * | * | KF775681 | * |

Appendix I. *Continued*

| Species | Taxonomic authority | DNA source | AG1 | CISP4 | CISP5 | <i>ndhA</i> | <i>petD-rpoA</i> | PRK | <i>psbK-trnS</i> | RBP2 | trnD | trnG | WRKY21 |
|-------------------------------|-----------------------------------|--------------------------|----------|----------|----------|-------------|------------------|----------|------------------|----------|----------|----------|----------|
| <i>Socratea exorrhiza</i> | (Mart.) H. Wendl. | H. Balslev 7905 (AAU) | KF776095 | KF776039 | KF776025 | KF775971 | KF775910 | KF775853 | KF775798 | KF775754 | KF775745 | KF775679 | KF775633 |
| <i>Socratea hecatonandra</i> | (Dugand) R. Bernal | R. Bernal 4867 (COL) | KJ540607 | KJ540593 | KJ540583 | * | * | KJ540568 | * | KJ540562 | KJ540551 | * | KJ540543 |
| <i>Socratea hecatonandra</i> | (Dugand) R. Bernal | G. Galeano 8119 (COL) | KF776096 | KF776041 | KF776024 | KF775969 | KF775912 | KF775854 | KF775800 | KF775752 | KF775748 | KF775678 | KF775630 |
| <i>Socratea karstenii</i> | F. W. Stauffer & Balslev | M. Sanin SN | * | KJ540591 | KJ540581 | * | * | * | * | KJ540560 | * | * | KJ540542 |
| <i>Socratea rostrata</i> | Burret | R. Bernal 2493 (COL) | * | KJ540594 | KJ540578 | * | * | KJ540569 | * | KJ540558 | # | * | * |
| <i>Socratea salazarii</i> | H.E. Moore | H. Balslev 7298 (AAU) | * | KJ540592 | KJ540580 | * | * | * | * | * | * | * | * |
| <i>Socratea salazarii</i> | H.E. Moore | H. Balslev 7364 (AAU) | KJ540609 | KJ540595 | KJ540585 | * | * | KJ540567 | * | KJ540559 | KJ540552 | * | KJ540544 |
| <i>Socratea salazarii</i> | H.E. Moore | H. Balslev 7310 (AAU) | * | * | KJ540582 | * | * | * | * | * | * | * | * |
| <i>Socratea salazarii</i> | H.E. Moore | H. Balslev 7594 (AAU) | KJ540608 | KJ540596 | KJ540579 | * | * | * | * | * | * | * | * |
| <i>Socratea salazarii</i> | H.E. Moore | H. Balslev 7662 (AAU) | * | KF776038 | * | KF775972 | KF775908 | KF775855 | KF775797 | * | KF775747 | KF775682 | KF775631 |
| <i>Wettinia aequatorialis</i> | R. Bernal | H. Balslev 6462 (AAU) | KF776113 | * | * | * | KF775914 | KF775857 | KF775794 | * | * | KF775651 | * |
| <i>Wettinia aequatorialis</i> | R. Bernal | F. Borchsenius 635 (AAU) | * | * | KF775997 | * | KF775915 | KF775856 | KF775788 | * | KF775698 | KF775675 | * |
| <i>Wettinia anomala</i> | (Burret) R. Bernal | R. Bernal 4632 (COL) | KJ540612 | KJ540598 | KJ540587 | * | * | KJ540572 | * | KJ540566 | KJ540549 | * | KJ540546 |
| <i>Wettinia anomala</i> | (Burret) R. Bernal | R. Bernal 2196 (COL) | * | KF776052 | * | * | KF775934 | KF775858 | KF775808 | * | * | KF775634 | * |
| <i>Wettinia augusta</i> | Poepp. & Endl. | H. Balslev 7355 (AAU) | KF776112 | KF776050 | KF775999 | KF775973 | KF775901 | KF775859 | KF775790 | KF775774 | KF775717 | KF775639 | * |
| <i>Wettinia augusta</i> | Poepp. & Endl. | H. Balslev 7556 (AAU) | KF776109 | KF776065 | * | KF775964 | KF775952 | KF775860 | KF775803 | KF775764 | KF775729 | KF775640 | * |
| <i>Wettinia augusta</i> | Poepp. & Endl. | H. Balslev 7696 (AAU) | KF776108 | KF776058 | KF776012 | KF775976 | KF775953 | KF775861 | KF775809 | KF775772 | KF775732 | KF775642 | KF775613 |
| <i>Wettinia augusta</i> | Poepp. & Endl. | H. Balslev 8017 (AAU) | KF776110 | KF776057 | KF775996 | KF775979 | KF775902 | KF775862 | KF775825 | KF775777 | KF775716 | KF775644 | KF775614 |
| <i>Wettinia augusta</i> | Poepp. & Endl. | H. Balslev 8031 (AAU) | KF776111 | KF776049 | * | KF775978 | KF775903 | KF775863 | KF775826 | KF775778 | KF775718 | KF775665 | KF775615 |
| <i>Wettinia castanea</i> | H.E. Moore & J. Drausf. | R. Bernal 2825 (COL) | * | KF776063 | KF776000 | KF775986 | KF775946 | * | KF775802 | KF775779 | KF775704 | KF775637 | KF775625 |
| <i>Wettinia castanea</i> | H.E. Moore & J. Drausf. | R. Bernal 4786 (COL) | KF776114 | KF776054 | KF776017 | KF775987 | KF775945 | KF775864 | KF775813 | * | KF775719 | KF775645 | KF775623 |
| <i>Wettinia disticha</i> | (R. Bernal) | R. Bernal 2838 (COL) | KJ540610 | KJ540599 | * | * | * | KJ540573 | * | KJ540565 | KJ540555 | * | * |
| <i>Wettinia disticha</i> | (R. Bernal) | R. Bernal 4774 (COL) | * | KF776062 | KF776015 | KF775965 | KF775947 | KF775865 | KF775827 | KF775760 | KF775720 | KF775674 | KF775604 |
| <i>Wettinia drudei</i> | (O.F. Cook & Doyle) A.J. Hend. | R. Bernal 2952 (COL) | * | KF776043 | KF776005 | KF775988 | KF775954 | KF775866 | KF775789 | * | KF775727 | KF775673 | KF775607 |

Appendix 1. Continued

| Species | Taxonomic authority | DNA source | AG1 | CISP4 | CISP5 | <i>ndhA</i> | <i>petD-rpoA</i> | PRK | <i>psbK-trnS</i> | RPB2 | trnDT | trnG | WRKY21 |
|------------------------------|-----------------------------------|---------------------------|----------|----------|----------|-------------|------------------|----------|------------------|----------|----------|----------|----------|
| <i>Wettinia drudei</i> | (O.F.Cook & Doyle) A.J.Hend. | H. Balslev 6996 (AAU) | KF776118 | * | * | KF775977 | KF775955 | KF775867 | KF775822 | * | KF775721 | KF775676 | KF775609 |
| <i>Wettinia drudei</i> | (O.F.Cook & Doyle) A.J.Hend. | H. Balslev 7261 (AAU) | KF776098 | KF776044 | KF776008 | KF775989 | KF775956 | KF775868 | KF775807 | * | KF775711 | KF775663 | KF775610 |
| <i>Wettinia drudei</i> | (O.F.Cook & Doyle) A.J.Hend. | H. Balslev 7266 (AAU) | * | * | KF775995 | KF775990 | KF775957 | KF775869 | KF775795 | * | KF775722 | KF775677 | KF775612 |
| <i>Wettinia drudei</i> | (O.F.Cook & Doyle) A.J.Hend. | H. Balslev 7309 (AAU) | KF776101 | KF776045 | KF776003 | KF775985 | KF775951 | KF775870 | KF775823 | KF775773 | KF775736 | KF775671 | KF775611 |
| <i>Wettinia equalis</i> | (O.F.Cook & Doyle) R.Bernal | C.D. Bacon SN (COL) | KJ540614 | KJ540597 | KJ540586 | * | * | KJ540570 | * | KJ540564 | KJ540553 | * | KJ540545 |
| <i>Wettinia equalis</i> | (O.F.Cook & Doyle) R.Bernal | G. Galeano 8158a (COL) | KF776104 | KF776056 | KF776009 | * | KF775948 | KF775871 | KF775815 | KF775763 | KF775728 | KF775662 | KF775603 |
| <i>Wettinia fascicularis</i> | (Burret) H.E.Moore & J.Dransf. | R. Bernal 2830 (COL) | * | * | * | * | KF775924 | KF775872 | KF775829 | * | KF775723 | KF775635 | * |
| <i>Wettinia fascicularis</i> | (Burret) H.E.Moore & J.Dransf. | R. Bernal 4728 (COL) | * | KF776068 | KF775998 | KF775980 | KF775917 | KF775873 | KF775828 | KF775767 | KF775712 | KF775670 | KF775622 |
| <i>Wettinia fascicularis</i> | (Burret) H.E.Moore & J.Dransf. | J. Betancur 7610 (COL) | * | * | * | * | KF775923 | KF775874 | KF775831 | * | * | KF775648 | KF775627 |
| <i>Wettinia hirsuta</i> | Burret | R. Bernal 2294 (COL) | * | * | * | * | KF775918 | KF775875 | KF775785 | * | * | KF775641 | * |
| <i>Wettinia hirsuta</i> | Burret | R. Bernal 4736 (COL) | KF776103 | KF776051 | KF776018 | KF775983 | KF775919 | KF775876 | KF775792 | KF775766 | KF775730 | KF775638 | KF775626 |
| <i>Wettinia hirsuta</i> | Burret | R. Bernal 4737 (COL) | * | KF776059 | KF776010 | KF775981 | KF775920 | KF775877 | KF775830 | KF775765 | KF775715 | KF775657 | * |
| <i>Wettinia kalbreyeri</i> | (Burret) R.Bernal | R. Bernal 2203 (COL) | * | * | * | * | KF775913 | * | KF775791 | * | KF775714 | KF775664 | * |
| <i>Wettinia kalbreyeri</i> | (Burret) R.Bernal | R. Bernal 2492 (COL) | * | * | * | * | KF775949 | KF775878 | KF775811 | * | KF775734 | KF775652 | * |
| <i>Wettinia kalbreyeri</i> | (Burret) R.Bernal | R. Bernal 4725 (COL) | KF776105 | * | KF776002 | * | KF775916 | KF775879 | KF775835 | KF775761 | KF775735 | KF775661 | KF775601 |
| <i>Wettinia kalbreyeri</i> | (Burret) R.Bernal | R. Bernal 4726 (COL) | KF776106 | KF776046 | KF776004 | * | KF775921 | KF775880 | KF775833 | KF775780 | KF775724 | KF775658 | * |
| <i>Wettinia kalbreyeri</i> | (Burret) R.Bernal | CDB MJS 5 (COL) | KF776102 | KF776070 | KF776013 | KF775982 | KF775900 | KF775881 | KF775834 | KF775771 | KF775702 | KF775666 | * |
| <i>Wettinia lanata</i> | R. Bernal | R. Bernal 2583 (COL) | KJ540615 | KJ540602 | * | * | * | KJ540571 | * | * | KJ540556 | * | * |
| <i>Wettinia lanata</i> | R. Bernal | R. Bernal 4775 (COL) | KJ540613 | KJ540601 | KJ540588 | * | * | * | * | KJ540563 | KJ540554 | * | KJ540547 |
| <i>Wettinia longipetala</i> | A.H.Gentry | H. Balslev 6545 (AAU) | KJ540611 | KJ540600 | KJ540584 | * | * | KJ540574 | * | KJ540561 | KJ540550 | * | * |
| <i>Wettinia maynensis</i> | Spruce | R. Bernal 2486 (COL) | * | KF776042 | KF776006 | KF775960 | KF775950 | KF775882 | KF775786 | KF775776 | KF775707 | KF775667 | * |
| <i>Wettinia maynensis</i> | Spruce | R. Bernal 4804 (COL) | * | KF776060 | KF776007 | * | KF775958 | KF775883 | KF775812 | KF775775 | KF775701 | KF775660 | * |
| <i>Wettinia maynensis</i> | Spruce | H. Balslev 6568 (AAU) | KF776107 | KF776061 | KF775994 | KF775975 | KF775959 | KF775884 | KF775784 | * | KF775713 | KF775649 | KF775608 |
| <i>Wettinia microcarpa</i> | (Burret) R.Bernal | R. Bernal 3481 (COL) | KF776120 | KF776069 | KF776021 | * | KF775944 | KF775885 | KF775843 | KF775781 | KF775705 | KF775643 | KF775602 |

Appendix 1. *Continued*

| Species | Taxonomic authority | DNA source | AG1 | CISP4 | CISP5 | <i>ndhA</i> | <i>petD-rpoA</i> | PRK | <i>psbK-trnS</i> | RPB2 | trnDT | trnG | WRKY21 |
|-----------------------------|--------------------------------|---------------------------|----------|----------|----------|-------------|------------------|----------|------------------|----------|----------|----------|----------|
| <i>Wettinia microcarpa</i> | (Burret) R.Bernal | R. Bernal 4831 (COL) | KF776117 | KF776066 | KF776020 | * | KF775943 | KF775886 | KF775844 | KF775770 | KF775700 | KF775655 | KF775619 |
| <i>Wettinia oxycarpa</i> | Galeano-Garcés & R.Bernal | R. Bernal 2498 (COL) | * | KF776047 | * | KF775991 | KF775937 | KF775887 | KF775839 | * | KF775706 | KF775668 | * |
| <i>Wettinia oxycarpa</i> | Galeano-Garcés & R.Bernal | Solarte 1 (COL) | * | * | KF776011 | * | KF775936 | * | KF775838 | * | * | KF775650 | KF775616 |
| <i>Wettinia praemorsa</i> | (Willd.) Wess.Boer | R. Bernal 2883 (COL) | KF776115 | KF776053 | KF776014 | KF775993 | KF775942 | KF775888 | KF775837 | KF775782 | KF775733 | KF775636 | KF775620 |
| <i>Wettinia praemorsa</i> | (Willd.) Wess.Boer | J. Betancur 7611 (COL) | * | KF776071 | KF776001 | KF775984 | KF775925 | KF775890 | KF775832 | KF775769 | KF775726 | KF775672 | KF775617 |
| <i>Wettinia praemorsa</i> | (Willd.) Wess.Boer | G. Galeano 8256a (COL) | KF776121 | KF776072 | KF776019 | KF775992 | KF775940 | KF775891 | KF775814 | KF775759 | KF775731 | KF775647 | KF775618 |
| <i>Wettinia praemorsa</i> | (Willd.) Wess.Boer | R. Bernal 4826 (COL) | * | KF776048 | KF776022 | KF775968 | KF775941 | KF775889 | KF775842 | KF775783 | KF775725 | KF775656 | KF775605 |
| <i>Wettinia praemorsa</i> | (Willd.) Wess.Boer | M. Sanin SN | KF776119 | KF776067 | KF776016 | * | KF775938 | KF775892 | * | * | * | * | * |
| <i>Wettinia quinaria</i> | (O.F.Cook & Doyle) Burret | G. Galeano 8168a (COL) | * | KF776075 | * | * | KF775939 | KF775893 | KF775841 | KF775762 | KF775708 | KF775669 | KF775606 |
| <i>Wettinia radiata</i> | (O.F.Cook & Doyle) R.Bernal | R. Bernal 2190 (COL) | * | KF776074 | * | * | KF775926 | * | KF775836 | * | * | KF775653 | KF775628 |
| <i>Wettinia radiata</i> | (O.F.Cook & Doyle) R.Bernal | R. Bernal 4794 (COL) | KF776116 | KF776055 | * | * | KF775922 | KF775894 | KF775824 | KF775768 | KF775699 | KF775646 | KF775621 |
| <i>Wettinia radiata</i> | (O.F.Cook & Doyle) R.Bernal | R. Bernal 4873 (COL) | KF776087 | * | * | * | KF775927 | # | * | * | KF775710 | * | * |
| <i>Wettinia radiata</i> | (O.F.Cook & Doyle) R.Bernal | G. Galeano 8155 (COL) | * | KF776073 | * | * | KF775928 | * | KF775793 | * | KF775709 | KF775654 | KF775629 |
| <i>Wettinia verruculosa</i> | H.E.Moore | R. Bernal 2500 (COL) | * | KF776064 | * | * | KF775935 | KF775895 | KF775840 | * | KF775703 | KF775659 | KF775624 |