



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

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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, CISP5 4 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

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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

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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.Barttram) Small; (Appendix 1). Our outgroup sampling represents all tribes of subfamily Arecoideae and exemplars from

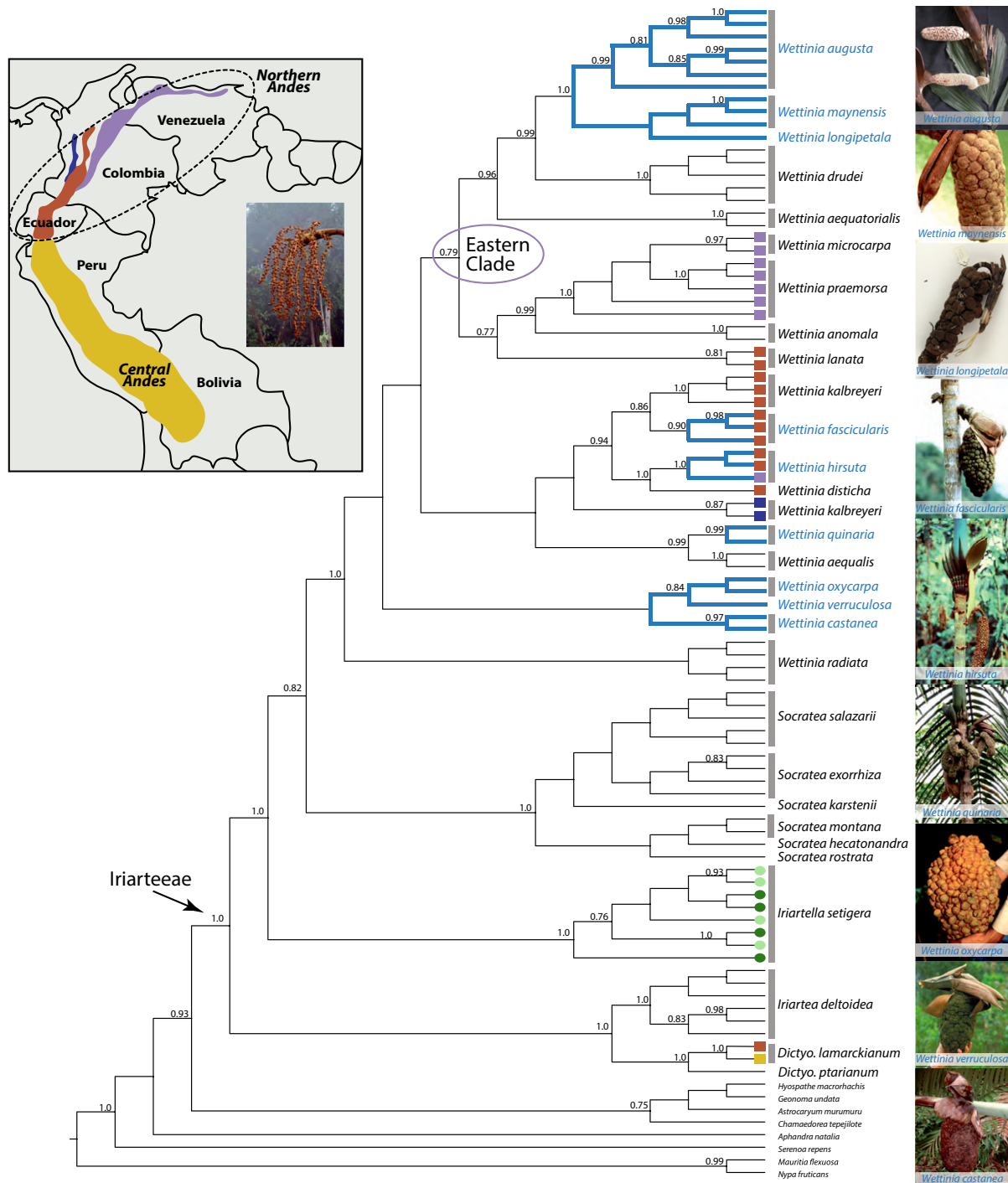


Figure 1. Phylogenetics of the palm tribe Iriarteae estimated using Bayesian inference implemented in BEAST. Clade support > 0.75 (Bayesian posterior probability) is displayed to the upper left of each node. Species are indicated with a grey bar when multiple individuals were sampled and those with a 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 Iriarteeae (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 Iriarteeae, 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.**

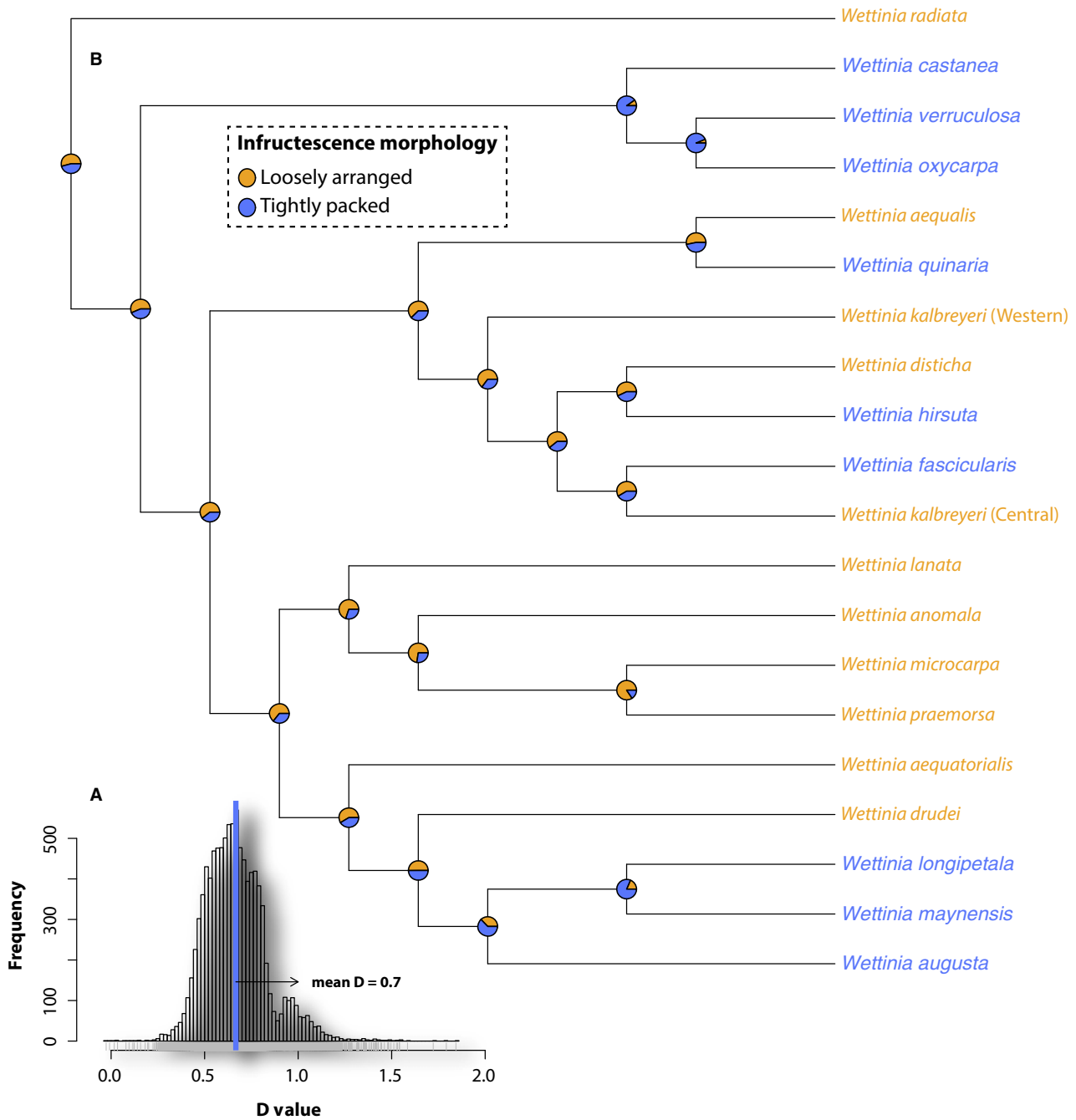


Figure 2. Trait evolution in *Wettinia* infructescences, where pie charts show the probability of each state at ancestral nodes. A, Distribution of the D statistic showing the mean in blue, indicating that infructescence type is not constrained phylogenetically. B, Stochastic mapping showing at least 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 *Iriarteia* (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 *Iriarteia*, with *Dictyocaryum lamarckianum* (Mart.) H.Wendl. replacing *Iriarteia 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 Chococoan 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 Iriarteae will benefit future studies on the interplay between members of Iriarteae 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*.

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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	<i>ndhA</i>	<i>petD-rpoA</i>	PRK	<i>psbK-trnS</i>	RPB2	trnDT	tmG	WRKY21
Dictyocaryum lamarkianum	(Mart.) H. Wendl.	H. Balslev 8319 (AAU)	KF776099	KF776077	KF776035	KF775961	KF775906	*	KF775810	KF775749	KF775743	KF775694	KF775599
Dictyocaryum lamarkianum	(Mart.) H. Wendl.	R. Bernal 4757 (COL)	*	KF776076	KF776034	KF775967	KF775904	KF775845	KF775801	*	KF775697	KF775692	*
Dictyocaryum ptarianum	(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 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>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	*	*	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.Dransf.	R. Bernal 2825 (COL)	*	KF776063	KF776000	KF775986	KF775946	*	KF775802	KF775779	KF775704	KF775637	KF775625
<i>Wettinia castanea</i>	H.E. Moore & J.Dransf.	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	trnD-T	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) R. Bernal 2583 (COL)	KF776102	KF776070	KF776013	KF775982	KF775900	KF775881	KF775834	KF775771	KF775702	KF775666	*
<i>Wettinia lanata</i>	R. Bernal	R. Bernal 4775 (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	KF775794	*	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 4881 (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	Solarie 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