RESEARCH ARTICLE

A densely sampled nuclear phylogenomic analysis of the coryphoid palms (Arecaceae: Coryphoideae)

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Abstract The palm family (Arecaceae) has a rich history of phylogenetic research, including several recent phylogenomic studies. However, densely sampled phylogenomic datasets for larger palm clades – such as subfamilies – are still few in number. We used target sequence capture to obtain data for 971 nuclear genes across 421 (ca. 80%) species in the subfamily Coryphoideae. We inferred a robust phylogenetic tree to address systematic issues in the subfamily, specifically the relationships among tribes Cryosophileae, Sabaleae, Phoeniceae and Trachycarpeae, the affinities of seven genera in Trachycarpeae that are not currently assigned to any subtribe, and the monophyly of genera across the subfamily. We recovered relationships among tribes that are in accordance with other major nuclear phylogenomic datasets, but that are incongruent with trees derived from plastome sequences. Importantly, the placement of tribe Phoeniceae (the date palms) remains contentious. Our tree recovered with high support the relationship of all unplaced Trachycarpeae genera, paving the way for an updated classification. Most genera were resolved as monophyletic except for *Livistona* and all three genera of tribe Caryoteae, calling for a revision of generic limits. Our tree clarifies the relationships of many fan palm species for the first time, allowing for future studies of diversification, trait evolution or biogeography.

Keywords Hyb-Seq; Palmae; phylogenetics; phylogenomics; target sequence capture; Trachycarpeae

Supporting Information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

The palm family (Arecaceae, 2516 species [POWO, 2024]) is widely used as a model group for studying the evolution, distribution and assembly of tropical rainforests (e.g., Couvreur & al., 2011; Kissling & al., 2012; Hagen & al., 2021). The value of palms as a model group derives from a deep history of research on palm taxonomy, phylogeny, traits and distribution (e.g., Dransfield & al., 2008; Baker & Dransfield, 2016; Faurby & al., 2016; Kissling & al., 2019). The inference of large-scale phylogenetic trees in particular (e.g., Baker & al., 2009; Faurby & al., 2016; Yao & al., 2023) has provided valuable insights into the evolution and ecology of the family (e.g., Couvreur & al., 2011; Baker & Couvreur, 2013; Onstein & al., 2017). Yet most of these studies focused on genus-level relationships (e.g., Baker & al., 2009) or relied heavily on morphology and taxonomic information to infer the placement of many species (e.g., Faurby & al., 2016). The next frontier in palm phylogenetics is therefore the inference of densely sampled species-level phylogenetic trees, which are still lacking for most larger clades, such as subfamilies (but see Kuhnhäuser, 2021).

With 519 species in 48 genera and 8 tribes (Baker & Dransfield, 2016; POWO, 2024), subfamily Coryphoideae (Fig. 1) accounts for roughly 20 percent of palms. It is overall characterized by palmate leaves with induplicate leaflets, but shows a remarkable diversity in leaf form including species with pinnate, bipinnate or entire leaves, as well as some

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Fig. 1. Selected species from the eight tribes of subfamily Coryphoideae, grouped by two major clades (**A–D**, CSPT clade; **E–H**, Syncarpous clade). **A**, *Coccothrinax montgomeryana* A.J.Hend. & al. in Cryosophileae; **B**, *Sabal domingensis* Becc. in Sabaleae; **C**, *Licuala grandis* (T.Moore) H.Wendl. in Trachycarpeae; **D**, *Phoenix dactylifera* L. in Phoeniceae; **E**, *Kerriodoxa elegans* J.Dransf. in Chuniophoeniceae; **F**, *Caryota rumphiana* Mart. in Caryoteae; **G**, *Corypha umbraculifera* L. in Corypheae; **H**, *Hyphaene compressa* H.Wendl. in Borasseae. — Photos: C.D. Bacon (A), J. Dransfield (B), O. Wrisberg (C, E), W.J. Baker (D, F, G), C. Godfray (H).

exceptional species with reduplicate leaflets (Dransfield & al., 2008). Coryphoid palms also inhabit a wider range of habitats and climates than any other subfamily of palms, and their distribution closely resembles that of the entire family (Dransfield & al., 2008). Building a species-level phylogenetic tree for the Coryphoideae would be a major step forward in understanding the evolution of palms and help shed light on the evolution of leaf shape and environmental adaptations.

Achieving a comprehensive species-level phylogenetic tree of Coryphoideae is now possible thanks to the availability of high-throughput sequencing and the development of specific target sequence capture probe sets for palms (Heyduk & al., 2016; Loiseau & al., 2019). Target sequence capture methods have enabled the sampling of hundreds of nuclear genes providing enough depth and breadth of data to accurately estimate species-level relationships (Andermann & al., 2019; Dodsworth & al., 2019). The target sequence capture method also unlocks the vast collections of specimens stored in herbaria, since it is less affected by DNA degradation than Sanger sequencing, making it more feasible to achieve the sampling required for near-complete or even complete species-level phylogenetic trees (Brewer & al., 2019). This approach has already been used across the palm family (Helmstetter & al., 2020; Bacon & al., 2021; Jiménez & al., 2021; Kuhnhäuser & al., 2021; Cano & al., 2022; Eiserhardt & al., 2022; Escobar & al., 2022), but so far studies using target sequence capture within the coryphoid subfamily have been limited to specific genera such as *Sabal* (Heyduk & al., 2016) and *Phoenix* (Pérez-Escobar & al., 2021) or only investigated relationships at the genus level and above (Bellot & al., 2024). By targeting nuclear genes, the target sequence capture approach can complement earlier studies which primarily used sequence data from the plastid genome (Bacon & al., 2012; Barrett & al., 2016; Faurby & al., 2016; Yao & al., 2023). This is especially important as the phylogenetic history of the plastid genome can differ substantially from the phylogenetic history of species due to hybridisation and chloroplast capture (e.g., Stull & al., 2020).

Although subfamily Coryphoideae has not yet been broadly investigated using target capture methods, it has a rich history of phylogenetic research. This includes both studies focusing on parts of the subfamily, and broader studies covering it entirely (Baker & al., 1999, 2009; Asmussen & al., 2000, 2006; Asmussen & Chase, 2001; Bacon & al., 2012, 2013; Faurby & al., 2016; Bellot & al., 2020; Kadam & al., 2023; Yao & al., 2023). Coryphoideae is split into eight tribes that form two well-established clades (Baker & Dransfield, 2016). The CSPT clade (Baker & Dransfield, 2016) includes tribes Cryosophileae, Sabaleae, Phoeniceae and Trachycarpeae, which comprise 85% of the subfamily's species. The second clade, known as the syncarpous clade (Dransfield & al., 2008), includes tribes Chuniophoeniceae, Caryoteae, Corypheae and Borasseae, and is morphologically supported by its gynoecia with completely fused carpels (Dransfield & al., 2008; Rudall & al., 2011). Within these two clades, systematic uncertainties remain at several levels, such as the relationships of the tribes within the CSPT clade, several genera of Trachycarpeae that are not placed to subtribe, and the relationships of previously unsampled and recently described species of Coryphoideae (Bacon & al., 2012; Baker & Dransfield, 2016; Faurby & al., 2016; Baker & al., 2022; Barfod & Heatubun, 2022; Henderson & Dựng, 2022; Henderson, 2023; Henderson & al., 2023; Yao & al., 2023).

While several studies have consistently found the same topology among the tribes of the syncarpous clade (Bayton, 2005; Asmussen & al., 2006; Baker & Dransfield, 2016; Bellot & al., 2020), the topology of the CSPT clade has been more challenging to pin down (Fig. 2A–C). It is primarily the placement of Phoeniceae that changes between studies. Several studies using predominantly plastid data have found Phoeniceae and Trachycarpeae to form a sister clade to Sabaleae and Cryosophileae (Fig. 2A) (Baker & al., 2009; Bacon & al., 2012; Barrett & al., 2016; Kadam & al., 2023; Yao & al., 2023). However, Phoeniceae on its own has also been found as sister to Cryosophileae and Sabaleae (Fig. 2B), and a family-wide all-evidence approach placed Cryosophileae alone as sister to Phoeniceae and Trachycarpeae (Fig. 2C) (Faurby & al., 2016). The differences in topologies might be caused by ancient hybridisation, as indicated by gene tree discordance that is inconsistent with incomplete lineage sorting (Bellot & al., 2024).

Within the tribe Trachycarpeae, seven genera are not assigned to any subtribe, partly due to ambiguity in their phylogenetic placement and partly due to the difficulty of integrating them morphologically into the existing subtribes (Dransfield & al., 2008; Baker & Dransfield, 2016). These genera are often referred to as the unplaced Trachycarpeae (Baker & Dransfield, 2016). The placement of *Acoelorrhaphe*, *Serenoa* and *Brahea* has been consistent across the latest studies, with *Acoelorrhaphe* and *Serenoa* forming a clade sister to Livistoninae, and *Brahea* being sister to Rhapidinae (Bacon, 2010; Bacon & al., 2012; Baker & al., 2022; Yao & al., 2023). The placement of the remaining four genera, *Colpothrinax*, *Copernicia*, *Pritchardia* and *Washingtonia*, has varied across studies (Fig. 2D–E) (Asmussen & al., 2006; Baker & al., 2009, 2022; Faurby & al., 2016; Yao & al., 2023). The difficulties in placing *Copernicia*, *Pritchardia* and *Washingtonia* could be due to ancient hybridisation and introgression between these lineages (Bellot & al., 2024). Clarifying the relationships of the unplaced Trachycarpeae is essential for understanding character evolution and diversification in the most species-rich tribe of Coryphoideae, and for allowing a complete tribal-level classification of the subfamily.

At the species level, many species of Coryphoideae have never been included in a phylogenetic analysis. Only 52% were represented in an all-evidence tree containing all Sanger sequencing data available at the time (Faurby & al., 2016). Specific groups such as the syncarpous clade, New World thatch palm clade, the tribes Trachycarpeae and Phoeniceae and genera such as *Brahea* and *Lanonia* have all been investigated with well-sampled species-level phylogenetic trees (Roncal & al., 2008; Henderson & Bacon, 2011; Bacon & al., 2012; Barrett & al., 2019; Bellot & al., 2020; Pérez-Escobar & al., 2021), but others have remained sparsely sampled. Although most accepted palm genera were supported by molecular phylogenetic evidence, some coryphoid genera (notably *Licuala*, *Livistona* and *Wallichia*) were found to be non-monophyletic, requiring new generic circumscriptions (Bacon & Baker, 2011; Henderson & Bacon, 2011; Jeanson, 2011). Additional issues with generic limits may become apparent when Coryphoideae are more comprehensively sampled at the species level.

In this study, we produced a densely sampled species-level phylogenomic tree of the Coryphoideae (85% of species sampled) using target sequence capture of both historical and recent collections. Based on this tree, we investigate outstanding systematic issues such as the topology of the CSPT clade and the placement of the unplaced Trachycarpeae genera, and test generic monophyly across the subfamily. Finally, we resolve many species-level relationships within the subfamily, deepening our understanding of the evolutionary history of the coryphoid subfamily and of the palm family as a whole.

■ METHODS

Taxon sampling. — In this study we utilized sequence data from 474 Coryphoideae specimens from 418 species (Appendix 1), following the World Checklist of Vascular Plants (Govaerts & al., 2021; Govaerts, 2023) with updates based on Henderson & al. (2023) and Baker & al. (2024). Data for 357 specimens were newly generated for this study. If possible, we sequenced leaf tissue samples that were collected in the wild and preserved in silica gel. Otherwise, we either collected leaf samples from living specimens in cultivation, or sampled herbarium specimens. In addition to our newly generated sequences, we used data for Coryphoideae from Bellot & al. (2024). The final dataset covers all tribes and subtribes, and 85% of species in the subfamily (Table 1). Most of the missing species belong to three big island radiations, *Coccothrinax* (49% missing), *Licuala* (35% missing) and *Pritchardia* (20% missing). For the outgroup we obtained one species from each of the four other subfamilies of palms from Bellot & al. (2024): *Aphandra natalia* (Balslev & A.J.Hend.) Barfod, *Chrysalidocarpus ambositrae* (Beentje) Eiserhardt & W.J. Baker, *Eugeissona tristis* Griff. and *Nypa fruticans* Wurmb.

DNA extraction and sequencing. — Leaf samples were pulverized using a tissue mill (Geno Grinder, SPEX, Metuchen, New Jersey, U.S.A.) or mortar and pestle with liquid nitrogen and sterile sand. DNA was extracted using the CTAB method (Doyle & Doyle, 1987) with adjusted incubation times, the Qiagen DNeasy Plant Mini Kit (Qiagen, Venlo, Netherlands), or the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany). The quality of the extracted DNA was assessed on standard agarose gels and/or an Agilent TapeStation (Agilent, Santa Clara, California, U.S.A.). A Quantus fluorometer (Promega, Madison, Wisconsin, U.S.A.) was used to determine DNA concentration. A Covaris ultrasonicator (Covaris, Woburn, Massachusetts, U.S.A.) was used to fragment DNA to a peak fragment length of ca. 400 bp, unless the DNA was already highly fragmented. Samples were further processed in one of two different ways: In one group of samples, total genomic DNA libraries were prepared using the NEBNext Ultra II DNA Library Prep kit for Illumina with dual index primers (New England Biolabs, Ipswich, Massachusetts, U.S.A.), and enriched for the target

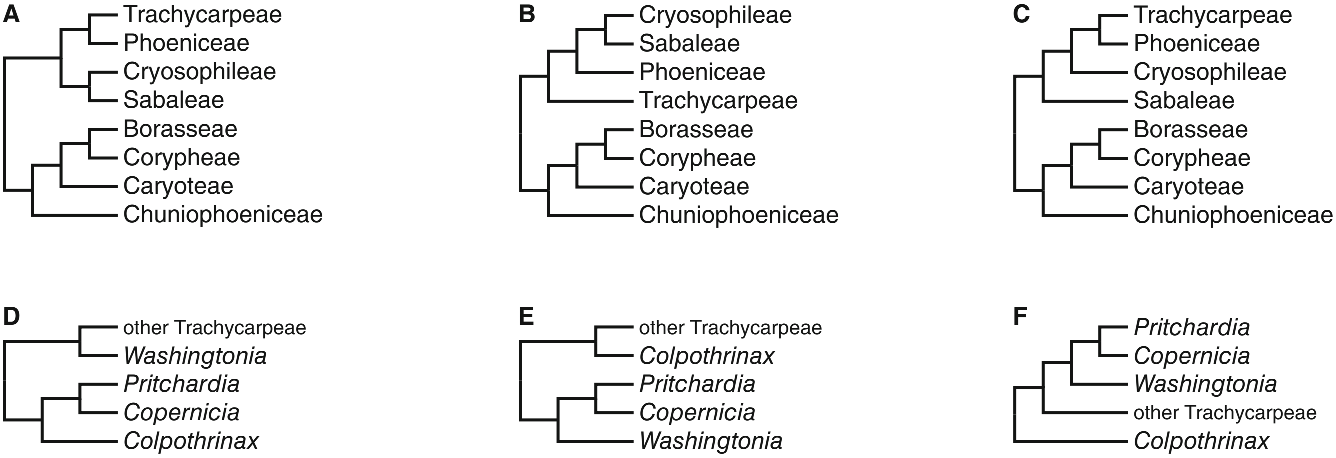

Fig. 2. Relationships among major groups of Coryphoideae recovered in previous studies. **A–C**, Relationships among the tribes; **D–F**, Placement of *Colpothrinax*, *Pritchardia*, *Copernicia* and *Washingtonia* within tribe Trachycarpeae. **A**, Found in an angiosperm-wide study using 353 nuclear loci (Baker & al., 2022), but a further analysis of the same dataset placed Phoeniceae as sister to Sabaleae but with low support (Zuntini & al., 2024); **B**, Found in several studies using few plastid and/or nuclear loci (Baker & al., 2009; Bacon & al., 2012; Barrett & al., 2016; Kadam & al., 2023; Yao & al., 2023) and in a study using plastomes (Yao & al., 2023); **C**, Found using a family-wide all-evidence approach (Faurby & al., 2016); **D**, Plastome phylogenetic tree of Arecaceae (Yao & al., 2023); **E**, Phylogenetic tree based on both nuclear and plastid DNA (Bacon & al., 2012); **F**, Phylogenomic tree based nuclear DNA (Baker & al., 2022; Zuntini & al., 2024).

Table 1. Sampling across all tribes and genera within the subfamily Coryphoideae.

Tribe	Genus	Species sampled / total species	Percentage sampled
Chuniophoeniceae (100%)	*Chuniophoenix* Burret	3 / 3	100%
	Kerriodoxa J.Dransf.	1 / 1	100%
	Nannorrhops H.Wendl.	1 / 1	100%
	Tahina J.Dransf. & Rakotoarin.	1 / 1	100%
Corypheae (80%)	*Corypha* L.	4 / 5	80%
Borasseae (91%)	*Bismarckia* Hildebr. & H.Wendl.	1 / 1	100%
	Borassodendron Becc.	2 / 2	100%
	Borassus L.	5 / 5	100%
	Hyphaene Gaertn.	6 / 8	75%
	Latania Comm. ex Juss.	3 / 3	100%
	Lodoicea Comm. ex H.Wendl	1 / 1	100%
	Medemia Württemb. ex H.Wendl.	1 / 1	100%
	Satranala J.Dransf & Beentje	1 / 1	100%
Caryoteae (87%)	*Arenga* Labill. ex DC.	21 / 24	86%
	Caryota L.	12 / 14	86%
	Wallichia Roxb.	7 / 8	88%
Phoeniceae (100%)	*Phoenix* L.	13 / 13	100%
Sabaleae (75%)	*Sabal* Adans.	14 / 16	87.5%
Cryosophileae (76%)	*Chelyocarpus* Dammer	4 / 4	100%
	Coccothrinax Sarg.	38 / 56	68%
	Cryosophila Blume	10 / 10	100%
	Hemithrinax Hook.f	3 / 3	100%
	Itaya H.E.Moore	1 / 1	100%
	Leucothrinax C.Lewis & Zona	1 / 1	100%
	Sabinaria R.Bernal & Galeano	1 / 1	100%
	Schippia Burret	1 / 1	100%
	Thrinax L.f. ex Sw.	3 / 3	100%
	Trithrinax Mart.	2 / 3	66%
	Zombia L.H.Bailey	1 / 1	100%
Trachycarpeae (77%)	*Acoelorrhaphe* H.Wendl.	1 / 1	100%
	Brahea Mart.	10 / 11	91%
	Chamaerops L.	1 / 1	100%
	Colpothrinax Schaedtler	2 / 3	66%
	Copernicia Mart. ex Endl.	18 / 22	82%
	Guihaia J.Dransf., S.K.Lee & F.N.Wei	2 / 4	50%
	Johannesteijsmannia H.E.Moore	4 / 4	100%
	Lanonia A.J.Hend. & C.D.Bacon	14 / 19	74%
	Licuala Wurmb.	121 / 167	72%
	Livistona R.Br.	23 / 28	82%
	Maxburretia Furtado	2 / 3	66%
	Pholidocarpus Blume	3 / 6	50%

(Continues)

Table 1. Continued.

Tribe	Genus	Species sampled / total species	Percentage sampled
	Pritchardia Seem. & H.Wendl.	23 / 29	79%
	Rhapidophyllum H.Wendl. & Drude	1 / 1	100%
	Rhapis L.f ex Aiton	11 / 11	100%
	Saribus Blume	8 / 9	89%
	Serenoa Hook.f.	1 / 1	100%
	Trachycarpus H.Wendl.	10 / 10	100%
	Washingtonia H.Wendl.	1 / 1	100%

The total number of species per genus is based on the World Checklist of Vascular Plants (Govaerts, 2023), resulting in *Wallichia* still being included as an accepted genus even though it has been found to be polyphyletic (Jeanson, 2011). In *Licuala*, we deviate from the World Checklist of Vascular Plants to reflect recent taxonomic changes made by Baker & al. (2024).

loci of Loiseau & al. (2019) using RNA baits (MyBaits, Arbor Biosciences, Ann Arbor, Michigan, U.S.A.) following manufacturer's protocols. In another group, library preparation and target enrichment were performed by a commercial service (Rapid Genomics, Gainesville, Florida, U.S.A.) using in-house protocols. These samples were enriched for the target loci of Heyduk & al. (2016) and de la Harpe & al. (2019), which include the loci of Loiseau & al. (2019). A single sample of *Sabal mauritiiformis* (H.Karst.) Griseb. & H.Wendl. was processed in a different way, preparing libraries using the NEXTflex DNA Rapid Sequencing Kit and NEXTflex DNA Barcodes (BIOO Scientific, Austin, Texas, U.S.A.) and enriching for the loci of Heyduk & al. (2016) only. Sequencing of enriched libraries was carried out on an Illumina MiSeq, HiSeq 300, or NovaSeq sequencer (Illumina, San Diego, California, U.S.A.). Details on the methods used for each sample can be found in the sample metadata on the Sequence Read Archive (see Appendix 1).

Sequence assembly. — We used Trimmomatic v.0.39 (Bolger & al., 2014) to remove adapter sequences (using palindrome mode) and low-quality nucleotides. The parameters for seed mismatches, palindrome clip threshold, simple clip threshold and minimum adapter length were set to the recommended values (Bolger & al., 2021). The quality of the reads was assessed using FASTQC v.0.11.9 (Andrews & al., 2019) before and after trimming. We used Hybpiper v.1.3.1 (Johnson & al., 2016) to assemble contigs from the cleaned reads. Hybpiper first mapped reads to the targeted loci using BWA v.0.7.17 (Li & Durbin, 2009), then contigs were assembled for each locus. We used "supercontigs" consisting of the target loci (exons) and flanking off-target regions, in our case non-coding regions such as introns and spacers. After assembly, we used BWA to map reads to the contigs and used Picard tools v.2.22.3 (Picard Toolkit, 2019) to de-duplicate the reads. We excluded parts of contigs covered by less than two reads following Eiserhardt & al. (2022).

Alignment. — Each locus was aligned using MAFFT v.7.475 (Katoh & Standley, 2013) with the global pair option. We used optrimAl (Shee & al., 2020) to trim the alignments with a range of gap trimming thresholds ranging from 0.1 to 0.95 with increments of 0.5. We then cleaned the alignments further using CIAlign v.1.0.18 (Tumescheit & al., 2022) using the divergent function to remove samples with highly divergent contigs for each alignment. We further used TAPER v.1.0.0 (Zhang & al., 2021) to find short segments of unusually divergent bases and trim these from the alignment.

Phylogenetic analysis. — Gene trees were inferred in IQ-TREE v.2.1.2 (Minh & al., 2020a) using partition models (Chernomor & al., 2016) with separate substitution models for exons and non-exonic regions. The boundaries between exons and non-exonic regions in each alignment were estimated based on exon contigs retrieved from HybPiper, choosing the two species with the longest exon contigs for each gene and mapping them to the supercontig alignment (Eiserhardt & al., 2022). ModelFinder (Chernomor & al., 2016; Kalyaanamoorthy & al., 2017) in IQ-TREE was used to determine the best-fitting substitution model for the exonic and non-exonic portions of each gene. We used ASTRAL-III v.5.7.7. (Zhang & al., 2018) to infer a species tree from the gene trees. To assess branch support we used the local posterior probability (LPP) provided by ASTRAL. Following Sayyari & Mirarab (2016), we classified branches with a LPP higher than 0.90 as resolved with strong support and branches with a lower LPP as resolved with weak support. The species tree was rooted on *Eugeissona tristis* Griff. (subfamily Calamoideae) based on the well-established relationships among palm subfamilies (Dransfield & al., 2008; Bellot & al., 2024). To assess the potential effect of paralogous gene copies, we conducted two ASTRAL-analyses: one with the full set of genes ("all-genes analysis"), and one only including 231 single-copy genes identified by Bellot & al. (2024) ("single-copy analysis"). We used IQ-TREE to calculate the gene concordance factor as a measure of agreement among informative gene trees for each node of the species tree, and the site concordance factor as a measure of agreement among alignment positions (Minh & al., 2020b). Finally, we added molecular branch lengths to the species tree using CASTLES-II (Tabatabaee & al., 2023). To evaluate support at the species level and above, we pruned the tree, so each species was represented only by a single sample, unless there was strong (LPP ≥ 0.9) evidence for a species to be polyphyletic, in which case multiple individuals were kept and treated as separate species for statistical purposes. Individuals with uncertain identification were also removed. In total, we removed 44 samples.

Analysis pipeline. — All scripts used for the analysis are available on https://github.com/pebgroup/coryphoideae_species_tree.

■ RESULTS

Dataset. — Across the whole dataset, ca. 29% of the raw reads are on target, with trimmed on-target reads amounting to ca. six million bases per sample on average (range: 130,311–37 million). The full dataset used to infer gene- and species trees contains sequences from 478 samples and 966 gene alignments (four loci had to be excluded due to very low contig recovery rates across all species). The average number of samples represented in each alignment is 396 (range: 67–460). Each sample is, on average, represented in 794 alignments (range: 1–965). Overall, this means that 82% of all possible sample-gene combinations are present. In total, the dataset contains 3,340,561 alignment positions, with an average alignment length of 3458 positions (range: 355–10,286). Across the whole dataset, 87% of alignment positions are variable, and 69% are parsimony informative. At the nucleotide level, the overall percentage of missing data is 31%.

Out of the total 482 samples, all but 4 are also represented in the 231 single-copy genes. Here, the average number of samples per alignment is 394 (range: 109–459), and each sample is on average represented in 190 alignments (range: 1–231), corresponding to 82% of possible sample-gene combinations being realised, as in the full dataset. In total, the 231 genes amount to 836,547 alignment positions, with an average alignment length of 3621 positions (range: 355–9128). Across the dataset, 86% of alignment positions are variable, and 66% are parsimony informative. The percentage of missing data is the same as in the full dataset, i.e. 31%.

Phylogenetic tree. — The species tree inferred from the single-copy genes (Figs. 3, 4) includes a total of 418 ingroup species and 22 subspecies and varieties. The tree inferred from all genes includes three additional species (suppl. Fig. S1). This corresponds to around 85% of species and 36% of infraspecific taxa in the coryphoid subfamily. The topologies resulting from all genes and the single-copy genes, respectively, are overall very similar, except in parts of the genus *Licuala* where support in both trees is very low (suppl. Fig. S2). The subfamily is found to be monophyletic and sister to a clade consisting of Ceroxyloideae and Arecoideae with maximum support in both analyses (Fig. 3 and suppl. Fig. S1). Molecular branch lengths inferred using CASTLES-II are shown in suppl. Fig. S3. The backbone of our phylogenetic tree is generally well supported, with all relationships among tribes having maximum support (Fig. 3 and suppl. Fig. S1). Branch support is overall high, with an average LPP of 0.81 (single-copy genes) or 0.88 (all genes) at the species level and above. This high support is achieved despite relatively high levels of gene tree conflict, as evident from quartet frequencies (suppl. Fig. S4), gene concordance factors (gCF, suppl. Fig. S5) and site concordance factors (suppl. Fig. S6). Overall, sCF values are mostly higher than gCF values (suppl. Fig. S7A), especially in the CSPT clade (suppl. Fig. S7B). Gene tree conflict overall varies significantly across the tree, with more conflict in the CSPT clade than in the syncarpous clade (suppl. Fig. S7A).

Tribes. — In both phylogenetic trees, all tribes are monophyletic and well supported and the relationships among the tribes are also identical across the trees (Fig. 3 and suppl. Fig. S1). In the syncarpous clade, Borasseae and Corypheae are sister clades and Caryoteae is then sister clade to Borasseae and Corypheae. Lastly, Chuniophoeniceae is sister to the rest of the syncarpous clade. In the CSPT clade we find Cryosophileae and Sabaleae to form a clade with Phoeniceae as its sister clade. Trachycarpeae is then sister to the aforementioned tribes.

Unplaced Trachycarpeae. — The unplaced Trachycarpeae are identically placed in both trees, with *Washingtonia*, *Copernicia* and *Pritchardia* forming a clade sister to the rest of Trachycarpeae, with *Washingtonia* as sister to *Copernicia* and *Pritchardia* (Fig. 3 and suppl. Fig. S1). These nodes are all maximally supported. The monotypic genera *Serenoa* and *Acoelorrhaphe* form a clade sister to Livistoninae with maximum support in both phylogenetic trees and *Colpothrinax* is sister to all Trachycarpeae except for *Washingtonia*, *Copernicia* and *Pritchardia* also with full support in both phylogenetic trees. Lastly, *Brahea* is sister to Rhapidinae with full support in both phylogenetic trees.

Monophyly of genera. — In both trees, most genera are recovered as monophyletic with good support. The exceptions are *Livistona*, *Sabal*, *Arenga*, *Caryota* and *Wallichia*. *Livistona exigua* J.Dransf. consistently groups outside the rest of the genus, maximally supported as sister to *Saribus*. The remainder of *Livistona* is monophyletic and maximally supported as such. *Sabal* is recovered as monophyletic, but with very low support (LPP = 0.44–0.46). *Arenga*, *Caryota* and *Wallichia* are intermixed, with *Wallichia* split into two clades, both nested in *Arenga*, and two species of the latter genus (*Arenga distincta* Mogea and *Arenga hastata* (Becc.) Whitmore) are nested within *Caryota*.

Species-level relationships. — The overall level of support for species-level relationships within genera differs slightly between the two trees (suppl. Table S1.), being higher in the all-genes tree (average LPP = 0.86) than in the single-copy tree (average LPP = 0.78). Species-level relationships are overall more strongly supported in the syncarpous clade (average LPP = 0.97 [all-genes], 0.92 [single-copy]) than in the CSPT clade (average LPP = 0.84 [all-genes], 0.76 [single-copy]). Support also varies substantially among

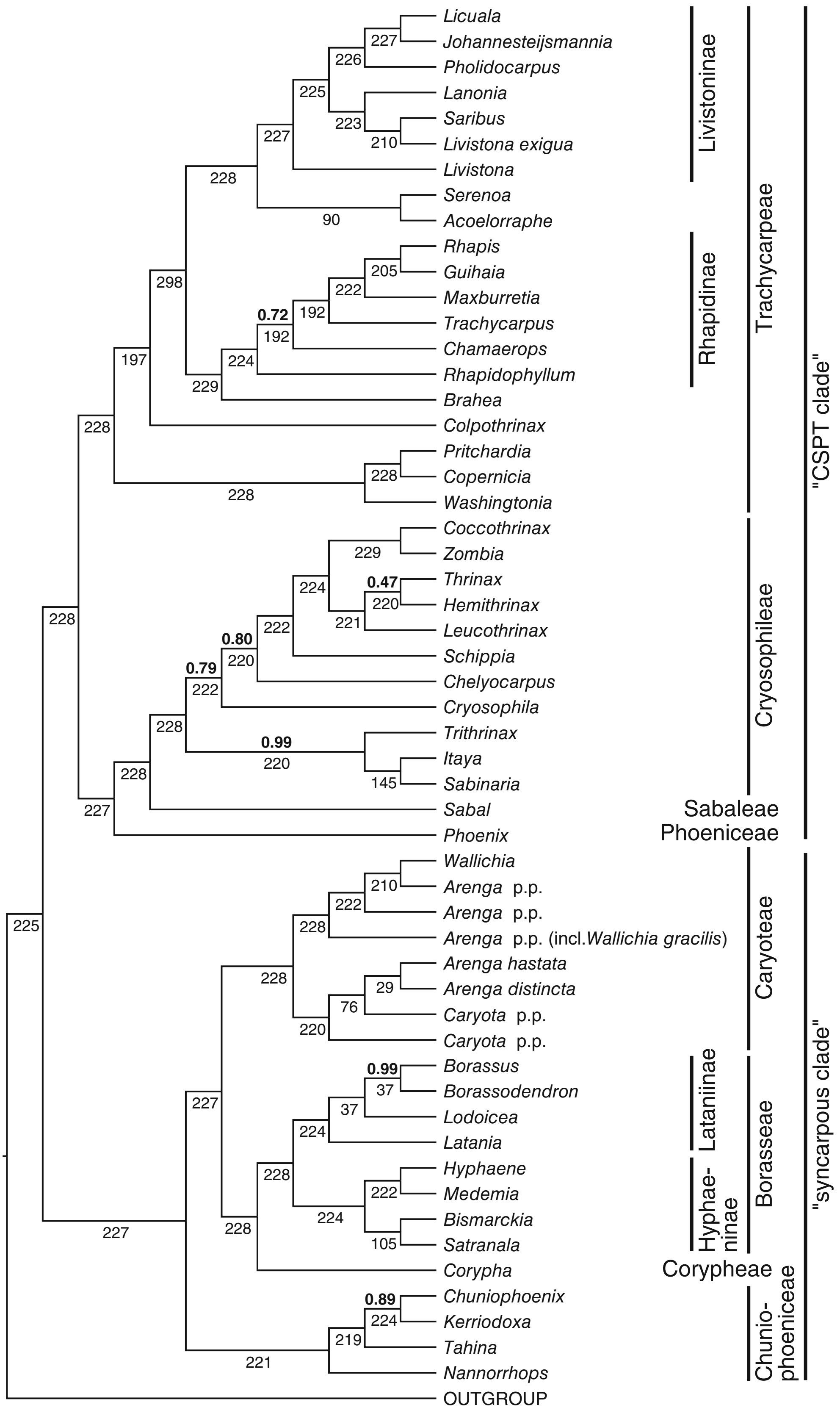

Fig. 3. Genus-level relationships within Coryphoideae as recovered in this study from 231 single-copy nuclear genes. Numbers below branches indicate the number of genes informing the branch (EN-value from ASTRAL-III). Bold numbers above branches are local posterior probability (LPP) for branches that have a LPP < 1.

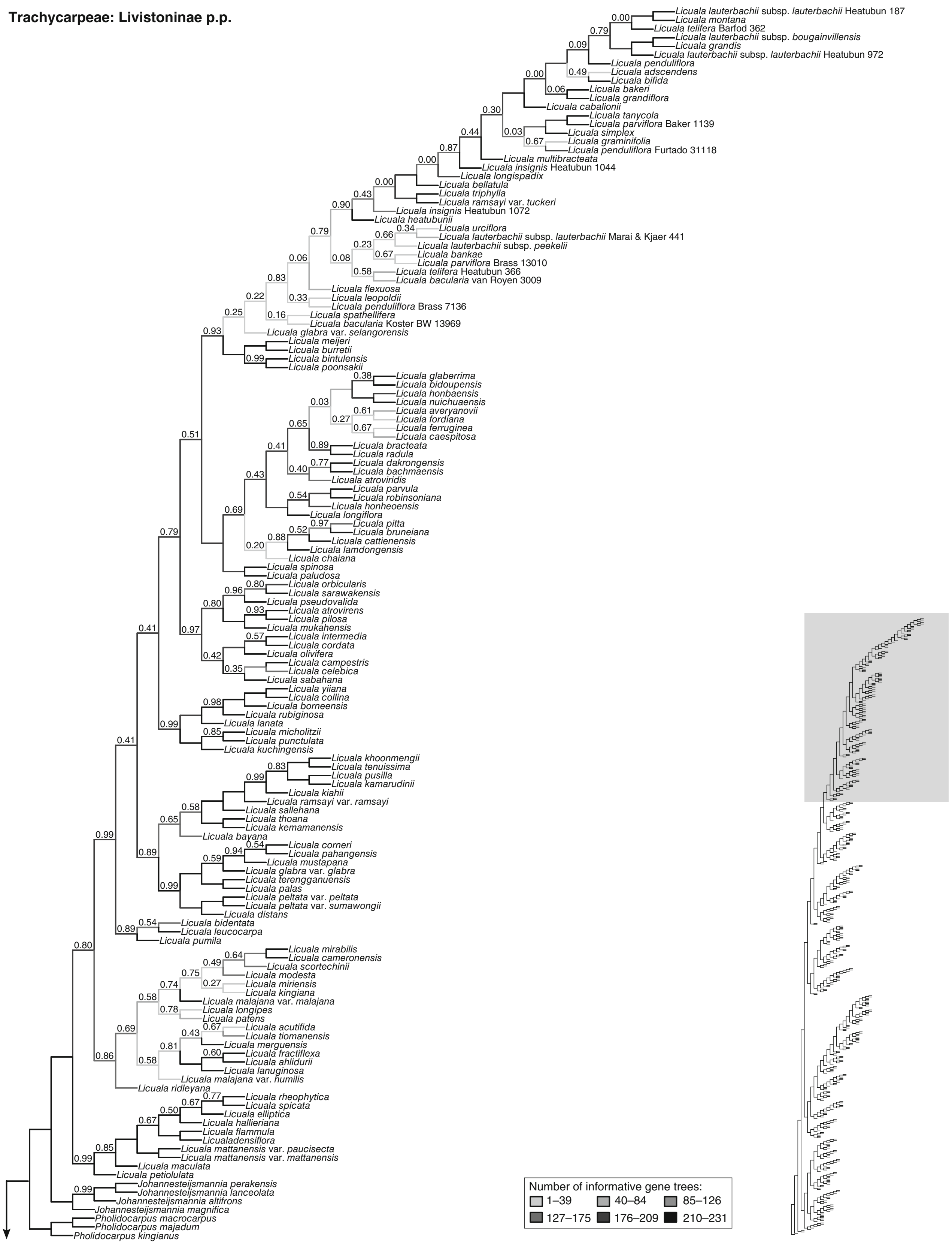

Fig. 4. Continued.

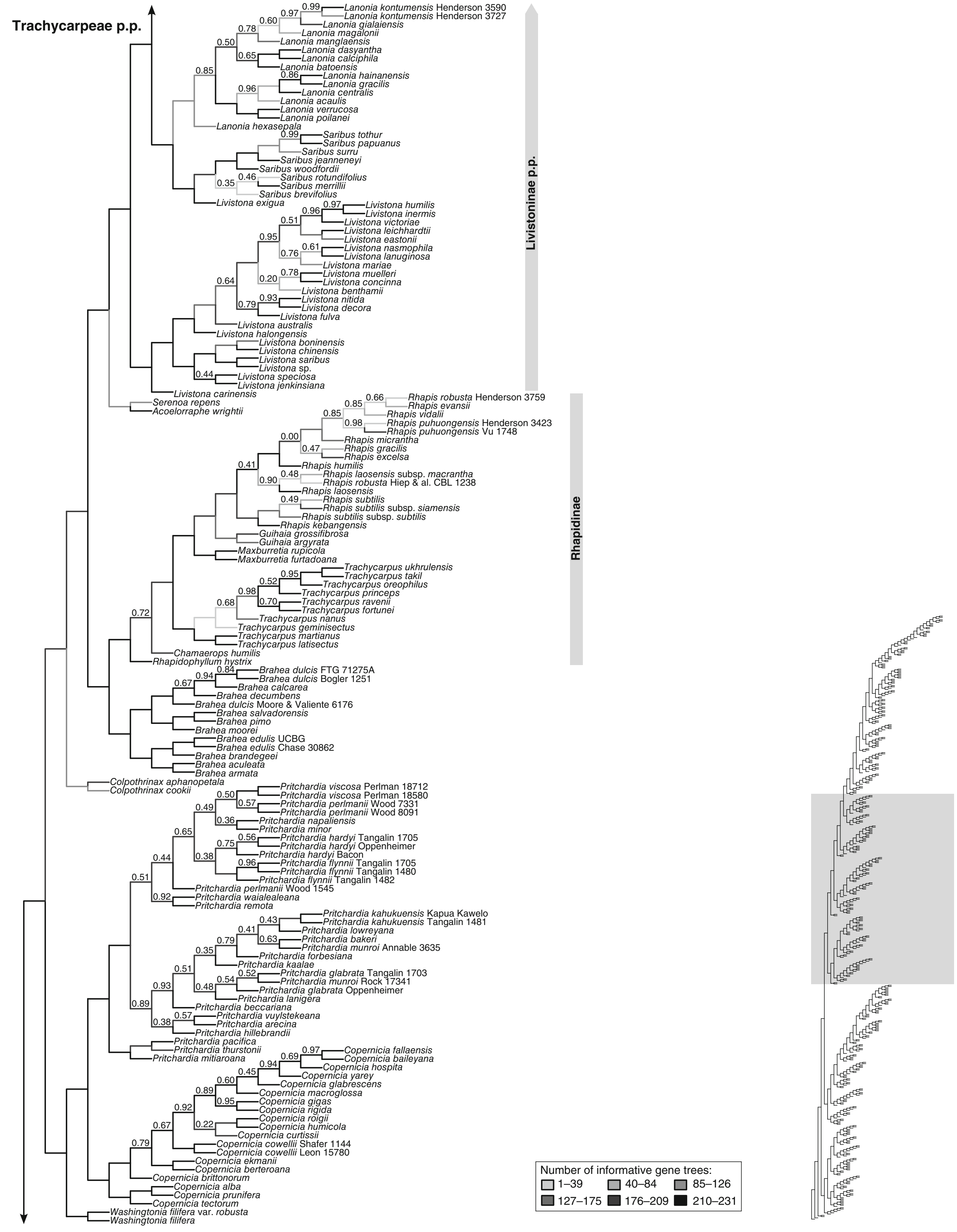

Fig. 4. Continued.

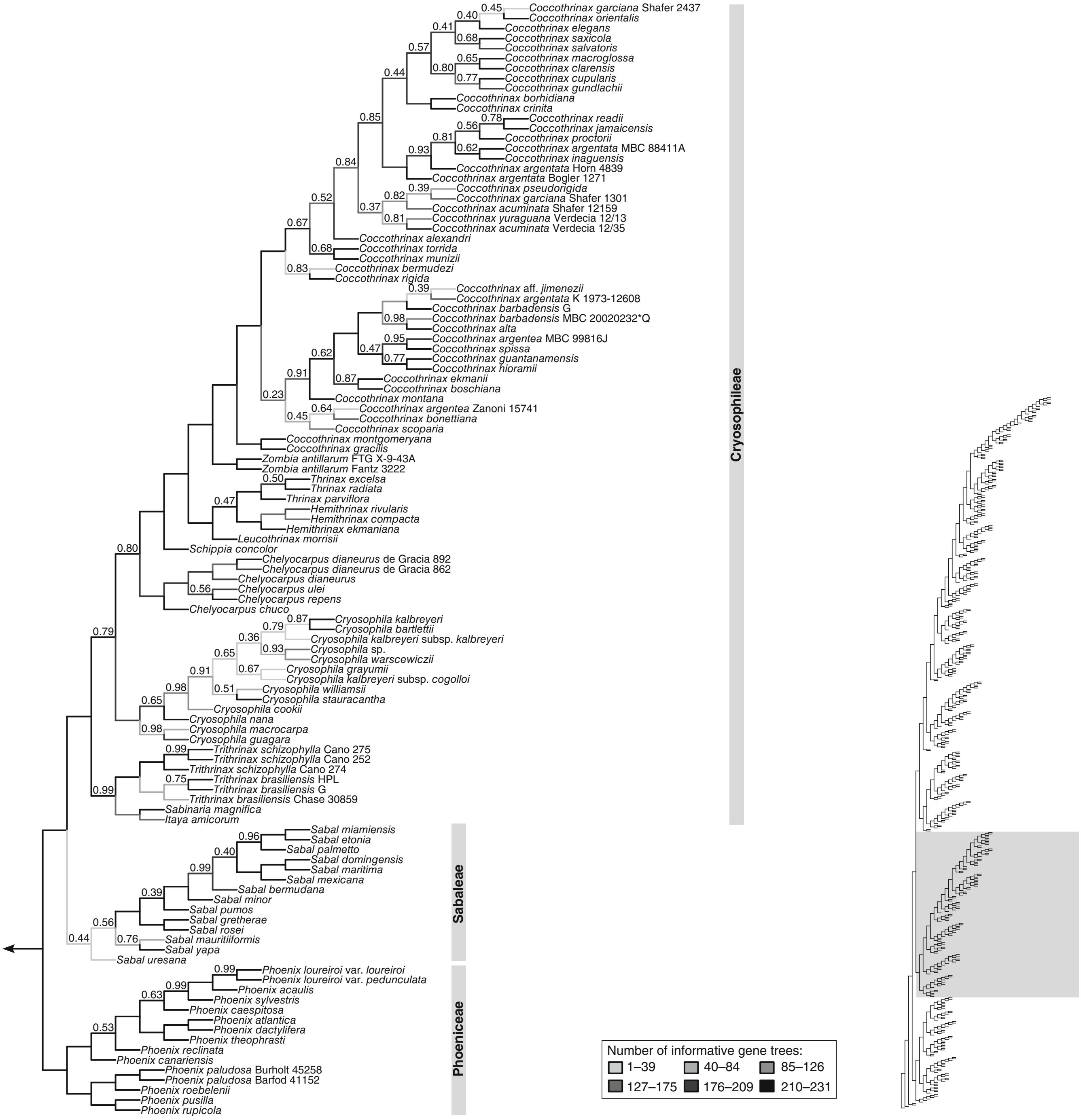

Fig. 4. Continued.

genera, ranging from LPP = 0.5 in *Thrinax* to maximum support in ten (all genes) or five (single-copy genes) genera. Relationships within larger genera, such as *Licuala* (average LPP = 0.79, all-genes tree) and *Coccothrinax* (0.80), are significantly less well-supported than relationships within smaller genera (Spearman's $r = -0.6623$, $P < 0.001$, all-genes tree, based on the number of species per genus from POWO, 2024). Average support of species-level relationships is not significantly related to the density of sampling, i.e., the proportion of species in each genus that is represented on our tree ($r = 0.31$, $P = 0.13$). *Coccothrinax*, *Corypha*, *Licuala*, *Pritchardia* and *Rhapis* are overall the least well-resolved genera with an average LPP of <0.9 in both trees.

Data availability. — Sequence data are deposited in the NCBI Sequence Read Archive BioProjects PRJNA966768, PRJNA1074667, PRJNA747880, PRJNA1131474 and

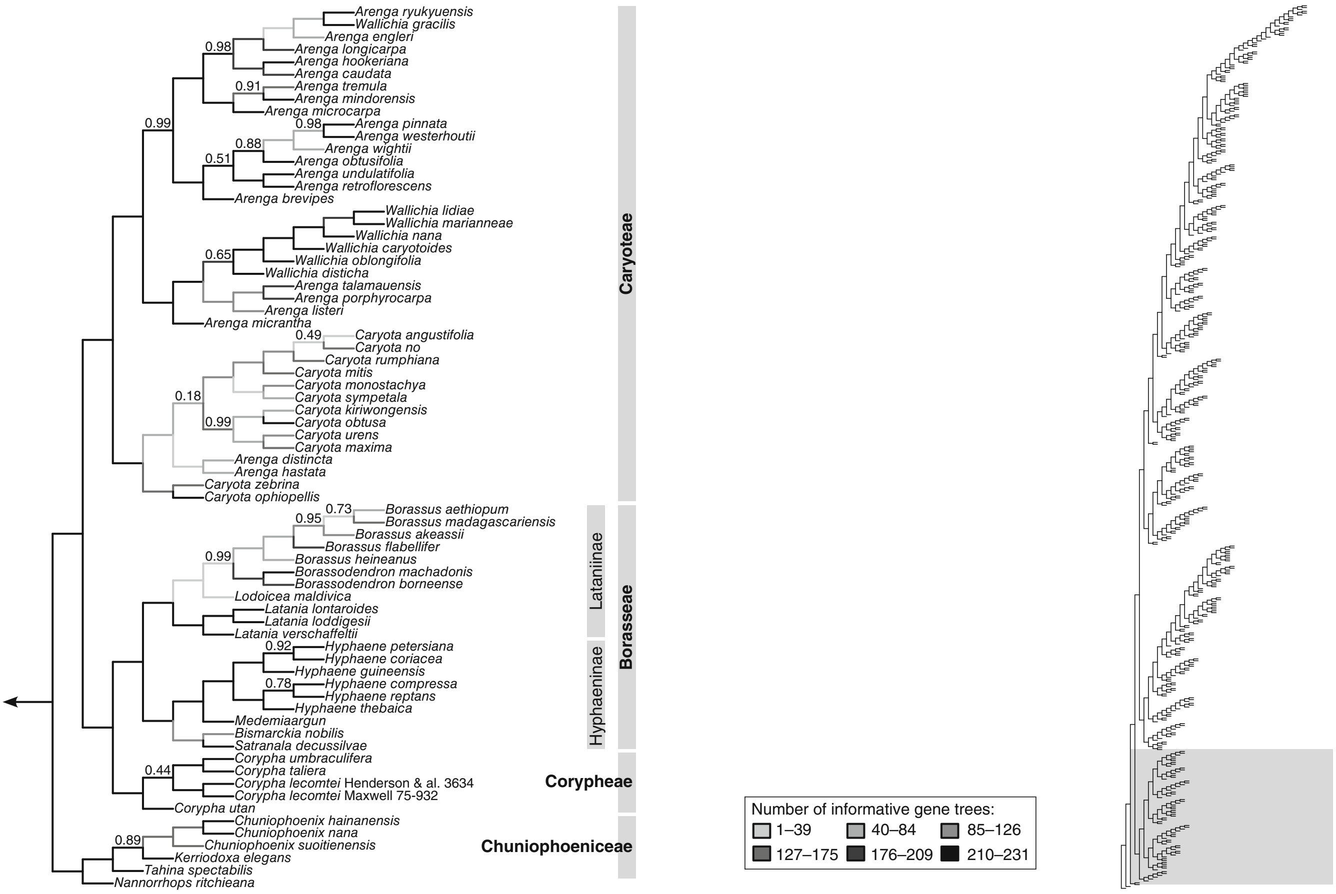

Fig. 4. Species tree of Coryphoideae inferred using 231 single-copy nuclear genes in ASTRAL-III. The colours of the branches correspond to the number of gene trees underpinning each branch. Support values are local posterior probabilities (LPP), values of 1 not shown.

PRJNA1077125 (see Appendix 1 for individual accession numbers). All other data, including alignments, gene trees and species trees can be found on Zenodo (https://zenodo.org/doi/10.5281/zenodo.13143053).

■ DISCUSSION

Subfamily Coryphoideae represents 20% of the diversity in the palm family but has until now not been investigated at the species level using phylogenomic methods. We increased the number of species sampled from around 50% (Faurby & al., 2016) to 85% and resolved many species-level relationships with strong support. We also increased the number of genes by almost two orders of magnitude from around 10 in earlier studies (Faurby & al., 2016) to ca. 1000 in our all-genes tree. Our findings confirmed many results from previous research, such as division of the subfamily into the CSPT and syncarpous clades, and the relationships among the tribes of the latter. With our greatly expanded sampling we have been able to address previously uncertain relationships with these data to determine the relationships among tribes Cryosophileae, Sabaleae, Phoeniceae and Trachycarpeae (CSPT clade), clarify the phylogenetic position of the unplaced Trachycarpeae genera, test the monophyly of genera and place more than 200 new species in the tree with strong support making this tree a robust resource for investigations into the evolution of Coryphoideae.

Our results determined that Trachycarpeae is sister to all the remaining members of the CSPT clade and that Phoeniceae is sister to a well-supported New World thatch palm clade (Cryosophileae, Sabaleae) (Fig. 3). The same topology was also found in a recent phylogenomic study of all palms at the genus level (Bellot & al., 2024). It was also found in a series of analyses of a growing angiosperm-wide dataset for 353 nuclear genes (Baker & al., 2022; https://treeoflife.kew.org release 3.0) (Fig. 2A), although a further analysis of this dataset found a poorly supported alternative placement for Phoeniceae as sister to Sabaleae (Zuntini & al., 2024). Thus, the balance of nuclear phylogenomic evidence strongly favours our findings. Why, then, did so many earlier studies recover a different topology where Phoeniceae and Trachycarpeae form a clade that is sister to Cryosophileae and Sabaleae (Fig. 2A) (Baker & al., 2009; Bacon & al., 2012; Barrett & al., 2016; Kadam & al., 2023; Yao & al., 2023)? While it is possible that the few nuclear genes included in those studies did not accurately reflect the phylogeny of the nucleus due to incomplete lineage sorting, it seems more likely that the divergent topology is due to evolutionary discordance between the nucleus and the plastid. This hypothesis is supported by a recent analysis of whole plastomes (Yao & al., 2023), which strongly supports the divergent topology. Discordance in the evolutionary history of the cytoplasmic and nuclear DNA could be caused by ancient hybridisation events (Soltis & Soltis, 2009; Stull & al., 2020). This was confirmed by a recent study of all palm genera which found that the discordance among gene trees for the placement of Phoeniceae was inconsistent with incomplete lineage sorting hinting at ancient gene flow (Bellot & al., 2024).

The positions of the unplaced Trachycarpeae genera are all resolved with high support in our tree using single-copy genes (Fig. 3). We find *Washingtonia*, *Copernicia* and *Pritchardia* to form a clade which is sister to the rest of Trachycarpeae (Fig. 3). *Colpothrinax* is sister to a clade comprising the rest of Trachycarpeae except the three aforementioned genera (Fig. 3). *Brahea* is found to be a sister clade to Rhapidinae while *Serenoa repens* and *Acoelorrhaphe wrightii* form a clade sister to Livistoninae. The placement of all the unplaced Trachycarpeae is the same across both the single-copy gene tree and the all-genes tree and identical to the findings of a study focusing on Trachycarpeae using three nuclear and three plastid genes (Bacon & al., 2012) and a study focusing on Arecaceae at the genus level (Bellot & al., 2024) using family-specific and universal angiosperm probe sets (Johnson & al., 2019; Loiseau & al., 2019). With a comprehensive nuclear phylogenomic species-level phylogenetic tree now in place, complementing plastid genomic evidence (Yao & al., 2023) and nuclear evidence (Bellot & al., 2024), we are now well-placed to identify taxonomic solutions for the unplaced genera in a future revision of the current phylogenetic classification of palms (Baker & Dransfield, 2016), which is in preparation.

Across both our trees, all but five genera were found to be monophyletic with good support. All three genera of tribe Caryoteae (i.e., *Arenga*, *Caryota* and *Wallichia*) were non-monophyletic. Two species of Bornean *Arenga*, *Arenga distincta* and *Arenga hastata*, were found to be nested within *Caryota*. Neither *A. distincta* or *A. hastata* have been included in a phylogenetic analysis with other species of *Arenga* and *Caryota* before, although they have been sequenced for studies of DNA barcoding and a study of Asparagales (Jeanson & al., 2011; Chen & al., 2013). As our analysis shows, they are closely related to each other, possibly hybridise in the wild (Mogea, 2003), and may in fact represent a single species (Jeanson & al., in press). Both species lack the doubly pinnate leaves which are unique to the genus *Caryota*, but they do share other leaf similarities, notably the divided eophyll (seedling leaf) and apical terminal leaflet (in adult leaves). Pollen of *A. hastata* also has an intectate clavate ectexine, as do some species of *Caryota*. The case for broadening *Caryota* to include these two species is strong and is supported by currently unpublished evidence from Sanger sequencing (Jeanson & al., in press), although work is needed to fully establish the morphological characters underpinning this new circumscription of the genus. Also in Caryoteae, *Wallichia* was found to be polyphyletic and nested within *Arenga*. This is unsurprising given earlier work (Jeanson, 2011) and it has already been suggested that *Wallichia* should be reduced into synonymy with *Arenga* (Baker & Dransfield, 2016). Our findings support this course of action, but further work is needed to address the morphological implications and implement the necessary nomenclatural changes (Jeanson & al., in press).

The genus *Livistona* (Trachycarpeae, Livistoninae) was also found to be polyphyletic due to one species, *Livistona exigua* from Borneo, being sister to *Saribus* Blume. *Livistona exigua* is known from only three collections from Brunei Darussalam in ridgetop kerangas forest (Dransfield, 1977). Morphologically, *L. exigua* is close to the genus *Livistona*, except for one morphological feature: it is a small, understorey palm, whereas all other species are robust, often tall tree palms (Dransfield, 1977). Our trees provide strong evidence that *L. exigua* is in fact not correctly placed in *Livistona*. One solution would be to include it within *Saribus*, but there are morphological inconsistencies with this genus, which comprises robust tree palms, with trifurcating inflorescences and large fruits. None of these characters is found in *L. exigua*. From a morphological perspective, it would be more reasonable to erect a new genus for *L. exigua*, a solution that would be consistent with the all-genes topology. Further work is required to test the phylogenetic placement of *L. exigua* before reaching a conclusion.

The species-level relationships in the phylogenetic tree using all genes were overall more strongly supported compared to the phylogenetic tree using only single-copy genes. One might have expected the opposite, if paralogous gene copies increase gene-tree discordance and thus reduce support in the all-genes tree. Instead, the superior resolution in the all-genes tree is likely caused by the higher number of genes providing additional resolution compared to the narrower selection of the single-copy genes. In large parts of the subfamily, there is little difference between the all-genes and single-copy trees (suppl. Fig. S2), suggesting that paralogous gene copies may have little effect on our results (Yan & al., 2022). However, in the largest genera, and especially *Licuala*, the two analyses differ notably (suppl. Fig. S2). These genera are also characterized by relatively low average support. It is tempting to think that a high rate of gene or genome duplications might be the cause of low support; however, in that case, support should increase when excluding multi-copy genes, which it does not (suppl. Table S1). Instead, it seems likely that fast diversification has led to low phylogenetic signal at the gene tree and/or high rates of incomplete lineage sorting level in these large genera. At least *Licuala* and *Coccothrinax* have previously been identified as having elevated diversification rates (Baker & Couvreur, 2013). A correlation between diversification rate and gene-tree conflict has recently been found in a phylogenomic analysis across all angiosperms (Zuntini & al., 2024). However, a time-calibrated phylogenetic tree would be required to formally disentangle these effects in Coryphoideae.

Although we were able to increase species-level sampling from ca. 50% (Faurby & al., 2016) to ca. 85%, not least due to target capture methodology rendering old specimens accessible (Brewer & al., 2019), many species remained beyond our reach. Although 12 of the non-monotypic genera are now fully sampled at the species level, most of these are small, *Phoenix* (13 spp.) being the largest one. In most genera with near-complete sampling, species are missing not because material was not available, but because the available herbarium material did not yield useful sequence data. Further sequencing of herbarium material could be attempted in these taxa. However, in other cases, we were unable to procure material, a problem that is best illustrated by the sparsely sampled genus *Coccothrinax*, a Caribbean radiation that is incompletely represented in European and North American herbaria. Focused studies on individual clades or regions are now needed to further improve the tree, ideally involving field work and/or visits to herbaria in areas where the missing species occur.

■ CONCLUSION

Our study is a significant leap forward in both species sampled and genes used for the Coryphoideae, giving us an unprecedented insight into the evolution of this important subfamily of palms. We find Trachycarpeae to be sister to a clade consisting of Phoeniceae, Sabaleae and Cryosophileae, a topology that differs from previous phylogenetic trees based on chloroplast data, hinting at ancient gene flow. We consolidate the placements of the unplaced Trachycarpeae and discover polyphyly in the genera *Arenga, Caryota* and *Wallichia* of Caryoteae, and *Livistona* of Trachycarpeae, paving the way for future taxonomic work on these genera. Our analysis sheds light on the species-level relationships of coryphoid palms and resolves these relationships with strong average support for 24 out of 31 genera. Consequently, our phylogenetic tree can act as a springboard for future studies into the general evolution and ecology of this important palm group. For example, the subfamily is famous for its several island radiations such as *Pritchardia* of the Hawaiian archipelago, *Coccothrinax* and *Copernicia* in Cuba and Hispaniola and *Licuala* in Melanesia and Malesia. Our phylogenetic tree will allow thorough investigations into the origin of these radiations and hence the drivers of island biodiversity. Other potential applications of the tree could include studies on the evolution of the very variable leaf morphology of the subfamily. However, many challenges still remain in phylogenomic research on the Coryphoideae, especially at the species level, and focused studies on individual clades should be the priority to fully unlock the potential of the subfamily for informing evolutionary research.

■ AUTHOR CONTRIBUTIONS

Conceptualisation: OW, PP, WJB, WLE; Formal analysis: OW, PdLF, WLE; Funding acquisition: WLE; Investigation: PP, AC, CDB, OW; Methodology: OW, SB, PdLF, WLE; Supervision: ASB, WJB, WLE; Visualisation: OW, WLE; Writing – original draft: OW; Writing – review & editing: all authors.

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Appendix 1. Specimens used for phylogenetic analysis of the coryphoid palms. Each specimen is described as "Taxon, country: *collector and collection number* (Herbarium)" or "Taxon, country (living collection and accession number)" where no voucher could be collected. Asterisk (*) indicates sequences newly obtained in this study.

Acoelorrhaphe wrightii H.Wendl. ex Becc., Belize: *Forest, F. 478* (K), SRR29749372. ***Aphandra natalia*** (Balslev & A.J.Hend.) Barfod., cultivated in the U.S.A.: *Baker, W.J. 985* (K), SRR29749267. ***Arenga brevipes*** Becc., Malaysia: *Hoare, A. 14* (K), SRR24760075*. ***Arenga caudata*** H.E.Moore, Vietnam: *Nguyen, V.D. 1705* (K), SRR31682203*. ***Arenga distincta*** Mogea, Malaysia: *B. Kuhnhäuser & al. 60* (K), SRR24760002*. ***Arenga engleri*** Becc., Taiwan: *Oldham, R. 626* (K), SRR24759936*. ***Arenga hastata*** Whitmore, Malaysia: *Utteridge, T.M.A. & al. 501* (K), SRR24760117*. ***Arenga hookeriana*** Whitmore, Malaysia: *Cooke 6* (K), SRR31682202*. ***Arenga listeri*** Becc., Australia: *Lister s.n.* (K), SRR24760108*. ***Arenga longicarpa*** C.F.Wei, China: *Jeanson, M. 85* (NY), SRR24759983*. ***Arenga micrantha*** C.F.Wei, India: *Pradhan s.n.* (K), SRR24760102*. ***Arenga microcarpa*** Becc., Papua New Guinea: *Baker, W.J. 577* (K), SRR24760072*. ***Arenga mindorensis*** Becc., Philippines: *McGregor, R.C. 12395* (K), SRR24760067*. ***Arenga obtusifolia*** Mart., Thailand: *Barfod, A.S. 141643* (AAU), SRR24760209*. ***Arenga pinnata*** Merr., Malaysia: *Petoe 52* (AAU), SRR24760183*. ***Arenga porphyrocarpa*** H.E.Moore, Indonesia: *Lobb 129/1* (K), SRR24760175*. ***Arenga retroflorescens*** H.E.Moore & Meijer, Malaysia: *Moore, H.E. 9162* (K), SRR24760048*. ***Arenga ryukyuensis*** A.J. Hend., Japan: *Furuse 2133* (K), SRR24760036*. ***Arenga talamauensis*** Mogea, Indonesia: *de Wilde, J.J.F.E. 16625* (K), SRR24760090*. ***Arenga tremula*** Becc., Philippines: *Merrill, E.D. 11635* (K), SRR24759971*. ***Arenga undulatifolia*** Becc., Malaysia: *Petoe 55* (AAU), SRR29749357. ***Arenga westerhoutii*** Griff., Vietnam: *Nguyen, V.D. 1443* (K), SRR31682191*. ***Arenga wightii*** Griff., India: *Saldanha 16818* (K), SRR24760079*. ***Bismarckia nobilis*** Hildebrandt & H.Wendl., cultivated in the U.K.: *Bayton, R.P. 43* (K), SRR29749360. ***Borassodendron borneense*** J.Dransf., Malaysia: *Dransfield, J. 5953* (K), SRR29749359. ***Borassodendron machadonis*** Becc., cultivated in the U.K. (K: 1989-3394), SRR24759921*. ***Borassus aethiopum*** Mart., Burkina Faso: *Bayton, R.P. 58* (K), SRR24760160*. ***Borassus akeassii*** Bayton, Ouédr. & Guinko, Burkina Faso: *Bayton, R.P. 68* (K), SRR24760014*. ***Borassus flabellifer*** L., Thailand: *Wilkin & al. 1160* (K), SRR29749358. ***Borassus heineanus*** Becc., Papua New Guinea: *Banka, R. s.n* (K), SRR24759962*. ***Borassus madagascariensis*** Bojer ex Jum. & H.Perrier, Madagascar: *Bayton, R.P. & Ranaivojaona, R. 52* (K), SRR24760149*. ***Brahea aculeata*** H.E.Moore, cultivated in the U.S.A. (Montgomery Botanical Center: 20040449Q), SRR28987074. ***Brahea armata*** S.Watson, cultivated in the U.S.A.: *Cano, Á. ACS301* (FTG), SRR28987124. ***Brahea brandegeei*** H.E.Moore, unknown origin: *HBG 89871; HNT 13043* (HBG), SRR24760137*. ***Brahea calcarea*** Liebm., cultivated in the U.S.A.: *Cano, Á. ACS300* (FTG), SRR28987121. ***Brahea decumbens*** Rzed., Mexico: *Dunkin, D., HBG 35650; HNT 13038* (HBG), SRR24759909*. ***Brahea dulcis*** Mart., cultivated in the U.S.A.: *Bogler 1251* (FTG), SRR28987123; Mexico: *Moore Jr., H.E. & Valiente M., A. 6176* (K), SRR24759950*; cultivated in the U.S.A. (FTG: 71275A), SRR28986786. ***Brahea edulis*** H.Wendl. ex S.Watson, cultivated in California (University of California Botanical Garden: 2003.0149; 1869963, UC 1971077), SRR24760004*; cultivated in the U.K.: *Chase, M.W. 30862* (K), SRR29749346. ***Brahea moorei*** L.H.Bailey ex H.E.Moore, cultivated in California (University of California Botanical Garden: 88.0345; UC 197077), SRR24759901*. ***Brahea pimo*** Becc., Mexico: *Green & Bredeson HBG 52194; HNT 13045* (HBG), SRR24759892*. ***Brahea salvadorensis*** H.Wendl. ex Becc., Guatemala: *Baker, W. 1028* (HBG), SRR24760125*. ***Caryota angustifolia*** Zumaidar & Jeanson, Indonesia: *Dransfield, J. 3730* (K), SRR24759890*. ***Caryota kiriwongensis*** Hodel, Thailand: *Jeanson, M. 79* (NY), SRR24759934*. ***Caryota maxima*** Blume, Thailand: *Barfod, A.S. 45210* (AAU), SRR24759933*. ***Caryota mitis*** Lour., Malaysia: *Petoe 48* (AAU), SRR24759935*. ***Caryota monostachya*** Becc., Vietnam: *Nguyen, V.D. 1337* (K), SRR31682180*. ***Caryota no*** Becc., Malaysia: *Eiserhardt, W.L. & al. 157* (AAU), SRR24759932*. ***Caryota obtusa*** Griff., Vietnam: *Henderson, A. 3412* (NY), SRR24759931*. ***Caryota ophiopellis*** Dowe, cultivated in the U.S.A.: *Baker, W.J. 987* (FTG), SRR31682170*. ***Caryota rumphiana*** Mart., Papua New Guinea: *Baker, W.J. 646* (K), SRR29749340. ***Caryota sympetala*** Gagnep., Vietnam: *Henderson, A. 3541* (NY), SRR24759930*. ***Caryota urens*** L., China: *Jeanson, M. 84* (NY), SRR24760222*. ***Caryota zebrina*** Hambali, Maturb., Heatubun & J.Dransf., Indonesia: *Heatubun, C. 273* (K), SRR31682169*. ***Chamaerops humilis*** L., cultivated in Spain: *Barrow, S. 76* (K), SRR29749338. ***Chelyocarpus chuco*** H.E.Moore, cultivated in the U.S.A.: *Bogler 1254* (FTG), SRR29749337. ***Chelyocarpus dianeurus*** H.E.Moore, cultivated in Colombia (Jardín Botánico del Quindío: 597), SRR28987111; *de Gracia Cruz, J.E. 862* (MO), SRR31682175*; Panama: *de Gracia Cruz, J.E. 892* (MO), SRR31682174*. ***Chelyocarpus repens*** F.Kahn & K.Mejia, cultivated in the U.S.A. (FTG: 88393A), SRR28987071. ***Chelyocarpus ulei*** Dammer, cultivated in the U.S.A.: *Frantz 3604* (FTG), SRR28987070. ***Chrysalidocarpus ambositrae*** (Beentje) Eiserhardt & W.J.Baker., Madagascar: *Rakotoarinivo, M. 169* (K), SRX11554836. ***Chuniophoenix hainanensis*** Burret, Vietnam: *Henderson, A. 3986* (NY), SRR24760221*. ***Chuniophoenix nana*** Burret, cultivated in the U.K.: *Bayton, R.P. 1A* (K), SRR29749336. ***Chuniophoenix suoitienensis*** A.J.Hend., Vietnam: *Henderson, A. 3659* (NY), SRR24760223.* ***Coccothrinax acuminata*** Sarg. ex Becc., Cuba: *Verdecia Pérez, R.M. 12/35* (NY), SRR24760220*; Cuba: *Shafer, J.A. 12159* (Harvard), SRR24760224*. ***Coccothrinax*** aff. ***jimenezii***, Haiti: *Zanoni, T.A. 33375* (NY), SRR24760113*. ***Coccothrinax alexandri*** León, cultivated in the U.S.A. (Montgomery Botanical Center: 20080412), SRR28987100. ***Coccothrinax alta*** Becc., cultivated in the U.S.A. (Montgomery Botanical Center: 20020232B), SRR28986781. ***Coccothrinax argentata*** L.H.Bailey, cultivated in the U.S.A.: *Horn, J.W. 4839* (FTG), SRR28986800; cultivated in the U.S.A.: *Bogler 1271* (FTG), SRR28986789; cultivated in the U.S.A. (Montgomery Botanical Center: 88411A), SRR28986785; cultivated in the U.K. (K: 1973-12608), SRR29749334. ***Coccothrinax argentea*** Sarg. ex K.Schum., cultivated in the U.S.A. (Montgomery Botanical Center: 99816J), SRR28987116; Dominican Republic: *Zanoni, T.A. 15741* (NY), SRR24759992*. ***Coccothrinax barbadensis*** Becc., cultivated in the U.S.A. (Montgomery Botanical Center: 20020232*Q), SRR28986801; cultivated in Switzerland (G), SRR28987115. ***Coccothrinax bermudezii*** León, Cuba: *Bro. León 18597* (Harvard), SRR24760219*. ***Coccothrinax bonettiana*** A.J.Hend., Elad.Fernández & C.D.Bacon, Dominican Republic: *Mejía Pimentel, M.M. 23684* (NY), SRR24760110*. ***Coccothrinax borhidiana*** O.Muñiz, cultivated in the U.S.A.: *Cano, Á. ACS270* (FTG), SRR28987132. ***Coccothrinax boschiana*** M.M.Mejía & R.G.García, Dominican Republic: *Garciá G., R.G. 6059* (NY), SRR24760121*. ***Coccothrinax clarensis*** León, cultivated in the U.S.A. (Montgomery Botanical Center: 96375A), SRR28987114. ***Coccothrinax crinita*** Becc., cultivated in the U.S.A. (FTG: 63412), SRR28987133. ***Coccothrinax cupularis*** O.Muñiz & Borhidi, cultivated in the U.S.A. (FTG: 87226G), SRR28987113. ***Coccothrinax ekmanii*** Burret, cultivated in the U.S.A. (Montgomery Botanical Center: 83205H), SRR28987112. ***Coccothrinax elegans*** O.Muñiz & Borhidi, cultivated in the U.S.A. (Montgomery Botanical Center: 20030771A), SRR28987110. ***Coccothrinax fragrans*** Burret, cultivated in the U.S.A. (FTG: 20020214C), SRR28987109. ***Coccothrinax garciana*** León, Cuba: *Shafer, J.A. 1301* (NYBG), SRR24760118*; Cuba: *Shafer, J.A. 2437* (Harvard), SRR24760119*. ***Coccothrinax gracilis*** Burret, cultivated in the U.S.A. (Montgomery Botanical Center: 99818A), SRR28987108. ***Coccothrinax guantanamensis*** O.Muñiz & Borhidi, cultivated in the U.S.A. (Montgomery Botanical Center: 20080413C), SRR28986780. ***Coccothrinax gundlachii*** León, cultivated in the U.S.A.: *Cano, Á. ACS267* (FTG), SRR28987131. ***Coccothrinax hioramii*** León, cultivated in the U.S.A. (Montgomery Botanical Center: 97227A), SRR28987082. ***Coccothrinax inaguensis*** Read, cultivated in the U.S.A. (Montgomery Botanical Center: 20020880), SRR28987107. ***Coccothrinax jamaicensis*** Read, cultivated in the U.S.A. (Montgomery Botanical Center: 931006B), SRR28986793. ***Coccothrinax macroglossa*** O.Muñiz & Borhidi, cultivated in the U.S.A. (Montgomery Botanical Center: 20100543A), SRR28986779. ***Coccothrinax montana*** Burret, cultivated in the U.S.A. (FTG: 20061125A), SRR28987081. ***Coccothrinax montgomeryana*** A.J.Hend., Elad.Fernández & C.D.Bacon, Dominican Republic: *Zanoni, T.A. 34387* (NY), SRR24760111*. ***Coccothrinax munizii*** Borhidi, cultivated in the U.S.A. (Montgomery Botanical Center: 20120063), SRR28987089. ***Coccothrinax orientalis*** O.Muñiz & Borhidi, cultivated in the U.S.A. (Montgomery Botanical Center: 20030772), SRR28987077. ***Coccothrinax proctorii*** Read, cultivated in the U.S.A. (Montgomery Botanical Center: 96211A), SRR28986799. ***Coccothrinax pseudorigida*** León, Cuba: *Shafer, J.A. 2924* (NYBG), SRR24760120*. ***Coccothrinax readii*** H.J.Quero, cultivated in the U.S.A. (FTG: 20040777B), SRR28986788. ***Coccothrinax rigida*** Becc., Cuba: *Wright, C. 3220* (K), SRR24760115*. ***Coccothrinax salvatoris*** León, cultivated in the U.S.A.: *Bogler 1273* (FTG), SRR28987098. ***Coccothrinax saxicola*** León, cultivated in the U.S.A. (Montgomery Botanical Center: 20030768D), SRR28986798. ***Coccothrinax scoparia*** Becc., Dominican Republic: *Zanoni, T.A. 33615* (NY), SRR24760114*. ***Coccothrinax spissa*** L.H.Bailey, cultivated in the U.S.A. (Montgomery Botanical Center: 97942F), SRR28987076. ***Coccothrinax torrida*** Morici & Verdecia, cultivated in the U.S.A. (Montgomery Botanical Center: 20120061), SRR28987105. ***Coccothrinax yuraguana*** León, Cuba: *Verdecia Pérez, R.M. 12/13* (NYBG), SRR24760112*; Cuba: *León 18468* (Harvard), SRR24760109*. ***Colpothrinax aphanopetala*** R.Evans, NA: *Henderson & Herrera 702* (K), SRR33916396. ***Colpothrinax cookii*** Read, Panama: *Croat, T.B. 22669* (K), SRR24759989*. ***Copernicia alba*** Morong, Paraguay: *Cano, Á. ACS308* (FTG), SRR28987083. ***Copernicia baileyana*** León, cultivated in the

Appendix 1. Continued.

U.S.A. (Montgomery Botanical Center: 931086H), SRR28987078. ***Copernicia berteroana*** Becc., cultivated in the U.S.A. (Montgomery Botanical Center: 20060681A), SRR28987104. ***Copernicia brittonorum*** León, Cuba: *Howard & al. 228* (A), SRR24759988*. ***Copernicia cowellii*** Britton & P.Wilson, Cuba: *Fr. León 15780* (NY), SRR24759990*; Cuba: *Shafer, J.A. 1144* (A), SRR24759987*. ***Copernicia curtissii*** Becc., Cuba: *Curtiss, A.H. 435* (K), SRR24759991*. ***Copernicia ekmanii*** Burret, cultivated in the U.S.A. (Montgomery Botanical Center: 20060039A), SRR28987103. ***Copernicia fallaensi***s León, cultivated in the U.S.A. (FTG: 88531F), SRR28987072. ***Copernicia gigas*** Ekman ex Burret, cultivated in the U.S.A. (FTG: 2000834A), SRR28987073. ***Copernicia glabrescens*** H.Wendl. ex Becc., cultivated in the U.S.A.: *Bogler 1284* (FTG), SRR28987120. ***Copernicia hospita*** Mart., cultivated in the U.S.A.: *Fantz, P.R. 4129* (FTG), SRR28987119. ***Copernicia humicola*** León, Cuba: *Fr. Leon 16379* (NY), SRR24759986*. ***Copernicia macroglossa*** Schaedtler, cultivated in the U.S.A. (Montgomery Botanical Center: 96372A), SRR28987102. ***Copernicia prunifera*** H.E.Moore, cultivated in the U.S.A. (Montgomery Botanical Center: 9797H), SRR28987101. ***Copernicia rigida*** Britton & P.Wilson, cultivated in the U.S.A. (FTG: 57725E), SRR28987099. ***Copernicia roigii*** León, Cuba: *Barboza, N. 824* (NY), SRR24759985*. ***Copernicia tectorum*** Mart., cultivated in the U.S.A.: *Bogler 1288* (FTG), SRR28987118. ***Copernicia yarey*** Burret, cultivated in the U.S.A.: *Bogler 1289* (FTG), SRR28987117. ***Corypha lecomtei*** Becc. ex Lecomte, Thailand: *Maxwell, J.F. 75-932* (AAU), SRR24759982*; Vietnam: *Henderson, A. & al. 3634* (K), SRR24759981*. ***Corypha taliera*** Roxb., cultivated in the U.S.A.: *Baker, W.J. 984* (FTG), SRR31682168*. ***Corypha umbraculifera*** L., cultivated in the U.K. (K: 1954-35301), SRR29749314. ***Corypha utan*** Lam., Indonesia: *Henderson, A. 4264* (NY), SRR24759980*. ***Cryosophila bartlettii*** R.J.Evans, Panama: *Cano, Á. ACS337* (G), SRR28987084. ***Cryosophila cookii*** Bartlett, Costa Rica: *Evans, R.J. 132* (NY), SRR24759984*. ***Cryosophila grayumii*** R.J.Evans, Costa Rica: *Evans, R.J. 241* (NY), SRR24759979*. ***Cryosophila guagara*** P.H.Allen, cultivated in the U.S.A.: *Cano, Á. ACS320* (FTG), SRR28987090. ***Cryosophila kalbreyeri*** Dahlgren, cultivated in the U.S.A.: *Cano, Á. ACS262* (FTG), SRR28987080. ***Cryosophila kalbreyeri*** subsp. ***cogolloi*** R.J.Evans, Colombia: *Bernal, R. & al. 933* (K), SRR24760202*. ***Cryosophila kalbreyeri*** Dahlgren subsp. ***kalbreyeri***, Colombia: *Moore Jr., H.E. & al. 10226* (K), SRR24760203*. ***Cryosophila macrocarpa*** R.J.Evans, Colombia: *Evans, R.J. 214* (NY), SRR24760201*. ***Cryosophila nana*** Blume, cultivated in the U.S.A.: *Cano, Á. ACS264* (FTG), SRR28987096. ***Cryosophila* sp.**, Panama: *de Gracia Cruz, J.E. 828* (MO), SRR31682173*. ***Cryosophila stauracantha*** R.J.Evans, cultivated in the U.S.A.: *Cano, Á. ACS266* (FTG), SRR28987097. ***Cryosophila warscewiczii*** Bartlett, cultivated in the U.K.: *Chase, M.W. 35984* (K), SRR31682176*. ***Cryosophila williamsii*** P.H.Allen, cultivated in the U.S.A.: *Cano, Á. ACS257* (FTG), SRR28987095. ***Eugeissona tristis*** Griff., Malaysia: *Baker, W.J. 501* (K), ERS5241171. ***Guihaia argyrata*** S.K.Lee, F.N.Wei & J.Dransf., cultivated in the U.K. (K: 1984-4478), SRR29749307. ***Guihaia grossefibrosa*** J.Dransf., S.K.Lee & F.N.Wei, Vietnam: *Henderson, A. 3377* (NY), SRR24760204*. ***Hemithrinax compacta*** Hook.f. ex Salomon, Cuba: *Wright, C. 3222* (K), SRR24760200*. ***Hemithrinax ekmaniana*** Burret, cultivated in the U.S.A.: *Cano, Á. ACS265* (FTG), SRR29749306. ***Hemithrinax rivularis*** León, Cuba: *Shafer, J.A. 4256* (NY), SRR24760205*. ***Hyphaene compressa*** H.Wendl., Tanzania: *Stauffer*, *F.W. 24.08.2016* (G), SRR24760199*. ***Hyphaene coriacea*** Gaertn., South Africa: *Stauffer, F.W. 05.09.2017* (G), SRR24760196*. ***Hyphaene guineensis*** Schumach. & Thonn., Ghana: *Stauffer, F.W. 14.05.2015* (G), SRR24760194*. ***Hyphaene petersiana*** Klotzsch ex Mart., Tanzania: *Stauffer, F.W. 30.08.2016* (G), SRR24760197*. ***Hyphaene reptans*** Becc., Somalia: *Gillett, J.B. 23018* (K), SRR24760193*. ***Hyphaene thebaica*** Mart., Djibouti: *Stauffer, F.W. 08.12.2015* (G), SRR24760198*. ***Itaya amicorum*** H.E.Moore, cultivated in the U.S.A.: *Baker, W.J. 990* (FTG), SRR31682172*. ***Johannesteijsmannia altifrons*** H.E.Moore, Malaysia: *Petoe 28* (AAU), SRR24760192*. ***Johannesteijsmannia lanceolata*** J.Dransf., Malaysia: *Dransfield, J. 861* (K), SRR24760107*. ***Johannesteijsmannia magnifica*** J.Dransf., Malaysia: *Wond, Y.K. 95088* (K), SRR24760104*. ***Johannesteijsmannia perakensis*** J.Dransf., Malaysia: *Saw, L.G. 36330* (K), SRR24760103*. ***Kerriodoxa elegans*** J.Dransf., cultivated in the U.K. (K: 1987-2685), ERS5241247. ***Lanonia acaulis*** A.J.Hend. & C.D.Bacon, Vietnam: *Henderson, A. 3309* (NY), SRR24760105*. ***Lanonia batoensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3819* (NY), SRR24760106*. ***Lanonia calciphila*** A.J.Hend. & C.D. Bacon, Vietnam: *Nguyen, V.D. 1309* (K), SRR31682167*. ***Lanonia centralis*** A.J.Hend. & C.D.Bacon, Vietnam: *Nguyen, V.D. 1854* (K), SRR31682166*. ***Lanonia dasyantha*** A.J.Hend. & C.D.Bacon, Vietnam: *Nguyen, V.D. 1620* (K), SRR31682165*. ***Lanonia gialaiensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 4221* (NY), SRR24760101*. ***Lanonia gracilis*** A.J.Hend. & C.D.Bacon, Indonesia: *Baker, W.J. 1353* (K), SRR29749274. ***Lanonia hainanensis*** A.J. Hend. & C.D.Bacon China: *Guo Lixiu 135* (NY), SRR24760100*. ***Lanonia hexasepala*** A.J.Hend. & C.D.Bacon, Vietnam: *Henderson, A. 3683* (NY), SRR24760097*. ***Lanonia magalonii*** A.J.Hend. & C.D.Bacon, Vietnam: *Henderson, A. 3268* (NY), SRR24760096*. ***Lanonia manglaensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3878* (AAU), SRR24760088*. ***Lanonia poilanei*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3643* (NY), SRR24760098*. ***Lanonia kontumensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3590* (NY), SRR24760099; Vietnam: *Henderson, A. 3727* (NY), SRR24760095*. ***Lanonia verrucosa*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 4079* (NY), SRR24760094*. ***Latania loddigesii*** Mart., cultivated in the U.K.: *Chase, M.W. 14248* (K), SRR29749273. ***Latania lontaroides*** H.E.Moore, cultivated in Réunion (CBNM: *WS 15-247*), SRR24759978*. ***Latania verschaffeltii*** Lem., cultivated in the U.K.: *Bayton, R.P. s.n.* (K), SRR24760071*. ***Leucothrinax morrisii*** C.Lewis & Zona, cultivated: *Forest 476* (K), SRR29749370. ***Licuala acutifida*** Mart., Malaysia: *Porter 8618B* (K), SRR24760073*. ***Licuala adscendens*** Barfod & Heatubun, Indonesia: *de Vogel, E.F. 4044* (K), SRR24760070*. ***Licuala ahlidurii*** Saw, Malaysia: *Saw, L.G. 39860* (K), SRR24760074*. ***Licuala atrovirens*** Saw, Malaysia: *Brunig*, *S8766* (K), SRR24760065*. ***Licuala atroviridis*** A.J.Hend., N.K.Ban & N.Q.Dung, Vietnam: *Henderson, A. 3300* (NY), SRR24760064*. ***Licuala averyanovii*** A.J. Hend., N.K.Ban & N.Q.Dung, Vietnam: *Averyanov, L. VH 5799* (LE), SRR24760066*. ***Licuala bachmaensis*** A.J.Hend., N.K.Ban & N.Q.Dung, Vietnam: *Henderson, A. 3254* (NY), SRR24760063*. ***Licuala bacularia*** Becc., Indonesia: *Koster, C. BW 13969* (L), SRR24760062*; Indonesia: *van Royen, P. 3009* (L), SRR24760019*. ***Licuala bakeri*** Barfod & Heatubun, Indonesia: *Baker, W.J. 1059* (AAU), SRR24760215*. ***Licuala bankae*** Barfod & Heatubun, Papua New Guinea: *Barfod, A. 449* (AAU), SRR24760216*. ***Licuala bayana*** Saw, Malaysia: *Saw, L.G. FRI 37583* (KEP), SRR24760214*. ***Licuala bellatula*** Becc., Indonesia: *Baker, W.J. 1054* (K), SRR31682201*. ***Licuala bidentata*** Becc., Malaysia: *Petoe 25* (AAU), SRR24760217*. ***Licuala bidoupensis*** A.J.Hend., N.K.Ban & N.Q.Dung, Vietnam: *Henderson, A. 3419* (NY), SRR24760213*. ***Licuala bifida*** Heatubun & Barfod, Indonesia: *Wally, E. 839* (K), SRR24760218*. ***Licuala bintulensis*** Becc., Malaysia: *Petoe 69* (AAU), SRR24760212*. ***Licuala borneensis*** Becc., Malaysia: *Petoe 66* (AAU), SRR24760211*. ***Licuala bracteata*** Gagnep., Vietnam: *Henderson, A. 3656* (NY), SRR24760210*. ***Licuala brevicalyx*** Becc., Indonesia: *Heatubun, C. 187* (K), SRR31682198*. ***Licuala bruneiana*** Saw, Brunei: *Gale 9* (AAU), SRR24760208*. ***Licuala burretii*** Saw, Malaysia: *Saikeh 82374* (K), SRR24760207*. ***Licuala cabalionii*** Dowe, Vanuatu: *Dowe, J.L. 48* (BRI), SRR24760206*. ***Licuala caespitosa*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 4211* (NY), SRR24760191*. ***Licuala cameronensis*** Saw, Malaysia: *Saw, L.G. FRI37383* (K), SRR24760190*. ***Licuala campestris*** Saw, Malaysia: *Kinsun Bakia 253* (K), SRR24760189*. ***Licuala cattienensis*** A.J. Hend., N.K.Ban & N.Q.Dung, Vietnam: *Henderson, A. 3407* (NY), SRR24760188*. ***Licuala celebica*** Miq., Indonesia: *Teijsmann, J.E. 200210* (L), SRR24760187*. ***Licuala chaiana*** Saw, Indonesia: *Chai, P. S.40051* (K), SRR24760186*. ***Licuala collina*** Saw, Indonesia: *Awa, D. S51191* (K), SRR24760182*. ***Licuala cordata*** Saw, Malaysia: *Ashton, P.S. S.18263* (K), SRR24760181*. ***Licuala corneri*** Furtado, Malaysia: *Rafidah, A.R. & Kueh, H.L. FRI 51632* (K), SRR24760184*. ***Licuala dakrongensis*** A.J.Hend., N.K.Ban & B.V.Thanh, Vietnam: *Henderson, A. 3498* (NY), SRR24760180*. ***Licuala densiflora*** Becc., cultivated in Malaysia: *Petoe 20* (AAU), SRR24760185*. ***Licuala distans*** Ridl., Thailand: *Barfod, A.S. 553* (AAU), SRR24760179*. ***Licuala elliptica*** Saw, Malaysia: *Dransfield, J. 6123* (K), SRR24760061*. ***Licuala ferruginea*** Becc., Malaysia: *Kunstler, H. 3041* (K), SRR24760058*. ***Licuala flammula*** Saw, Malaysia: *Yii S.42003* (K), SRR24760059*. ***Licuala flexuosa*** Burret, Indonesia: *de Vogel, E.F. 3074* (L), SRR24760056*. ***Licuala fordiana*** Becc., China: *Chun, N.K. 44716* (K), SRR24760055*. ***Licuala fractiflexa*** Saw, Malaysia: *Saw, L.G. FRI 37585* (K), SRR24760054*. ***Licuala glaberrima*** Gagnep., Vietnam: *Henderson, A. 3677* (NY), SRR24760053*. ***Licuala glabra*** Griff. var. ***glabra***, Malaysia: *Saw, L.G. FRI 37717* (K), SRR24760052*. ***Licuala glabra*** var. ***selangorensis*** Becc., Malaysia: *Ridley 12117* (K), SRR24760051*. ***Licuala graminifolia*** Heatubun & Barfod, Indonesia: *van Royen, P. 7345* (K), SRR24760050*. ***Licuala grandiflora*** Ridl., Indonesia: *Dransfield, J. & al. 7719* (K), SRR31682200*. ***Licuala grandis*** H.Wendl., Vanuatu: *Cribb, P. 10* (K), SRR24760049*. ***Licuala hallieriana*** Becc., Indonesia: *Awmack, C. 327* (K), SRR24760178*. ***Licuala heatubunii*** Barfod & Baker, Papua New Guinea: *Versteegh BW 4711* (L), SRR24760177*. ***Licuala honbaensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3694* (NY), SRR24760176*. ***Licuala honheoensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3666* (NY), SRR24760172*. ***Licuala insignis*** Becc., Indonesia: *Heatubun, C. 1044* (K), SRR31682199*; Indonesia: *Heatubun, C. 1072* (K), SRR24760083*. ***Licuala intermedia*** Saw, Malaysia: *Aban, G. SAN 95384* (K), SRR24760171*. ***Licuala***

Appendix 1. Continued.

kamarudinii Saw, Malaysia: *Saw, L.G. FRI 37533* (K), SRR24760173*. ***Licuala kemamanensis*** Furtado, Malaysia: *Saw, L.G. FRI 44998* (K), SRR24760170*. ***Licuala khoonmengii*** Saw, Malaysia: *Saw, L.G. FRI 37634* (K), SRR24760174*. ***Licuala kiahii*** Furtado, Malaysia: *Dransfield, J. & Fong, F.W. 5039* (K), SRR24760169*. ***Licuala kingiana*** Becc., Malaysia: *Kunstler, H. 471* (K), SRR24760168*. ***Licuala kuchingensis*** Saw, Malaysia: *Beaman, J.H. & al. 11862* (K), SRR24760165*. ***Licuala lamdongensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3635* (NY), SRR24760166*. ***Licuala lanata*** J.Dransf., Malaysia: *Chai, P. 39527* (K), SRR24760167*. ***Licuala lanuginosa*** Ridl., Malaysia: *Saw, L.G. 37426* (K), SRR24760047*. ***Licuala lauterbachii*** Dammer & K.Schum. subsp. ***lauterbachii***, Indonesia: *Heatubun C. 972* (K), SRR24760046*; Papua New Guinea: *Marai & Kjaer 441* (AAU), SRR24760044*. ***Licuala lauterbachii*** subsp. ***peekelii*** unpublished, Papua New Guinea: *Coode, M. NGF 29831* (K), SRR24760043*. ***Licuala lauterbachii*** subsp. ***bougainvillensis*** Becc., Papua New Guinea: *Gideon, O.E. LAE 78494* (K), SRR24760042*. ***Licuala leopoldii*** Saw, Malaysia: *Madani, L. 130688* (K), SRR24760041*. ***Licuala leucocarpa*** Saw, cultivated in Malaysia: *Petoe 24* (AAU), SRR24760040*. ***Licuala longiflora*** A.J.Hend., N.K.Ban & N.Q.Dung, Vietnam: *Henderson, A. 3641* (NY), SRR24760035*. ***Licuala longipes*** Griff., Malaysia: *Griffith s.n.* (K), SRR24760037*. ***Licuala longispadix*** Banka & Barfod, Papua New Guinea: *Barfod, A. 508* (AAU), SRR24760093*. ***Licuala maculata*** Saw, Malaysia: *Baker, W.J. 719* (K), SRR24760038*. ***Licuala malajana*** var. ***humilis*** Saw, Malaysia: *Whitmore FRI 20554* (KEP), SRR24760092*. ***Licuala malajana*** Becc. var. ***malajana***, Malaysia: *Dransfield, J. 6786* (K), SRR24760091*. ***Licuala mattanensis*** Becc. var. ***mattanensis***, cultivated in Malaysia: *Petoe 68* (AAU), SRR24760089*. ***Licuala mattanensis*** var. ***paucisecta*** Becc., cultivated in Malaysia: *Petoe 70* (AAU), SRR24760086*. ***Licuala meijeri*** Saw, Malaysia: *Meijer, W. SAN 19588* (K), SRR24760085*. ***Licuala merguensis*** Becc., Thailand: *Barfod, A.S. 527* (AAU), SRR24760084*. ***Licuala micholitzii*** Saw, Malaysia: *Lee, B. S.41907* (K), SRR24760081*. ***Licuala mirabilis*** Furtado, Malaysia: *Dransfield, J. 6785* (K), SRR24760080*. ***Licuala miriensis*** Saw, Malaysia: *Au S.16794* (K), SRR24760082*. ***Licuala modesta*** Becc., Malaysia: *Kunstler, H. 3243* (K), SRR24759977*. ***Licuala montana*** Dammer & K.Schum., Papua New Guinea: *Baker, W.J. 576* (K), SRR31682197*. ***Licuala mukahensis*** Saw, Malaysia: *Yahud S.77309* (K), SRR24759972*. ***Licuala multibracteata*** Barfod & Heatubun, Papua New Guinea: *Schodde, R. 2542* (K), SRR24760026*. ***Licuala mustapana*** Saw, Malaysia: *Saw, L.G. FRI 39878* (K), SRR24759973*. ***Licuala nuichuaensis*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3642* (NY), SRR24759974*. ***Licuala olivifera*** Becc., Brunei: *Forman, L. 900* (AAU), SRR24759970*. ***Licuala orbicularis*** Becc., Malaysia: *Petoe 26* (AAU), SRR24759975*. ***Licuala pahangensis*** Furtado, Malaysia: *Damahuri FRI 46251* (K), SRR24759969*. ***Licuala palas*** Saw, Malaysia: *Saw, L.G. FRI 39889* (K), SRR24759965*. ***Licuala paludosa*** Griff., cultivated in the U.K.: *Baker, W.J. 1359* (K), SRR31682196*. ***Licuala parviflora*** Dammer ex Becc., Papua New Guinea: *Baker, W.J. 1139* (K), SRR24759966*; Indonesia: *Brass, L.J. 13010* (A), SRR24760156*. ***Licuala parvula*** A.J.Hend. & N.Q.Dung, Vietnam: *Henderson, A. 3457* (NY), SRR24759964*. ***Licuala patens*** Ridl., Malaysia: *Wray Jr., L. 3928* (K), SRR24759967*. ***Licuala peltata*** Roxb. ex Buch.-Ham. var. ***peltata***, Thailand: *Barfod, A.S. 45278* (AAU), SRR24759968*. ***Licuala peltata*** var. ***sumawongii*** Saw, Thailand: *Smith, G. GC 148* (K), SRR24760029*. ***Licuala penduliflora*** Zipp. ex Blume, Indonesia: *Heatubun, C. & al. 359* (K), SRR24760028*; cultivated in in Singapore: *Furtado 31118* (L), SRR24760068*; Papua New Guinea: *Brass, L.J. 7136* (BRI), SRR24760034*. ***Licuala petiolulata*** Becc., Malaysia: *Petoe 22* (AAU), SRR24760030*. ***Licuala pilosa*** Saw, Malaysia: *Chai, P. 40055* (K), SRR24760027*. ***Licuala pitta*** Vatch. ex Barfod & Pongsatt., Thailand: *Barfod, A.S. 727* (AAU), SRR24760031*. ***Licuala poonsakii*** Hodel, Thailand: *Barfod, A.S. 732* (AAU), SRR24760025*. ***Licuala pseudovalida*** Saw, Malaysia: *Kutuh KP 58/5* (K), SRR24760022*. ***Licuala pumila*** Blume, Indonesia: *Mogea, J.P. 2991* (K), SRR24760021*. ***Licuala punctulata*** Burret, Malaysia: *Dransfield, J. 6001* (K), SRR24760023*. ***Licuala pusilla*** Becc., Malaysia: *Tsuruda 2* (K), SRR24760024*. ***Licuala radula*** Gagnep., Vietnam: *Henderson, A. 3807* (NY), SRR24760078*. ***Licuala ramsayi*** Domin var. ***ramsayi***, Australia: *Dowe & Barfod 600* (AAU), SRR24760077*. ***Licuala ramsayi*** var. ***tuckeri*** Barfod & Dowe, Australia: *Dowe & Barfod 602* (AAU), SRR24759927*. ***Licuala rheophytica*** Saw, Malaysia: *Petoe 31* (AAU), SRR24759926*. ***Licuala ridleyana*** Becc., Malaysia: *Ridley 14112* (K), SRR24759928*. ***Licuala robinsoniana*** Becc., Vietnam: *Henderson 3457* (NY), SRR24759925*. ***Licuala rubiginosa*** Saw, Brunei: *Dransfield, J. 6629* (K), SRR24759929*. ***Licuala sabahana*** Saw, Malaysia: *Saw, L.G. FRI 39981* (K), SRR24759920*. ***Licuala sallehana*** Saw, Malaysia: *Saw, L.G. FRI 39877* (K), SRR24759919*. ***Licuala sarawakensis*** Becc., Malaysia: *Chai, P. S.64672* (K), SRR24759922*. ***Licuala scortechinii*** Becc., Malaysia: *Dransfield, J. 5097* (K), SRR24760163*. ***Licuala simplex*** Becc., Papua New Guinea: *Barfod, A. 505* (AAU), SRR24759923*. ***Licuala spathellifera*** Becc., Malaysia: *Beccari, O. PB 3699* (K), SRR24760162*. ***Licuala spicata*** Becc., Malaysia: *Christensen, H. 1749* (AAU), SRR24760161*. ***Licuala spinosa*** Wurmb, Vietnam: *Henderson, A. 3633* (NY), SRR24760158*. ***Licuala suprafolia*** Barfod & Heatubun, Papua New Guinea: *Barfod, A. 462* (AAU), SRR24760159*. ***Licuala telifera*** Becc., Papua New Guinea: *Barfod, A. 362* (AAU), SRR24760155*; Indonesia: *Heatubun, C. 366* (K), SRR24760045*. ***Licuala tenuissima*** Saw, Malaysia: *Saw, L.G. FRI 39881* (K), SRR24760154*. ***Licuala terengganuensis*** Saw, Malaysia: *Saw, L.G. FRI 39864* (K), SRR24760151*. ***Licuala thoana*** Saw & J.Dransf., Malaysia: *Saw, L.G. FRI 36354* (K), SRR24760150*. ***Licuala tiomanensis*** Furtado, Malaysia: *Nur 18611* (K), SRR24760152*. ***Licuala triphylla*** Griff., Malaysia: *Dransfield, J. 6505* (K), SRR24760020*. ***Licuala urciflora*** Barfod & Heatubun, Indonesia: *Maturbongs, R.A. 497* (K), SRR24760153*. ***Licuala yiiana*** Saw, Malaysia: *Yii, P.C. S.55818* (K), SRR24760018*. ***Livistona australis*** Mart., Australia: *Irvine 1929* (K), SRR29749269. ***Livistona benthamii*** F.M.Bailey, Australia: *Blake, S.T. 16967* (K), SRR24760016*. ***Livistona boninensis*** Nakai, Japan: *Furuse, M. 7719* (K), SRR24760013*. ***Livistona carinensis*** J.Dransf. & N.W.Uhl, Somalia: *Barbier, C. 972* (K), SRR24760017*. ***Livistona chinensis*** R.Br. ex Mart., cultivated in the U.K. (K: 1982-5601), SRR24760012*. ***Livistona concinna*** Dowe & Barfod, Australia: *Dowe, J.L. 607* (AAU), SRR24760011*. ***Livistona decora*** Dowe, Australia: *Rodd, A. 3069* (K), SRR24760008*. ***Livistona eastonii*** C.A.Gardner, Australia: *Gardner, C.A. 1544* (K), SRR24760009*. ***Livistona exigua*** J.Dransf., Brunei: *Dransfield, J. 6568* (K), SRR24760010*. ***Livistona fulva*** Rodd, Australia: *Rodd, A. 3062* (K), SRR24759961*. ***Livistona halongensis*** T.H.Nguyên & Kiew, Vietnam: *Henderson, A. 3802* (NY), SRR24759960*. ***Livistona humilis*** R.Br., Australia: *Martensz AE 618* (K), SRR24759959*. ***Livistona inermis*** R.Br., Australia: *Evans, M. 3544* (K), SRR24759958*. ***Livistona jenkinsiana*** Griff., Thailand: *Barfod, A.S. 714* (AAU), SRR24759955*. ***Livistona lanuginosa*** Rodd, Australia: *Irvine, A.K. 1912* (K), SRR24759954*. ***Livistona leichhardtii*** F.Muell., Australia: *Rodd, A. 2871* (K), SRR24759956*. ***Livistona mariae*** F.Muell., Australia: *Rodd, A. 3216* (K), SRR24759953*. ***Livistona muelleri*** F.M.Bailey, Australia: *Clarkson, J.R. 4359* (K), SRR24759957*. ***Livistona nasmophila*** Dowe & D.L.Jones, Australia: *Rodd, A. 2868* (K), SRR24759952*. ***Livistona nitida*** Rodd, Australia: *Rodd, A. 3051* (K), SRR24760146*. ***Livistona saribus*** Merr. ex A.Chev., Vietnam: *Henderson, A. 3557* (NY), SRR24760147*. ***Livistona* sp.**, Vietnam: *Henderson, A. 3730* (NY), SRR31682171*. ***Livistona speciosa*** Kurz, Thailand: *Damborg, A. 2* (AAU), SRR24760144*. ***Livistona victoriae*** Rodd, Australia: *Rodd, A. 2934* (K), SRR24760143*. ***Lodoicea maldivica*** Pers., cultivated in Madagascar: *Bayton 56* (K), SRR29749268. ***Maxburretia furtadoana*** J.Dransf., Thailand: *Dransfield, J. 2350* (K), SRR29749328. ***Maxburretia rupicola*** Furtado, Malaysia: *Saw, L.G. FRI 39811* (K), SRR24760139*. ***Medemia argun*** Württemb. ex H.Wendl., Egypt: *Haitham Ibrahim 1* (K), SRR24760138*. ***Nannorrhops ritchieana*** Aitch., cultivated: *Chase, M.W. 1890* (K), SRR29749326. ***Nypa fruticans*** Wurmb, cultivated in the U.K.: *Chase, M.W. 12603* (K), ERS5241246. ***Phoenix acaulis*** Roxb., Nepal: *Watson 9615* (E), SRR31682195*. ***Phoenix atlantica*** A.Chev., Cape Verde: *Henderson, S. & al. 277* (K), SRR24760140*. ***Phoenix caespitosa*** Chiov., Somalia: *Thulin 9016* (K, UPS), SRR31682194*. ***Phoenix canariensis*** H.Wildpret, Spain: *Barrow, S. 75* (K), SRR31682193*. ***Phoenix dactylifera*** L., Spain: *Barrow, S. 77* (K), SRR31682192*. ***Phoenix loureiroi*** Kunth var. ***loureiroi***, Thailand: *Barrow, S. 23* (K), SRR31682190*. ***Phoenix loureiroi*** var. ***pedunculata*** Govaerts, India: *Barrow, S. 57* (K), SRR31682189*. ***Phoenix paludosa*** Roxb., Thailand: *Barfod, A.S. 41152* (AAU), SRR24760141*; Thailand: *T. Burholt 45258* (K), SRR24760136*. ***Phoenix pusilla*** Gaertn., Sri Lanka: *Barrow, S. 66* (K, PDA), SRR31682188*. ***Phoenix reclinata*** Jacq., Zimbabwe: *Wilkin 724* (K), SRR29749315. ***Phoenix roebelenii*** O'Brien, cultivated in the U.K.: *Chase, M.W. 1400* (K), SRR31682187*. ***Phoenix rupicola*** T.Anderson, India: *Barrow, S. 73* (K), SRR31682186*. ***Phoenix sylvestris*** Roxb., India: *Barrow, S. 59* (K), SRR31682185*. ***Phoenix theophrasti*** Greuter, Turkey: *Barrow, S. 37* (K), SRR31682184*. ***Pholidocarpus kingianus*** Ridl., Malaysia: *Dransfield, J. 876* (K), SRR24759916*. ***Pholidocarpus macrocarpus*** Becc., Thailand: *Smith, G. & Sumawong, W. GC 95* (K), SRR24759914*. ***Pholidocarpus majadum*** Becc., Malaysia: *Petoe 27* (AAU), SRR24759917*. ***Pritchardia arecina*** Becc. cultivated in the U.K.: *Baker, W.J. 1183* (K), SRR29749294. ***Pritchardia bakeri*** Hodel, U.S.A.: *Kapua Kawelo, H. s.n.* (Environmental Division, Directorate of Public Works, USAG-HI), SRR24759912*. ***Pritchardia beccariana*** Rock, U.S.A.: *Degener, O. 9716* (NY), SRR24759908*. ***Pritchardia flynnii*** Lorence & Gemmill, U.S.A.: *Tangalin, N. 1705* (PTBG), SRR24759907*; U.S.A.: *Tangalin, N. 1482* (PTBG), SRR24759910*; U.S.A.: *Tangalin, N. 1480* (PTBG), SRR24759906*. ***Pritchardia forbesiana*** Rock, U.S.A.: *Annable, C.R. 3815* (NY), SRR24759911*.

Appendix 1. Continued.

Pritchardia glabrata Becc. & Rock, U.S.A.: *Oppenheimer, H. s.n.* (HAW), SRR24759918*; U.S.A.: *Tangalin, N. 1703* (PTBG), SRR24759905*. ***Pritchardia hardyi*** Rock, U.S.A.: *Oppenheimer, H. s.n.* (HAW), SRR24759951*; U.S.A.: *Bacon, C.D. s.n.* (GB), SRR24759948*; U.S.A. *Tangalin, N. 1705* (PTBG), SRR24759947*. ***Pritchardia hillebrandii*** Becc., U.S.A.: *Rock, J. 822-59.82204* (K), SRR24759949*. ***Pritchardia kaalae*** Rock, U.S.A.: *Degener, O. 20784* (K), SRR24759946*. ***Pritchardia kahukuensis*** Caum, U.S.A.: *Kapua Kawelo, H. s.n.* (Environmental Division, Directorate of Public Works, USAG-HI), SRR24759945*; U.S.A.: *Tangalin, N. 1481* (NTBG), SRR24759944*. ***Pritchardia lanigera*** Becc., U.S.A.: *Rock, J.F. 17349* (A), SRR24759941*. ***Pritchardia lowreyana*** Rock ex Becc., U.S.A.: *Tangalin, N. NT001* (K), SRR24759940*. ***Pritchardia minor*** Becc., cultivated in U.S.A.: *Chapin, M.H. & Wood, K.R. 82* (K), SRR24759939*. ***Pritchardia mitiaroana*** J.Dransf. & Y.Ehrh., Cook Islands: *Luttrell, C. 126* (K), SRR24759943*. ***Pritchardia munroi*** Rock, U.S.A.: *Annable, C.R. 3635* (NY), SRR24759938*; U.S.A.: *Rock, J.F. 17341* (A), SRR24760006*. ***Pritchardia napaliensis*** H.St.John, cultivated in the U.S.A.: *Chapin, M. 75* (K), SRR24760003*. ***Pritchardia pacifica*** Seem. & H.Wendl., cultivated in the U.K. (K: 1952-355501), SRR24760001*. ***Pritchardia perlmanii*** Gemmill, U.S.A.: *Wood, K. 1545* (PTBG), SRR24760005*; U.S.A.: *Wood, K. 8091* (PTBG), SRR24760000*; U.S.A.: *Ken Wood, K. 7331* (PTBG), SRR24759999*. ***Pritchardia remota*** Becc., U.S.A.: *Chapin, M.H. 59* (K), SRR32316733. ***Pritchardia thurstonii*** F.Muell. & Drude, cultivated in the U.K.: *Baker, W.J. 1362* (K), SRR32316732. ***Pritchardia viscosa*** Rock, U.S.A.: *Perlman, S. 18580* (PTBG), SRR24759996*; U.S.A.: *Perlman, S. 18712* (PTBG), SRR24759995*. ***Pritchardia vuylstekeana*** H.Wendl., cultivated in the U.K. (K), SRR24759994*. ***Pritchardia waialealeana*** Read, U.S.A.: *Lorence, D.H. & al. s.n.* (K), SRR24759998*. ***Rhapidophyllum hystrix*** H.Wendl. & Drude, cultivated in the U.S.A. (Montgomery Botanical Center: 94648K), SRR28987079. ***Rhapis evansii*** A.J.Hend., Laos: *Evans, T. 56* (K), SRR32316721. ***Rhapis excelsa*** A.Henry, Vietnam: *Henderson, A. 3787* (NY), SRR24759993*. ***Rhapis gracilis*** Burret, China: *Tsiang, Y. 2751* (NY), SRR24759902*. ***Rhapis humilis*** Blume, China: *Xianghou, S. 135* (K), SRR24759900*. ***Rhapis kebangensis*** A.J.Hend., Vietnam: *Henderson, A. 4048* (NY), SRR24759903*. ***Rhapis laosensis*** Becc., Thailand: *Barfod, A. 724* (AAU), SRR24759899*. ***Rhapis laosensis*** subsp. ***macrantha*** A.J.Hend., Vietnam: *Henderson, A. 3756* (NY), SRR24759904*. ***Rhapis micrantha*** Becc., Vietnam: *Henderson, A. 4182* (NY), SRR24759898*. ***Rhapis puhuongensis*** M.S.Trudgen, T.P.Anh & A.J.Hend., Vietnam: *Henderson, A. 3423* (NY), SRR24759894*; Vietnam: *Vu, X.P. 1748* (K), SRR24759895*. ***Rhapis robusta*** Burret, Vietnam: *Henderson, A. 3759* (NY), SRR24759893*; Vietnam: *Hiep, N.T. & al. CBL 1238* (K), SRR24759896*. ***Rhapis subtilis*** Becc., cultivated in the U.K. (K: 1995-4001), SRR29749288. ***Rhapis subtilis*** subsp. ***siamensis*** A.J.Hend., cultivated in Thailand: *Henderson, A. 4022* (NY), SRR24759891*. ***Rhapis subtilis*** Becc. subsp. ***subtilis***, Thailand: *Barfod, A.S. & al. 45205* (K), SRR24759897*. ***Rhapis vidalii*** Aver., T.H.Nguyên & P.K.Lôc, Vietnam: *Henderson, A. 4183* (NY), SRR24760132*. ***Sabal bermudana*** L.H.Bailey, Bermuda: *Greene, L. HS1* (K), SRR29749285. ***Sabal domingensis*** Becc., cultivated in the U.S.A. (Montgomery Botanical Center: 20120482 215 SD), SRR28987126. ***Sabal etonia*** Swingle ex Nash, cultivated in the U.S.A.: *Noblick, L. 5586* (FTG), SRR28986784. ***Sabal gretherae*** H.J.Quero, Mexico: *Balslev, H. 8171* (AAU), SRR24760131*. ***Sabal maritima*** Burret, cultivated in the U.S.A.: *Noblick, L. 5584* (FTG), SRR28987125. ***Sabal mauritiiformis*** Griseb. & H.Wendl., Panamá: *Horn, J.W. 4784* (G), SRR28987134. ***Sabal mexicana*** Mart., cultivated in the U.S.A.: *Fantz, P.R. 3536* (FTG), SRR28986783. ***Sabal miamiensis*** Zona, cultivated in the U.S.A.: *Pena, A. 2013-13* (FTG), SRR28987088. ***Sabal minor*** Pers., cultivated in the U.S.A.: *Noblick, L. 5589* (FTG), SRR28986795. ***Sabal palmetto*** Lodd. ex Schult. & Schult.f., cultivated in Switzerland (G: 19701758), SRR28987122. ***Sabal pumos*** Burret, cultivated in the U.S.A.: *Horn, J.W. 4806* (FTG), SRR28987086. ***Sabal rosei*** Becc., cultivated in the U.S.A.: *Cano, Á. ACS325* (FTG), SRR28987085. ***Sabal uresana*** Trel., cultivated in the U.S.A.: *Bogler 1310* (FTG), SRR28986794. ***Sabal yapa*** Becc., cultivated in the U.S.A.: *Horn, J.W. 4784* (FTG), SRR28986782. ***Sabinaria magnifica*** Galeano & R.Bernal, Colombia: *Bernal, R. 4949* (G), SRR29749284. ***Saribus brevifolius*** Bacon & W.J.Baker, Indonesia: *Takeuchi, W. JPM 8171* (K), SRR24760133*. ***Saribus jeanneneyi*** Bacon & W.J.Baker, cultivated in France: *Pintaud, J.C. 315* (P), SRR24760134*. ***Saribus merrillii*** Bacon & W.J.Baker, Philippines: *Ramos, M. 33759* (K), SRR24760129*. ***Saribus papuanus*** Kuntze, Indonesia: *Baker, W.J. 851* (K), SRR29749283. ***Saribus rotundifolius*** Blume, Indonesia: *Dransfield, J. 3831* (K), SRR24760128*. ***Saribus surru*** Bacon & W.J.Baker, Papua New Guinea: *Barfod, A.S. 390* (AAU), SRR24760124*. ***Saribus tothur*** Bacon & W.J.Baker, Papua New Guinea: *Damborg, A. 418* (AAU), SRR24760126*. ***Saribus woodfordii*** Bacon & W.J.Baker, Papua New Guinea: *Brass, L.J. 28281* (K), SRR24760123*. ***Satranala decussilvae*** Beentje & J.Dransf., Yemen: *Beentje & Dransfield 4810* (K), SRR29749356. ***Schippia concolor*** Burret, cultivated in the U.S.A.: *Baker 995* (FTG), SRR28986796. ***Serenoa repens*** Small, cultivated in the U.K.: *Chase, M.W. 34476* (K), SRR29749353. ***Tahina spectabilis*** J.Dransf. & Rakotoarin., Madagascar: *Rakotoarinivo 337* (K), SRR29749348. ***Thrinax excelsa*** Lodd. ex Mart., Jamaica: *Britton, N.L. 373* (NY), SRR24760127*. ***Thrinax parviflora*** Sw., cultivated in the U.S.A.: *Bogler 1315* (FTG), SRR28987094. ***Thrinax radiata*** Lodd. ex Schult. & Schult.f., cultivated in the U.S.A.: *Cano, Á. ACS326* (FTG), SRR28987130. ***Trachycarpus fortunei*** H.Wendl., cultivated in the U.K.: *Chase, M.W. 30051* (K), SRR29749369. ***Trachycarpus geminisectus*** Spanner, Gibbons, V.D.Nguyen & T.P.Anh, Vietnam: *Gibbons, M. 1* (K), SRR31682179*. ***Trachycarpus latisectus*** Spanner, Noltie & Gibbons, India: *Gibbons, M. s.n.* (K), SRR24760122*. ***Trachycarpus martianus*** H.Wendl., India: *Gibbons, M. s.n.* (K), SRR24759887*. ***Trachycarpus nanus*** Becc., China: *Gibbons, M. s.n.* (K), SRR24759888*. ***Trachycarpus oreophilus*** Gibbons & Spanner, Thailand: *Niyomdham, C. 5036* (K), SRR24759886*. ***Trachycarpus princeps*** Gibbons, Spanner & San Y.Chen, China: *Gibbons, M. 14441* (K), SRR24759889*. ***Trachycarpus ravenii*** Aver. & K.S.Nguyen, Laos: *Averyanov, L. 725* (LE), SRR24759885*. ***Trachycarpus takil*** Becc., India: *Gibbons, M. 0* (K), SRR31682178*. ***Trachycarpus ukhrulensis*** M.Lorek & K.C.Pradhan, India: *Lorek, M. s.n.* (HBG), SRR24759884*. ***Trithrinax brasiliensis*** Mart., cultivated in Switzerland (G), SRR28987106; cultivated in Brazil (HPL), SRR28986787; cultivated in the U.K.: *Chase, M.W. 30859* (K), SRR33916395. ***Trithrinax schizophylla*** Drude, Argentina: *Cano, Á. ACS274* (G), SRR28986791; cultivated in the U.S.A.: *Cano, Á. ACS252* (FTG), SRR28987092; Argentina: *Cano, Á. ACS275* (G), SRR28986790. ***Wallichia caryotoides*** Roxb., Myanmar: *Armstrong, K. 1248* (NY), SRR24759880*. ***Wallichia disticha*** T.Anderson, Thailand: *Dransfield, J. 7343* (K), SRR24759881*. ***Wallichia gracilis*** Becc., Vietnam: *Jeanson, M. 55* (NY), SRR24759879*. ***Wallichia lidiae*** A.J.Hend., Myanmar: *Henderson, A. 3212* (NY), SRR24759882*. ***Wallichia marianneae*** Hodel, Thailand: *Barfod, A.S. 43895* (AAU), SRR24759878*. ***Wallichia nana*** Griff., Myanmar: *Armstrong, K. 2574* (NY), SRR24759883*. ***Wallichia oblongifolia*** Griff., cultivated in the U.K.: *Bayton 2* (K), SRR31682177*. ***Washingtonia filifera*** H.Wendl. ex de Bary var. ***filifera***, cultivated in the U.K.: *Chase, M.W. 30863* (K), SRR29749367. ***Washingtonia filifera*** var. ***robusta*** Parish, cultivated in the U.K.: *N.N. 000-73.12610* (K), SRR24759877*. ***Zombia antillarum*** L.H.Bailey, cultivated in the U.S.A.: *Fantz, P.R. 3222* (FTG), SRR33999139; cultivated in the U.S.A. (FTG: X-9-43A), SRR28987091.