Annals of Botany **108**: 1417–1432, 2011
doi:10.1093/aob/mcr020, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY
Founded 1887

PART OF A SPECIAL ISSUE ON PALM BIOLOGY

Phylogenetic relationships among arecoid palms (Arecaceae: Arecoideae)

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Received: 28 October 2010 Returned for revision: 22 November 2010 Accepted: 8 December 2010 Published electronically: 16 February 2011

• *Background and Aims* The Arecoideae is the largest and most diverse of the five subfamilies of palms (Arecaceae/Palmae), containing >50 % of the species in the family. Despite its importance, phylogenetic relationships among Arecoideae are poorly understood. Here the most densely sampled phylogenetic analysis of Arecoideae available to date is presented. The results are used to test the current classification of the subfamily and to identify priority areas for future research.
• *Methods* DNA sequence data for the low-copy nuclear genes *PRK* and *RPB2* were collected from 190 palm species, covering 103 (96 %) genera of Arecoideae. The data were analysed using the parsimony ratchet, maximum likelihood, and both likelihood and parsimony bootstrapping.
• *Key Results and Conclusions* Despite the recovery of paralogues and pseudogenes in a small number of taxa, *PRK* and *RPB2* were both highly informative, producing well-resolved phylogenetic trees with many nodes well supported by bootstrap analyses. Simultaneous analyses of the combined data sets provided additional resolution and support. Two areas of incongruence between *PRK* and *RPB2* were strongly supported by the bootstrap relating to the placement of tribes Chamaedoreeae, Iriarteeae and Reinhardtieae; the causes of this incongruence remain uncertain. The current classification within Arecoideae was strongly supported by the present data. Of the 14 tribes and 14 sub-tribes in the classification, only five sub-tribes from tribe Areceae (Basseliniinae, Linospadicinae, Oncospermatinae, Rhopalostylidinae and Verschaffeltiinae) failed to receive support. Three major higher level clades were strongly supported: (1) the RRC clade (Roystoneeae, Reinhardtieae and Cocoseae), (2) the POS clade (Podococceae, Oranieae and Sclerospermeae) and (3) the core arecoid clade (Areceae, Euterpeae, Geonomateae, Leopoldinieae, Manicarieae and Pelagodoxeae). However, new data sources are required to elucidate ambiguities that remain in phylogenetic relationships among and within the major groups of Arecoideae, as well as within the Areceae, the largest tribe in the palm family.

Key words: Arecaceae, Areceae, Arecoideae, coconut, *Cocos*, *Elaeis*, incongruence, low-copy nuclear DNA, oil palm, Palmae, paralogy, phylogeny, pseudogene.

INTRODUCTION

The Arecoideae is the largest and most diverse of the five subfamilies recognized in the palm family (Arecaceae/Palmae; Dransfield *et al.*, 2008). Almost 60 % of palm genera (107 out of 183) and >50 % of species (approx. 1300 out of approx. 2400) are included in this group. Arecoid palms are widespread in the tropics and sub-tropics, occurring principally in rain forest and, to a lesser extent, in some seasonally dry habitats. They display exceptional levels of endemism, most notably in the Americas and the Indo-Pacific region (including Madagascar). Ranging from minute forest floor palms to giant canopy trees and even climbers, arecoid palms often play a prominent role in determining forest composition (e.g. Peters *et al.*, 2004) and biotic interactions (e.g. Galetti *et al.*, 2006). Some of the most important economic palms fall within the Arecoideae, such as oil palm (*Elaeis guineensis*), coconut (*Cocos nucifera*), betel nut palm (*Areca catechu*), peach palm (*Bactris gasipaes*) and many important species in the global horticultural trade (e.g. *Dypsis lutescens*, *Howea forsteriana* and *Roystonea regia*). Many taxa have important uses at local levels (Balick and Beck, 1990).

The monophyly of subfamily Arecoideae as circumscribed in the current classification (Dransfield *et al.*, 2005, 2008) is strongly supported by a substantial body of phylogenetic evidence (Uhl and Dransfield, 1987; Asmussen *et al.*, 2000, 2006; Asmussen and Chase, 2001; Lewis and Doyle, 2002; Baker *et al.*, 2009). Morphological characters that define the arecoid clade and distinguish it from other subfamilies include the presence of reduplicately pinnate leaves, highly differentiated primary inflorescence bracts and floral triads. The floral triad is a cluster of three unisexual flowers, comprising a central female flower flanked by two male flowers. All arecoid palms bear triads or a derivative thereof, with the exception of tribe Chamaedoreeae, which produces a unique

floral cluster known as an acervulus (Uhl and Moore, 1978) or solitary flowers. Outside arecoids, triads are only found in tribe Caryoteae (Coryphoideae), which is the main reason for the erroneous placement of this tribe within Arecoideae in the earlier classification of Uhl and Dransfield (1987). The differentiated primary inflorescence bracts of Arecoideae contrast with those of most other subfamilies, which are usually conspicuous and relatively uniform throughout the main axis of the inflorescence. In arecoids, however, the primary bracts subtending the first-order branches (rachis bracts) are always highly reduced, and well-developed bracts occur only on the peduncle. This feature is shared with subfamily Ceroxyloideae, the sister of Arecoideae (Asmussen and Chase, 2001; Asmussen *et al.*, 2006; Baker *et al.*, 2009).

Many aspects of phylogenetic relationships among arecoid palms remain poorly understood (Dransfield *et al.*, 2008), which creates a substantial obstacle to comparative research on this important group of plants. Phylogenetic relationships among arecoid palms have primarily been investigated within broader family-wide studies (e.g. Asmussen and Chase, 2001; Asmussen *et al.*, 2006), including the most recent study of this kind that includes all genera (Baker *et al.*, 2009). The two studies (Hahn, 2002*a*; Savolainen *et al.*, 2006) in which phylogenies of Arecoideae were specifically reconstructed lacked adequate sampling and a full systematic analysis, respectively. Nevertheless, this research, along with important contributions on sub-clades of Arecoideae (Gunn, 2004; Roncal *et al.*, 2005; Loo *et al.*, 2006; Norup *et al.*, 2006; Cuenca and Asmussen-Lange, 2007; Cuenca *et al.*, 2008, 2009), provided sufficient evidence for the circumscription of monophyletic tribes and sub-tribes in the current classification (Dransfield *et al.*, 2005, 2008). In total, 14 tribes and 14 sub-tribes are recognized (Table 1). The largest tribe, Areceae, contains 11 of the 14 sub-tribes and includes ten genera that have not yet been placed to sub-tribe due to inadequate phylogenetic evidence. The remaining three sub-tribes fall within tribe Cocoseae. Although the majority of the clades recognized in the classification of Arecoideae are well supported, some groups (e.g. subtribes Basseliniinae and Dypsidinae) are less robust. Published studies have failed to provide consistent assessments of relationships among the major lineages of arecoids. Only two highly supported major clades stand out, namely a group comprising Areceae, Euterpeae, Geonomateae, Leopoldinieae, Manicarieae and Pelagodoxeae, termed the core arecoid clade by Dransfield *et al.* (2008; Hahn, 2002*a*, *b*; Lewis and Doyle, 2002; Baker *et al.*, 2009), and a group consisting of Podococceae, Oranieae and Sclerospermeae, here termed the POS clade (Uhl *et al.*, 1995; Hahn, 2002*b*; Lewis and Doyle, 2002; Dransfield *et al.*, 2008; Baker *et al.*, 2009).

In this paper, we present the most densely sampled phylogenetic analysis of subfamily Arecoideae yet published based on DNA sequence data from low-copy nuclear DNA regions. We use our phylogenetic hypotheses to evaluate the systematic evidence for the classification of Dransfield *et al.* (2005, 2008) and explore relationships among tribes and sub-tribes, reviewing our results in the context of existing phylogenetic data. The aim is to provide an assessment of confidence in phylogenetic hypotheses for arecoid groups and determine priorities for future research.

TABLE 1. *Classification of subfamily Arecoideae (Dransfield et al., 2005, 2008)*

Tribe	Sub-tribe	Genus
Iriarteeae		*Dictyocaryum*, *Iriartea*, *Iriartella*, *Socratea*, *Wettinia*
Chamaedoreeae		*Chamaedorea*, *Gaussia*, *Hyophorbe*, *Synechanthus*, *Wendlandiella*
Podococceae		*Podococcus*
Oranieae		*Orania*
Sclerospermeae		*Sclerosperma*
Roystoneeae		*Roystonea*
Reinhardtieae		*Reinhardtia*
Cocoseae	Attaleinae	*Allagoptera*, *Attalea*, *Beccariophoenix*, *Butia*, *Cocos*, *Jubaea*, *Jubaeopsis*, *Lytocaryum*, *Parajubaea*, *Syagrus*, *Voanioala*
	Bactridinae	*Acrocomia*, *Astrocaryum*, *Aiphanes*, *Bactris*, *Desmoncus*
	Elaeidinae	*Barcella*, *Elaeis*
Manicarieae		*Manicaria*
Euterpeae		*Euterpe*, *Hyospathe*, *Neonicholsonia*, *Oenocarpus*, *Prestoea*
Geonomateae		*Asterogyne*, *Calyptrogyne*, *Calyptronoma*, *Geonoma*, *Pholidostachys*, *Welfia*
Leopoldinieae		*Leopoldinia*
Pelagodoxeae		*Pelagodoxa*, *Sommieria*
Areceae	Archontophoenicinae	*Actinokentia*, *Actinorhytis*, *Archontophoenix*, *Chambeyronia*, *Kentiopsis*
	Arecinae	*Areca*, *Nenga*, *Pinanga*
	Basseliniinae	*Basselinia*, *Burretiokentia*, *Cyphophoenix*, *Cyphosperma*, *Lepidorrhachis*, *Physokentia*
	Carpoxylinae	*Carpoxylon*, *Satakentia*, *Neoveitchia*
	Clinospermatinae	*Clinosperma*, *Cyphokentia*
	Dypsidinae	*Dypsis*, *Lemurophoenix*, *Marojejya*, *Masoala*
	Linospadicinae	*Calyptrocalyx*, *Howea*, *Laccospadix*, *Linospadix*
	Oncospermatinae	*Acanthophoenix*, *Deckenia*, *Oncosperma*, *Tectiphiala*
	Ptychospermatinae	*Adonidia*, *Balaka*, *Brassiophoenix*, *Carpentaria*, *Drymophloeus*, *Normanbya*, *Ponapea*, *Ptychococcus*, *Ptychosperma*, *Solfia*, *Veitchia*, *Wodyetia*
	Rhopalostylidinae	*Hedyscepe*, *Rhopalostylis*
	Verschaffeltiinae	*Nephrosperma*, *Phoenicophorium*, *Roscheria*, *Verschaffeltia*
	Areceae unplaced to sub-tribe	*Bentinckia*, *Clinostigma*, *Cyrtostachys*, *Dictyosperma*, *Dransfieldia*, *Heterospathe*, *Hydriastele*, *Iguanura*, *Loxococcus*, *Rhopaloblaste*

MATERIALS AND METHODS

Taxon sampling

Representatives of all 14 tribes and 14 sub-tribes of subfamily Arecoideae recognized in the classification of Dransfield *et al.*

(2005, 2008) were included in this study. Notably, 103 of the 107 genera (96 %) of Arecoideae were sampled (see Appendix). Including outgroups, 190 palm species were included. In contrast to previous studies, more than one exemplar species was included for many genera, targeting those groups with reported delimitation problems. In addition, representatives of all tribes of subfamily Ceroxyloideae, the sister group of Arecoideae, were sampled. Six outgroups were selected from the three remaining subfamilies, Calamoideae, Coryphoideae and Nypoideae. Trees were rooted on *Eremospatha wendlandiana* (Calamoideae) based on the expanding body of evidence that Calamoideae are sister to all remaining palms (Asmussen *et al.*, 2006; Baker *et al.*, 2009).

DNA sequence data were gathered from two low-copy nuclear regions, intron 4 of *PRK*, the gene encoding the Calvin cycle enzyme phosphoribulokinase, and intron 23 of *RPB2*, the gene for the second largest subunit of RNA polymerase II. Both have been widely used in palm molecular phylogenetic studies (Lewis and Doyle, 2002; Gunn, 2004; Roncal *et al.*, 2005, 2008, 2010; Loo *et al.*, 2006; Norup *et al.*, 2006; Savolainen *et al.*, 2006; Thomas *et al.*, 2006; Trénel *et al.*, 2007; Cuenca *et al.*, 2008, 2009; Eiserhardt *et al.*, 2011), providing robust evidence for relationships at intermediate and lower taxonomic levels that more slowly evolving plastid regions have failed to reveal. These DNA regions have also been exploited in other angiosperm groups (Denton *et al.*, 1998; Oxelman and Bremer, 2000; Popp and Oxelman, 2001, 2004; Oxelman *et al.*, 2004; Pfeil *et al.*, 2004; Popp *et al.*, 2005; Eggens *et al.*, 2007; Fijridiyanto and Murakami, 2009; Frajman *et al.*, 2009; Schulte *et al.*, 2009; Russell *et al.*, 2010; Sass and Specht, 2010).

DNA extraction, amplification and sequencing

Extraction, polymerase chain reaction (PCR) amplification and sequencing protocols are described in detail by Norup *et al.* (2006). For the amplification of *PRK*, we used the primers of Lewis and Doyle (2002) that are specific to their *PRK* paralogue 2. The primers amplify *PRK* intron 4 and partial exons 4 and 5 (717F, 5′-GTGATATGGAAGAA CGTGG-3′; 969R, 5′-ATTCCAGGGTATGAGCAGC-3′). Primers published by Roncal *et al.* (2005) and Loo *et al.* (2006) were used for *RPB2* (forward, 5′-CAACTTATTGAGT GCATCATGG-3′; reverse, 5′-CCACGCATCTGATATCC AC-3′). Where preliminary amplification or sequence results suggested the presence of more than one copy of either region, PCR products were cloned as described by Norup *et al.* (2006) and up to five clones were sequenced. GenBank/EMBL accession numbers for all sequences are given in the Appendix.

DNA sequence alignment and phylogenetic analysis

DNA sequences were assembled using Sequencher 4.1.2 software (Gene Codes Corp, Ann Arbor, MI, USA). Alignments of *PRK* and *RPB2* were built upon the published data sets of Norup *et al.* (2006) into which new sequences were incorporated manually. All variable positions were verified against raw sequence data files to identify and correct base-calling errors. Ambiguously aligned regions were excluded from further analysis. Alignments may be downloaded from TreeBASE (www.treebase.org; accession number S11041).

The two data partitions were analysed separately and in combination. Phylogenetic analyses were conducted under maximum parsimony (MP) and maximum likelihood (ML) optimality criteria. Maximum parsimony analyses were conducted using the parsimony ratchet (Nixon, 1999), a highly efficient method for analysis of large data sets that reliably finds optimal trees. PAUPRat (Sikes and Lewis, 2001) was used to implement the parsimony ratchet searches in PAUP* 4·0b10 (Swofford, 2002). Twenty ratchet searches were conducted on each data set, with each search comprising 200 ratchet iterations with 15 % of characters perturbed in each iteration and a single tree saved per iteration. Characters were treated as unordered and equally weighted (Fitch, 1971), and indels were handled as missing data. On completion, the most parsimonious trees from all 20 searches were compiled into a single file and filtered to retain only the shortest trees. Branch lengths and statistics were calculated with parsimony-uninformative characters excluded and DELTRAN character optimization. Node support was assessed with PAUP* by conducting 1000 bootstrap iterations, each comprising a single search with simple taxon entry order and TBR swapping, saving a maximum of five trees per search (Salamin *et al.*, 2003). The results were summarized in a 50 % majority rule consensus tree.

Maximum likelihood analyses were conducted using RAxML version 7·2·7 (Stamatakis, 2006; Stamatakis *et al.*, 2008) on the CIPRES portal teragrid (www.phylo.org; Miller *et al.*, 2010). Maximum likelihood bootstrap analyses and the inference of the optimal tree were conducted simultaneously. The optimal tree was inferred using a GTR + Γ model, whereas a similar yet more computationally efficient model was employed for the 1000 bootstrap iterations (GTR with optimization of substitution rates and site-specific evolutionary rates categorized into 25 distinct rate categories).

The congruence among data sets was assessed by scrutinizing the phylogenetic results carefully to identify highly supported [bootstrap percentage (BP) >85 %] conflicting relationships (e.g. Wiens, 1998). The partition homogeneity test (incongruence length difference test; Farris *et al.*, 1994, 1995) was not used because its results have been shown to be misleading (Dolphin *et al.*, 2000; Lee, 2001; Reeves *et al.*, 2001; Yoder *et al.*, 2001; Barker and Lutzoni, 2002; Darlu and Lecointre, 2002).

RESULTS

PRK *and* RPB2 *DNA sequences*

Edited DNA sequences of *PRK* and *RPB2* were highly variable in length. *PRK* sequences ranged from 354 bp (*Pinanga coronata* and *P. simplicifrons*) to 1112 bp (*Dypsis lanceolata*) with a mean length of 607 bp (total: 208 sequences). *RPB2* varied from 554 bp (*Cocos nucifera*) to 1115 bp (*Syagrus smithii*) with a mean of 802 bp (total: 206 sequences). Due to this length variation, many indels were introduced into the alignment of both data sets. In some regions, DNA sequences could not be aligned unambiguously due to high levels of sequence divergence. For this reason, 140 and 248 bp were excluded from analyses of *PRK* and *RPB2* data sets,

respectively. The remaining 1562 bp of the *PRK* alignment contained 615 variable positions and 360 parsimony-informative characters. For *RPB2*, the 1273 unambiguously aligned positions included 615 variable positions and 451 parsimony-informative characters (Table 2).

Cloning proved necessary in five taxa for *PRK* (*Clinosperma lanuginosa*, *Cyphophoenix alba*, *Masoala kona*, *M. madagascariensis* and *Pseudophoenix vinifera*) and seven taxa for *RPB2* (*Burretiokentia grandiflora*, *Ceroxylon quindiuense*, *Dypsis ambilaensis*, *D. hiarakae*, *Lemurophoenix halleuxii*, *Marojejya insignis* and *Roystonea regia*). In both DNA regions, clonal variation was characterized by rare single nucleotide polymorphisms and, less frequently, short indels. In all but two instances (*PRK*, *Pseudophoenix vinifera*; *RPB2*, *Roystonea regia*) more than two copy types were identified, indicating that allelic variation alone cannot account for clonal diversity. In most cases, clones were resolved as exclusive groups in our phylogenetic analyses (Supplementary Data Figs. S1 and S2, available online) or, if not as a group, these nodes were poorly supported (Figs 1 and 2). In two pairs of closely related taxa (*PRK*, *Masoala kona* and *M. madagascariensis*; *RPB2*, *Dypsis ambilaensis* and *D. hiarakae*) some highly supported intermixing of clones was identified. In addition, all clones of *PRK* for *Masoala kona* and *M. madagascariensis* (Areceae: Dypsidinae) isolated in this study formed a highly supported group on a long branch in a position sister to all remaining Areceae (Fig. 2). Closer inspection revealed stop codons in the exons of clones 2–5 of *M. kona* and clones 1 and 4 of *M. madagascariensis*, suggesting that these divergent clones may represent pseudogenes. An additional, apparently functional *PRK* sequence of *M. madagascariensis* published previously (Lewis and Doyle, 2002) was resolved with strong support among the remaining Areceae with other members of sub-tribe Dypsidinae, in which the genus *Masoala* is placed in the classification of Dransfield *et al.* (2005, 2008).

Taxa lacking sequences for either of the DNA regions were excluded from the combined analysis. Where multiple clones were available, one clone selected at random was incorporated into the combined data set. Due to the divergent and apparently pseudogenic nature of the *Masoala* clones and the systematically consistent nature of the *M. madagascariensis* data generated by Lewis and Doyle (2002), the latter sequence was selected for the combined analysis. The combined data set comprised 2835 bp of unambiguously aligned sequence data for 173 species, including 1076 variable positions and 771 parsimony-informative characters

Phylogenetic analyses

For MP analyses, >90 % of the trees saved in the parsimony ratchet searches of the *PRK*, *RPB2* and combined data sets attained the shortest tree length. For each data set, all 20 ratchet searches converged on the same shortest tree length. A strict consensus of the MP trees is given for each data set in Figs 1–4, annotated with MP and ML BPs >50 % that are consistent with this topology. These topologies may also be downloaded from TreeBASE (www.treebase.org; accession number S11041). The optimal ML tree recovered for each data set is provided in Supplementary Data Figs S1–S3 (available online). Tree statistics for all analyses are provided in Table 2. The results of MP and ML analyses were highly congruent, with a high degree of correspondence between bootstrap percentages. Two incongruences between *PRK* and *RPB2* were highly supported (BP >85 % for both ML and MP BPs). These related to the placement of tribes Reinhardtieae, Iriarteeae and Chamaedoreeae (see below for further discussion).

The parsimony analyses of both *PRK* [MP tree length, 1460; consistency index (CI), 0·45; retention index (RI), 0·78; rescaled consistency index (RC), 0·35] and *RPB2* (MP tree length, 1562; CI, 0·52; RI, 0·79; RC, 0·41) yielded generally well-resolved strict consensus trees with numerous nodes supported with BP >50 %. Topologies and bootstrap support were strongly consistent with results of ML analyses (*PRK*, log likelihood −11 864·24; *RPB2*, log likelihood −12 435·05). Subfamily Arecoideae, all of its tribes and seven out of the 14 sub-tribes of Arecoideae were supported by *PRK*. Results from *RPB2* were similar, except that tribe Cocoseae was not resolved as monophyletic. Despite generally good resolution, major polytomies occurred near to the base of Arecoideae in general and within tribe Areceae in particular. The strict consensus tree of the combined analysis (MP tree length, 2855; CI, 0·48; RI, 0·74; RC, 0·36) was more highly resolved than that of either *PRK* or *RPB2* analyses, included more nodes supported with BP >50 %, and was consistent with ML results (log likelihood −23 307·22). The monophyly of Arecoideae, all tribes except for Cocoseae and nine of the 14 sub-tribes (excluding Basseliniinae, Linospadicinae, Oncospermatinae, Rhopalostylidinae and Verschaffeltiinae) was supported. However, while relationships at the base of Arecoideae were better resolved, large polytomies were still present within tribe Areceae. Full details of the relationships recovered by our analyses are discussed below.

DISCUSSION

PRK *and* RPB2 *in arecoid palms*

In common with all preceding studies, we found *PRK* and *RPB2* to be highly informative DNA regions for phylogeny reconstruction in palms. Both regions yielded substantial numbers of informative characters, and resultant topologies were both well resolved and strongly supported, with a few exceptions such as in tribe Areceae. Paralogous copies of both regions were discovered in a small proportion of taxa, but the fact that different copy types largely formed monophyletic groups (or more rarely group with a closely related species) and show minimal divergence suggests that they result from recent duplication events or a combination of allelic variation and recent duplication. We acknowledge that PCR error may also account for some of this diversity (Pfeil *et al.*, 2004). No evidence was found to suggest that we had accidentally isolated either the longer paralogue 1 of *PRK* reported by Lewis and Doyle (2002) or the divergent paralogue 3 of Thomas *et al.* (2006). The basal divergence in Areceae between the cloned *PRK* putative pseudogenes of *Masoala kona* and *M. madagascariensis* (Fig. 2) implies an older duplication event within the tribe and subsequent change rendering most, if not all, of these copies non-

TABLE 2. *Data set and tree statistics for analyses of* PRK *and* RPB2

Data partition	Number of taxa	Total characters	Variable characters	Parsimony-informative characters	MP tree length	MP tree number	CI	RI	RC	ML log likelihood
PRK	208	1562	500	360	1460	3856	0·45	0·78	0·35	−11 864·24
RPB2	206	1273	615	451	1562	3742	0·52	0·79	0·41	−12 435·05
PRK + *RPB2*	173	2835	1076	771	2855	3662	0·48	0·74	0·36	−23 307·22

MP, maximum parsimony; ML, maximum likelihood.
Total characters excludes ambiguously aligned regions.

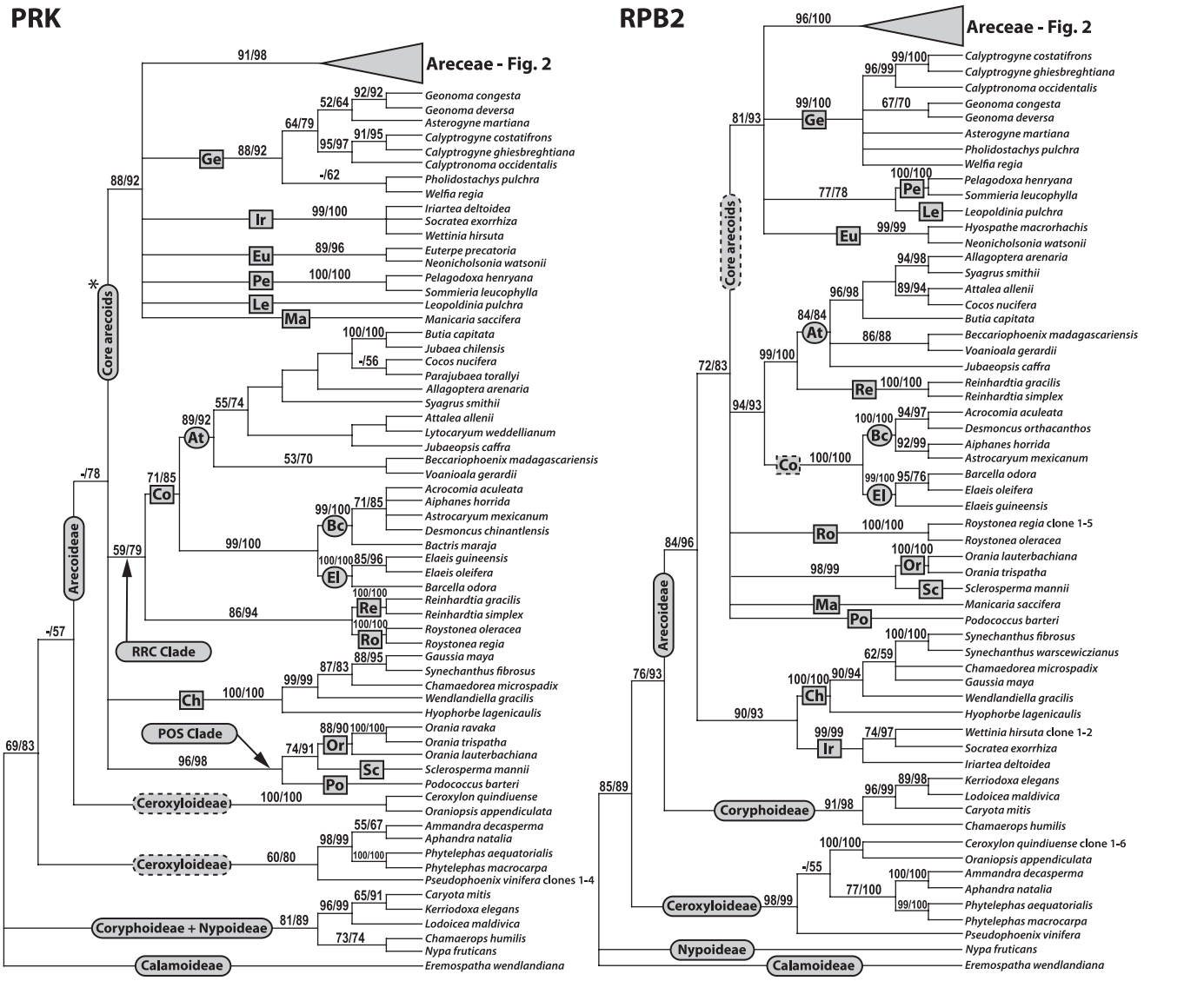

FIG. 1. Strict consensus trees from parsimony ratchet analyses of the *PRK* (number of MP trees, 3856; MP tree length, 1460; CI, 0·45; RI, 0·78; RC, 0·35) and *RPB2* (number of MP trees, 3742; MP tree length, 1562; CI, 0·52; RI, 0·79; RC, 0·41) data sets. Values above the branches are MP/ML bootstrap percentages. Groups recognized in the classification of Dransfield *et al.* (2005, 2008) and major clades mentioned in the text are indicated. The asterisk indicates that the core arecoid clade in this tree also includes tribe Iriarteeae. Labels with a dotted line indicate that the group is only resolved in part. Key to abbreviations, Ar, Areceae; Arc, Archontophoenicinae; Are, Arecinae; At, Attaleinae; Ba, Basseliniinae; Bc, Bactridinae; Ca, Carpoxylinae; Ch, Chamaedoreeae; Cl, Clinospermatinae; Co, Cocoseae; Dy, Dypsidinae; El, Elaeidinae; Eu, Euterpeae; Ge, Geonomateae; Ir, Iriarteeae; Le, Leopoldinieae; Li, Linospadicinae; Ma, Manicarieae; On, Oncospermatinae; Or, Oranieae; Pe, Pelagodoxeae; Po, Podococceae; Pt, Ptychospermatinae; Re, Reinhardtieae; Ro, Roystoneeae; Sc, Sclerospermeae; Ve, Verschaffeltiinae.

functional. Putative *PRK* pseudogenes have also been recovered previously in tribe Chamaedoreeae (Thomas *et al.*, 2006). It is puzzling that we failed to recover a sequence for *Masoala* that corresponded to that obtained by Lewis and Doyle (2002) despite using the same source of DNA and primers. Variation in PCR protocols may have resulted in

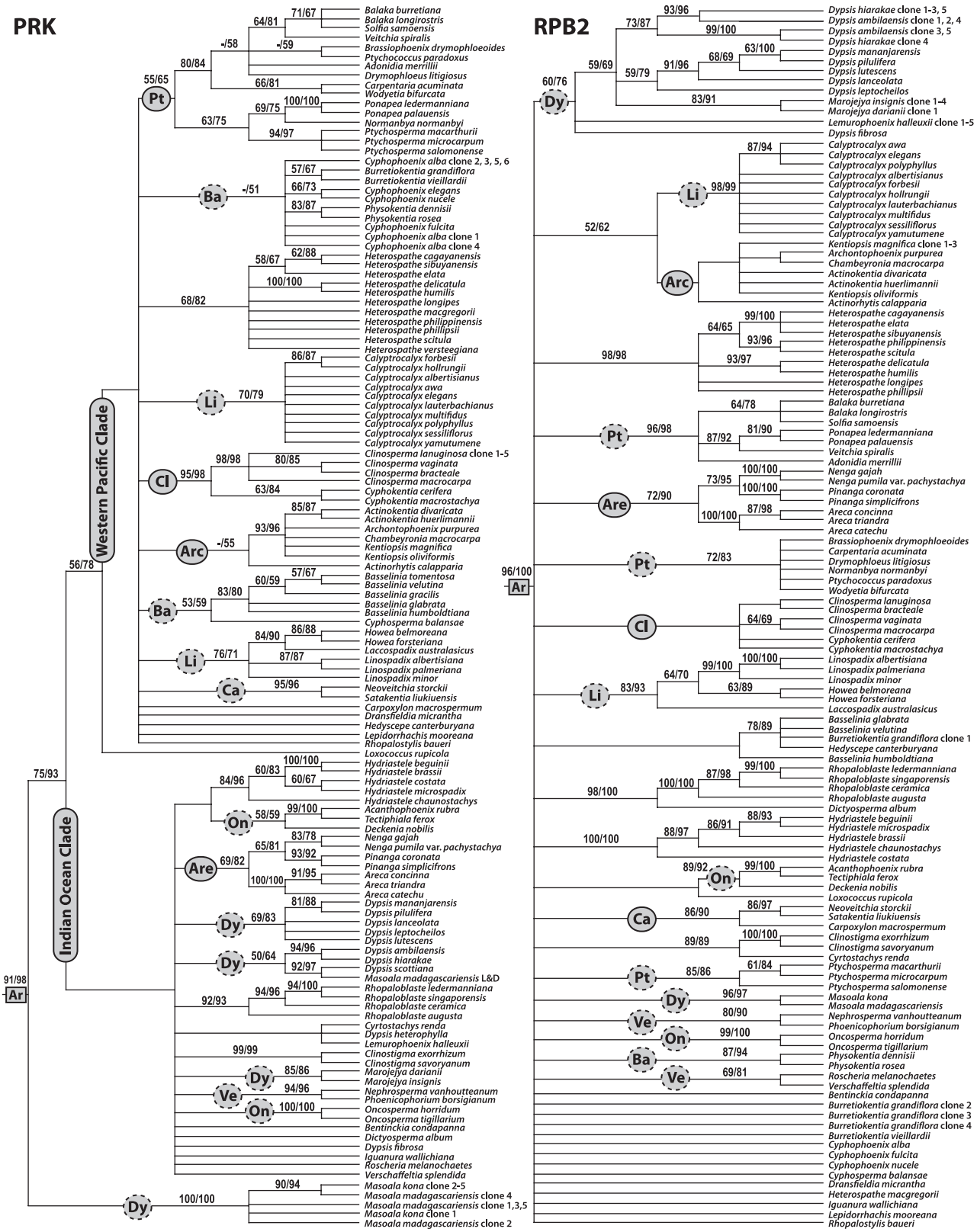

FIG. 2. Strict consensus trees from parsimony ratchet analyses of the *PRK* and *RPB2* data sets, tribe Areceae only, continued from Fig. 1. See legend to Fig. 1 for further details and key to abbreviations. The taxon labelled *Masoala madagascariensis* L&D represents the *PRK* sequence published by Lewis and Doyle (2002).

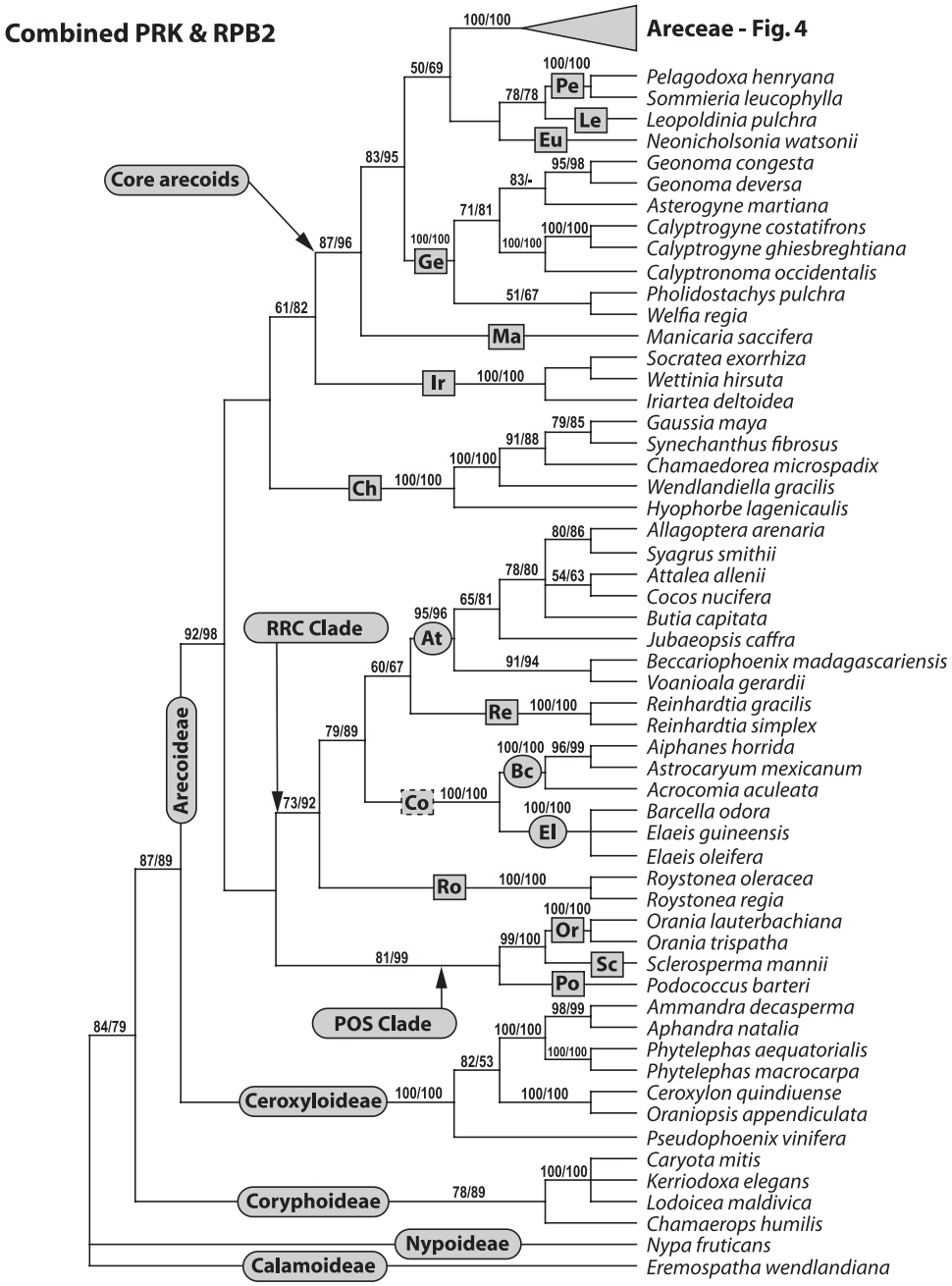

FIG. 3. Strict consensus trees from parsimony ratchet analyses of the combined analysis of *PRK* and *RPB2* (number of MP trees, 3662; MP tree length, 2855; CI, 0·48; RI, 0·74; RC, 0·36). See legend to Fig. 1 for further details and key to abbreviations.

biases towards different copy types, although no further evidence of this is seen elsewhere in our data. In the large majority of taxa, however, we experienced no difficulty in amplifying what appears to be a single copy of each target region, consistent with the finding of several other palm studies utilizing these genes (Roncal *et al.*, 2005, 2008; Loo *et al.*, 2006; Trénel *et al.*, 2007; Cuenca *et al.*, 2008, 2009).

Although numerous topological differences exist between *PRK* and *RPB2* phylogenetic trees, we regard only two as strongly supported incongruence (Fig. 1). First, tribe Iriarteeae falls in a clade with the six tribes of the core arecoid clade (88/92 BP; MP BP/ML BP), whereas *RPB2* places it as sister to tribe Chamaedoreeae (90/93 BP). The combined analysis reaches an intermediate solution, with Iriarteeae sister to the core arecoid clade and then forming a group that is sister to Chamaedoreeae, but these relationships are not as strongly supported as those recovered in the analyses of separate data partitions. Secondly, Reinhardtieae are sister to Roystoneeae in the *PRK* tree (86/94 BP), but nested within Cocoseae as sister to Attaleinae in the *RPB2* tree (99/

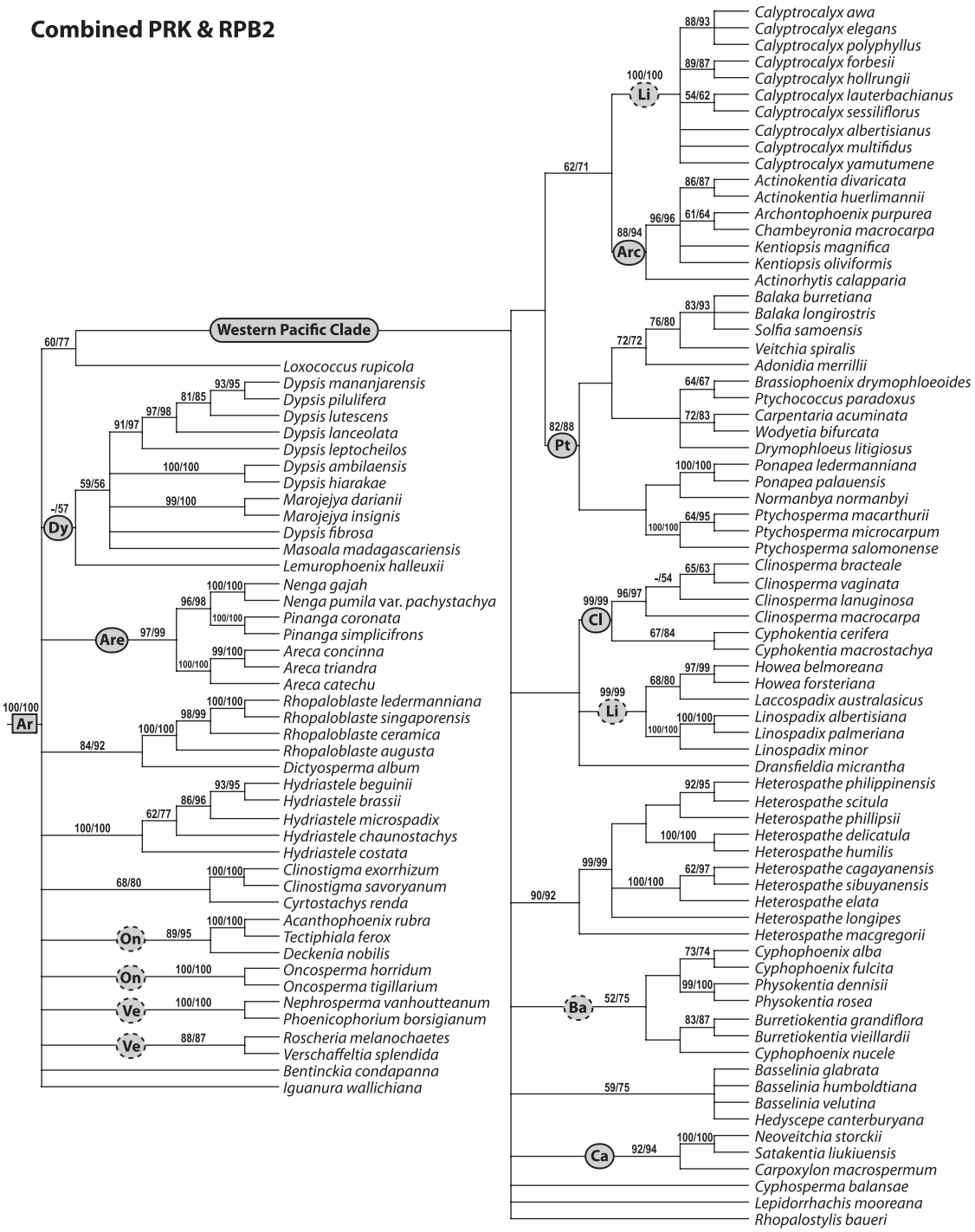

FIG. 4. Strict consensus trees from parsimony ratchet analyses of the combined analysis of *PRK* and *RPB2*, tribe Areceae only, continued from Fig. 3. See legend to Fig. 1 for further details and key to abbreviations.

100 BP). Here, the combined analysis retains the sister group relationship between Reinhardtieae and Attaleinae as recovered by *RPB2*, but with lower support (60/67 BP). The reduction in bootstrap support for relationships of these groups in the combined analysis makes it clear that these are incongruent results. The causes of this incongruence are uncertain.

Higher-level relationships

Monophyly of subfamily Arecoideae is supported by both *PRK* and *RPB2* independently and receives high support in the combined analysis. The combined analysis places Arecoideae sister to Ceroxyloideae, as suggested by the broadest family-wide studies (Asmussen and Chase, 2001;

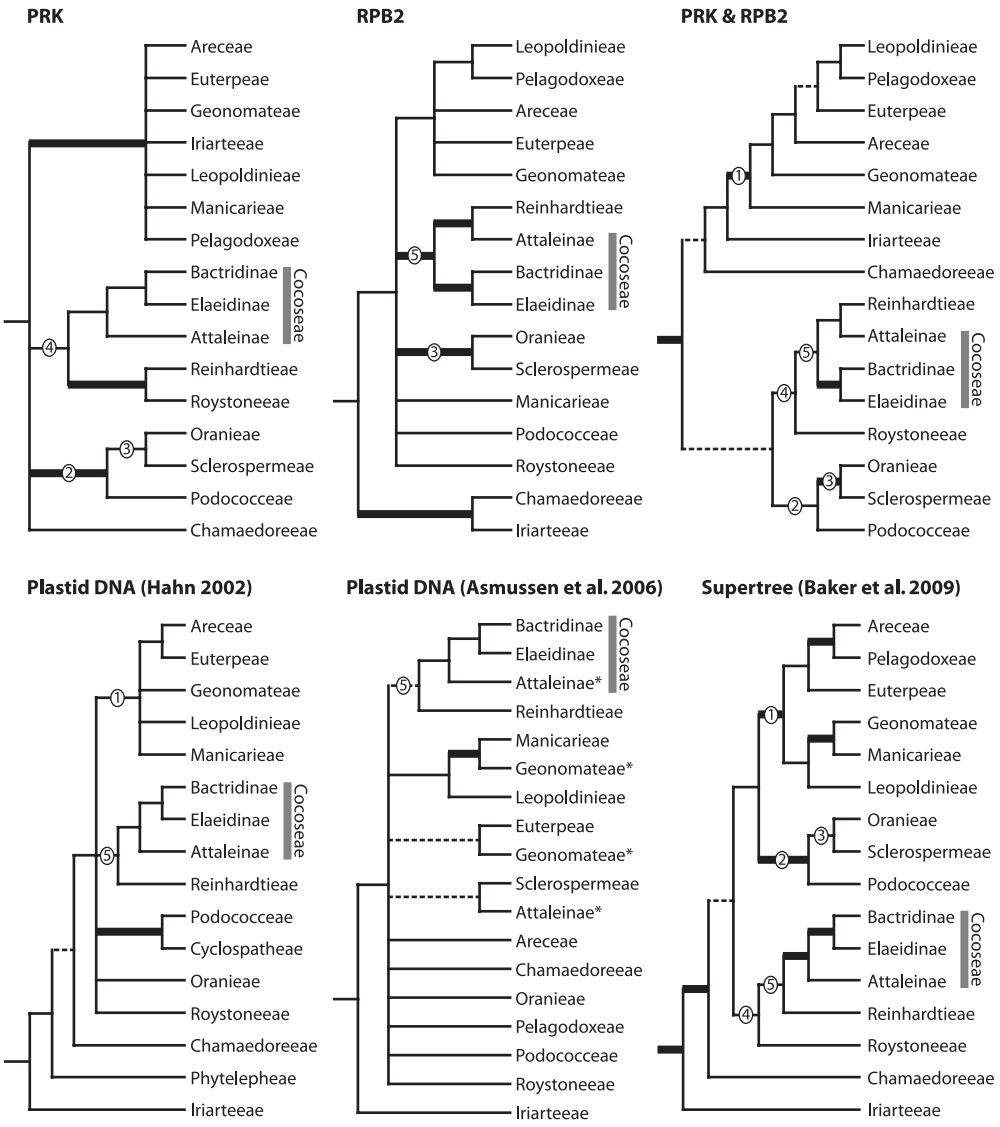

FIG. 5. Summary trees depicting inter-tribal relationships resolved in this study compared with the three most relevant previous studies (Hahn, 2002*a*; Asmussen *et al.*, 2006; Baker *et al.*, 2009). Note that tribe Pelagodoxeae was not sampled by Hahn (2002*a*). Plastid DNA regions sampled by Hahn (2002*a*) were *atpB*, *rbcL*, *ndhF*, *trnQ–rps16* and *trnD–trnT*, and those sampled by Asmussen *et al.* (2006) were *matK*, *rbcL*, *rps16* intron, *trnL* intron and *trnL–F* spacer. Baker *et al.* (2009) combined 16 published data sets including those of Hahn and Asmussen *et al.* and existing data for *PRK* and *RPB2* (e.g. Norup *et al.*, 2006; Savolainen *et al.*, 2006). Bold branches indicate relationships supported by bootstrap percentages ≥85 % (for both MP and ML, where available). For the supertree of Baker *et al.* (2009), bold branches indicate relationships supported by five or more input trees ($s \geq 5$). Remaining branches are supported by <85 BP (or for the supertree $s < 5$) except for dotted branches that are not supported by >50 BP (or for the supertree $s = 1$). * indicates tribes that are not resolved as monophyletic. Sub-tribes of Areceae are not shown here. Key to clade annotations: 1, core arecoid clade (Areceae, Euterpeae, Geonomateae, Leopoldinieae, Manicarieae and Pelagodoxeae); 2, POS clade (Podococceae, Oranieae and Sclerospermeae); 3, Oranieae–Sclerospermeae clade; 4, RRC clade (Roystoneeae, Reinhardtieae and Cocoseae); and 5, Reinhardtieae–Cocoseae clade.

Asmussen *et al.*, 2006; Baker *et al.*, 2009), although alternative topologies are suggested by *PRK*, which renders Ceroxyloideae as paraphyletic with poor support, and *RPB2*, which resolves Coryphoideae as sister to Arecoideae with moderate to high support. These findings do not substantially undermine the body of evidence supporting the sister relationship of Arecoideae and Ceroxyloideae, but indicate that alternative hypotheses may yet come to light from the nuclear genome that contradict the status quo, which has been heavily influenced by large plastid DNA data sets.

We compared the inter-tribal relationships recovered in this study with those found by previous authors (Fig. 5). It is important to note that these studies are not entirely independent of each other. For example, the plastid DNA analyses of Hahn (2002*a*) and Asmussen *et al.* (2006) overlap because both used *rbcL*, and all eight of the plastid regions used in these studies, as well as *PRK* and *RPB2*, were among the 16 data sets analysed by Baker *et al.* (2009). Nevertheless, because data sampling, taxon sampling and methodologies varied among these studies, the similarities

and differences in their results provide an indication of confidence in the resultant phylogenetic hypothesis. Several higher level relationships stand out, notably the core arecoid clade, the POS clade and the Roystoneeae–Reinhardtieae–Cocoseae clade (here termed the RRC clade), and these are discussed below.

Iriarteeae and Chamaedoreeae

Our results strongly support monophyly of Chamaedoreeae and Iriarteeae. As explained above, incongruent placements of tribe Iriarteeae are resolved by *RPB2* and *PRK*. These results contrast with those obtained by previous family-wide studies that moderately supported Iriarteeae as sister to all other Arecoideae (Asmussen and Chase, 2001; Hahn, 2002*a*; Asmussen *et al.*, 2006; Baker *et al.*, 2009) and Chamaedoreeae as sister to all Arecoideae excluding Iriarteeae (Hahn, 2002*a*; Baker *et al.*, 2009). However, the high support for alternatives given by *PRK* and *RPB2* is a cause for concern and merits closer scrutiny with new data.

The intergeneric relationships within Chamaedoreeae found by other authors in analyses of *PRK*, *RPB2* and a number of plastid regions (Thomas *et al.*, 2006; Cuenca and Asmussen-Lange, 2007; Cuenca *et al.*, 2008, 2009) are largely consistent with our findings. Only the moderately supported sister relationship between *Gaussia* and *Synechanthus* (combined, 79/85 BP) conflicts with prior studies which resolved a moderately supported sister relationship between *Gaussia* and *Chamaedorea* (Cuenca *et al.*, 2008, 2009).

The RRC clade: Roystoneeae, Reinhardtieae and Cocoseae

In partitioned and combined analyses we find moderate support for a clade comprising tribes Roystoneeae, Reinhardtieae and Cocoseae (Fig. 5, clade 4; combined, 73/92 BP; *PRK*, 59/70 BP; *RPB2*, $<50/<50$ BP, but resolved in the *RPB2* ML tree, see Supplementary Data Fig. S2, available online). The RRC clade was also resolved by Baker *et al.* (2009) with moderate support, but apart from scant evidence from plastid DNA (e.g. *trnL–trnF* analyses of Asmussen and Chase, 2001), this relationship is only recovered in studies that include data from *PRK* and *RPB2*. However, our confidence in these relationships is strengthened because *PRK* and *RPB2* independently support the RRC clade. Alternatives hypotheses, summarized by Dransfield *et al.* (2008), are not strongly supported.

As outlined above, *PRK* and *RPB2* yield highly supported incongruent placements of Reinhardtieae within the RRC clade, the former placing it sister to Cocoseae (Fig. 5, clade 5), the latter nested with Cocoseae sister to sub-tribe Attaleinae. However, the sister group relationship of Reinhardtieae to Cocoseae is widely supported in other studies (Hahn, 2002*a*; Asmussen *et al.*, 2006; Baker *et al.*, 2009), including independent analyses based on plastid DNA data, which increases our confidence in this relationship. Potential morphological synapomorphies for this relationship include the fibrous leaf sheath, incomplete splits near the rachis (windows) in the leaf and the well-developed staminodial ring in the female flower.

Within Cocoseae, *PRK*, *RPB2* and combined analyses support the monophyly of the three sub-tribes and the sister relationship between Elaeidinae and Bactridinae that has been identified previously (Hahn, 2002*a*; Gunn, 2004; Asmussen *et al.*, 2006; Baker *et al.*, 2009; Eiserhardt *et al.*, 2011). In contrast to the study of Gunn (2004) of *PRK* in Cocoseae, in which a divergent copy of *PRK* was isolated from *Barcella* that did not resolve with *Elaeis*, the remaining genus of Elaeidinae, our *Barcella PRK* sequences resolved as sister to *Elaeis*. Our results also support earlier findings that the Neotropical genera of Attaleinae and pantropical *Cocos* form a monophyletic group to the exclusion of the Madagascan (*Beccariophoenix* and *Voanioala*) and African (*Jubaeopsis*) genera (Gunn, 2004; Baker *et al.*, 2009; Meerow *et al.*, 2009; Eiserhardt *et al.*, 2011).

The POS clade: Podococceae, Oranieae, Sclerospermeae

The POS clade (Podococceae, Oranieae and Sclerospermeae) is supported by our combined analysis (Fig. 5, clade 2; 81/99 BP), adding confidence to a relationship that has been recovered partially or completely by several other studies (Uhl *et al.*, 1995; Hahn, 2002*b*; Lewis and Doyle, 2002; Baker *et al.*, 2009). Our study and that of Baker *et al.* (2009) provide strong support for a sister relationship between Oranieae and Sclerospermeae (Fig. 5, clade 3; 99/100 BP), although weak support for a sister relationship between Sclerospermeae and Podococceae was found by Lewis and Doyle (2002). The strongly supported relationship between Podococceae and Cyclospatheae (Ceroxyloideae) of Hahn (2002*a*) appears to be anomalous. The three tribes of the POS clade are highly distinctive morphologically, and synapomorphies for the group have not been identified. Each tribe comprises a single genus, with *Podococcus* and *Sclerosperma* endemic to the rain forest of tropical West Africa, and *Orania* disjunctly distributed between Madagascar and South-East Asia. Our study provides weak evidence that the POS clade is sister to the RRC clade, whereas Baker *et al.* (2009) provided stronger support for a sister relationship to the core arecoid clade.

Core arecoid clade

Our combined analysis strongly supports the core arecoid clade (Dransfield *et al.*, 2008), comprising Areceae, Euterpeae, Geonomateae, Leopoldinieae, Manicarieae and Pelagodoxeae (Fig. 5, clade 1; 87/96 BP). The MP strict consensus of the *PRK* analysis includes a strongly supported clade of the core arecoid tribes plus Iriarteeae, but the core arecoid clade itself is not resolved. However, the ML bootstrap analysis of *PRK* does support the core arecoid clade (70 BP), which is also present in the ML tree (Supplementary Data Fig. S1). *RPB2* moderately supports the clade, excluding Manicarieae. The appearance of this group in numerous phylogenetic studies (Uhl *et al.*, 1995; Lewis and Doyle, 2001, 2002; Hahn, 2002*a*; Norup *et al.*, 2006; Savolainen *et al.*, 2006; Baker *et al.*, 2009) indicates that a variety of independent data sources point to the same relationship. Morphological synapomorphies for this apparently robust clade have not yet been identified.

The monophyly of the tribes within the core arecoid clade is strongly supported (excluding monogeneric Leopoldinieae and Manicarieae). Within the core arecoids, various contrasting

topologies have been resolved. Only a sister relationship between Geonomateae and Manicarieae is highly supported in multiple studies (Asmussen *et al.*, 2006; Baker *et al.*, 2009), although our combined analysis places Manicarieae as sister to the remaining core arecoid tribes (83/95 BP). Moderately supported clades involving Areceae and Euterpeae appear in several studies, for example Hahn (2002*a*) and, with the addition of Pelagodoxeae, Baker *et al.* (2009). A weakly supported clade including Areceae, Euterpeae, Leopoldinieae and Pelagodoxeae is resolved by our combined analysis (50/69 BP), apparently due to signal from the *RPB2* partition. Although molecular data indicate that Areceae, Euterpeae and Pelagodoxeae are well supported and distinct lineages (Dransfield *et al.*, 2008), the lack of morphological differentiation between the three groups supports the hypothesis of relationships. These three tribes share a distinctive pseudomonomerous gynoecium structure in which only one of three carpels contains a fertile ovule, whereas the remaining core arecoids (and most other Arecoideae) possess a more conventional anatomy with all three carpels containing a functional ovule [the 'triovulate–tricarpellate' gynoecium of Dransfield *et al.* (2008)].

Areceae and Geonomateae

Two of the core arecoid tribes, Areceae and Geonomateae, have been the focus of in-depth phylogenetic studies based on *PRK* and *RPB2* in the past (Roncal *et al.*, 2005, 2010; Norup *et al.*, 2006). Our sampling of Geonomateae was less dense than that of Roncal *et al.*, but the findings of the two studies are entirely congruent. For Areceae, however, we substantially augmented the sampling of Norup *et al.*, who had included only one species per genus, except for their focal genera *Heterospathe* and *Rhopaloblaste*. The Areceae includes 59 genera and is the largest tribe of palms. We sampled all 59 genera and 123 of the 660 species, facilitating a wide assessment of sub-tribal and generic monophyly.

As expected, our findings are broadly congruent with those of Norup *et al.* (2006). We recovered the western Pacific clade (Archontophoenicinae, Basseliniinae, Carpoxylinae, Clinospermatinae, Linospadicinae, Ptychospermatinae, Rhopalostylidinae, *Dransfieldia* and *Heterospathe*) in the *PRK* and combined analyses but with <50 BP, although the sister position of Sri Lankan *Loxococcus* to this group was moderately supported (*PRK*, 56/78 BP; combined, 60/77 BP). The presence of only three staminodes in the female flower is a synapomorphy for the group comprising the western Pacific clade and *Loxococcus* (Nadot *et al.*, 2011). The Indian Ocean clade that Norup *et al.* (2011) recovered with <50 BP in their combined analysis was resolved only in our *PRK* analysis, again with weak support. Despite the biogeographic integrity of these clades (Baker and Couvreur, 2011), additional taxon sampling has not improved phylogenetic confidence in them. In general, large polytomies pervade our results for Areceae, precluding many further inferences regarding deeper relationships among sub-tribes.

Despite widespread phylogenetic ambiguity, evidence for monophyly of six of the 11 subtribes of Areceae is obtained. Archontophoenicinae are resolved with weak support in separate analyses and highly supported in the combined analysis (88/94 BP). All three analyses indicate that *Actinorhytis* is sister to the remaining Archontophoenicinae comprising the Australian and New Caledonian genera (*Actinokentia*, *Archontophoenix*, *Chambeyronia* and *Kentiopsis*; combined, 94/96 BP), a result not found by Norup *et al.* (2006). *RPB2* and the combined analysis place Archontophoenicinae sister to *Calyptrocalyx*, albeit with weak support (*RPB2*, 52/62 BP; combined, 62/71 BP; see below). All analyses provide strong support for the monophyly of Arecinae and the component genera, and for the sister relationship between *Nenga* and *Pinanga*, consistent with the findings of Loo *et al.* (2006). All three data sets support the monophyly of Carpoxylinae (combined, 92/94 BP) and the sister relationship of *Neoveitchia* and *Satakentia* (combined, 100/100 BP). They also support monophyly of Clinospermatinae (combined, 99/99 BP) and its two genera, *Clinosperma* (combined, 96/97 BP) and *Cyphokentia* (combined, 67/84 BP), compatible with a recent re-classification of the group (Pintaud and Baker, 2008). Monophyly of Ptychospermatinae is supported by all three analyses (combined, 82/88 BP), although only sub-clades of the group appear in the MP strict consensus tree of the *RPB2* analysis. Some weakly to moderately supported incongruences in intergeneric relationships occur within the subtribe that may be resolved by sampling more densely. Madagascan Dypsidinae are resolved as monophyletic, but only in the combined analysis and with weak support (<50/57 BP). Disregarding the clade of putative paralogues from *Masoala*, the analyses of *PRK* and *RPB2* do not contradict the sub-tribe's monophyly, but resolve various sub-clades with differing levels of support. Beyond shared geographical distribution, morphological synapomorphies for Dypsidinae have not been identified. Our results also indicate that the large and variable *Dypsis* may not be monophyletic, echoing earlier findings of Lewis and Doyle (2002) and calling into question the lumping of several smaller genera into a broadly defined genus *Dypsis* by previous workers (Dransfield and Beentje, 1995).

The present data suggest that three sub-tribes of Areceae, Basseliniinae, Linospadicinae and Rhopalostylidinae, are not monophyletic. The *PRK* analysis provides equivocal results for Basseliniinae, resolving two weakly supported sub-clades of the group and a third comprising *Lepidorrhachis* only at a basal polytomy in the western Pacific clade. The *RPB2* analysis is even less informative, except that a clade of *Basselinia* species and *Burretiokentia grandiflora* clone 1 is recovered in which *Hedyscepe canterburyana* (Rhopalostylidinae) is embedded (78/89 BP), rendering both Basseliniinae and Rhopalostylidinae non-monophyletic. A similar relationship persists in the combined analysis (excluding *Burretiokentia grandiflora*) with lower support (59/75 BP). Here, the group comprises a basal polytomy within the western Pacific clade with a clade comprising *Burretiokentia*, *Cyphophoenix* and *Physokentia*, and two lineages comprising *Cyphosperma* and *Lepidorrhachis* alone. *Basselinia* and *Cyphophoenix* are not monophyletic, though non-monophyly is not strongly supported. Nevertheless, the revised circumscriptions for these genera proposed by Pintaud and Baker (2008) are not fully corroborated here. Additional data are required to determine whether or not delimitation of Basseliniinae and its genera requires reconsideration.

More surprising than Basseliniinae is the non-monophyly of Linospadicinae. This group of four genera is well defined by shared vegetative characters as well as unique reproductive morphology within Areceae in which inflorescences are spicate with flowers developing in pits in the inflorescence axis. Non-monophyly for this group was first discovered by Norup *et al.* (2006) and later confirmed by Baker *et al.* (2009), although strong support for this finding has not yet been recovered. We addressed this problem by substantially increasing species-level sampling in the group, especially in the largest genus *Calyptrocalyx*. We found all genera to be strongly supported (disregarding monotypic *Laccospadix*), but found no support for monophyly of the sub-tribe. Rather, we found moderate support for a sister relationship between *Calyptrocalyx* and Archontophoenicinae (combined, 62/71 BP), whereas the remaining genera form a robustly supported clade (combined, 99/99 BP) within a weakly supported group with Clinospermatinae and *Dransfieldia*. These findings call into question the delimitation of Linospadicinae and the interpretation of their putative morphological synapomorphies. Nevertheless, changes to the current limits of the sub-tribe cannot yet be justified due to remaining phylogenetic uncertainty and the need for evidence from alternative DNA regions.

Monophyly of two further sub-tribes, Oncospermatinae and Verschaffeltiinae, was not supported in our analyses. For these groups, highly supported sub-clades resolved at polytomies or as sister to other groups with no bootstrap support. Monophyly of these sub-tribes has been supported in previous analyses (e.g. Baker *et al.*, 2009), and our analyses provide insufficient evidence to undermine those findings.

Our results provide some insights into the relationships of the ten genera not yet placed to sub-tribe. *Dransfieldia* and *Heterospathe* fall within the western Pacific clade to which *Loxococcus* is sister. All remaining unplaced genera are part of the Indian Ocean group that is recovered as a clade only in the *PRK* analysis. *Cyrtostachys* is moderately supported as sister to *Clinostigma* (combined, 68/80 BP), whereas *Dictyosperma* is sister to *Rhopaloblaste* (combined, 84/92 BP).

Prospects

Our results provide widespread support for the majority of groups recognized formally in the current classification of Arecoideae (Dransfield *et al.*, 2005, 2008). They also give many insights into the relationships among these groups and corroborate findings obtained from other data sets. In particular, they provide confidence in three major clades, the core arecoid clade, the POS clade and the RRC clade. However, many areas of ambiguity remain: (*a*) relationships among the three major clades and tribes Chamaedoreeae and Iriarteeae; (*b*) relationships among the tribes of the core arecoid clade; and (*c*) relationships among the genera and sub-tribes of tribe Areceae. These three areas require research attention as a matter of priority, perhaps as part of a concerted research campaign on Arecoideae as a whole.

It is clear that available data sets are not sufficiently informative to answer all phylogenetic questions in Arecoideae, and new data sources are required. Despite the fact that plastid DNA is reported to be highly conserved in palms (Wilson *et al.*, 1990; Gaut *et al.*, 1992, 1996; Baker *et al.*, 1999), it has recently been used successfully to resolve relationships at lower taxonomic levels (Cuenca and Asmussen-Lange, 2007). Nevertheless, low-copy nuclear DNA regions have been shown to be more effective sources of data in palms (e.g. Trénel *et al.*, 2007). It is important that new regions of the nuclear genome are now investigated (e.g. Bacon *et al.*, 2008) to build on existing understanding. However, conventional molecular phylogenetic approaches may prove insufficient to resolve these currently intractable groups. A substantial up-scaling of data production exploiting new genomic methods may be required to generate a much more robust phylogenetic hypothesis for this important group of palms.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following figures. Figure S1: maximum likelihood tree from analysis of the *PRK* data set (log likelihood −11 864·24). Figure S2: maximum likelihood tree from analysis of the *RPB2* data set (log likelihood −12 435·05). Figure S3: maximum likelihood tree from simultaneous analysis of the combined *PRK* and *RPB2* data sets (log likelihood −23 307·22).

ACKNOWLEDGEMENTS

We thank John Dransfield, Sophie Nadot and an anonymous reviewer for useful comments on the manuscript, and the staff at the Jodrell Laboratory, RBG Kew, for technical assistance. Conny Asmussen-Lange, Roy Banka, Rudi Maturbongs, Jack Wanggai, Charlie Heatubun, Paul Forster, Scott Zona, Fairchild Tropical Botanic Garden, Flecker Botanic Gardens and Brisbane Botanic Gardens supplied DNA samples. This work was supported by grants from the Leverhulme Trust, Royal Society and the UK Natural Environment Research Council to W.J.B. and V.S., from the British American Tobacco Biodiversity Partnership to W.J.B., from the European Commission to V.S., and from the Oticon Foundation and the University of Aarhus to M.V.N.

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APPENDIX

List of taxa sampled in this study with voucher herbarium specimen details (or source publication reference where appropriate) and GenBank/EMBL accession numbers for all DNA sequences. Accession numbers are given as *PRK*/*RPB2*. Where multiple clones have been included, the clone number is indicated by superscript numbers. Clones included in the combined analysis are underlined.

Acanthophoenix rubra (Lewis 98-067 [BH]): AF453329/AJ830020; ***Acrocomia aculeata*** (Baker 1000 [FTG]): AJ831344/AJ830151; ***Actinokentia divaricata*** (Pintaud 300 [K]): AJ831221/FR729727; ***Actinokentia huerlimannii*** (Pintaud 465 [NOU]): AJ831222/AJ830023; ***Actinorhytis calapparia*** (Lewis 97-011 [FTG]): AF453330/AJ830024; ***Adonidia merrillii*** (Zona 874 [FTG]): AJ831224/AJ830193; ***Aiphanes horrida*** (Gunn, 2004; Cuenca *et al*., 2008): AY601211/EF491155; ***Allagoptera arenaria*** (Lewis 99-014 [BH]): AF453331/AJ830152; ***Ammandra decasperma*** (Lewis 99-039 [BISH]): AF453332/AY543096; ***Aphandra natalia*** (Baker 985 [K]): AJ831345/AJ830153; ***Archontophoenix purpurea*** (Pintaud 492 [TL]): AJ831227/AJ830028; ***Areca catechu*** (PRK, Lewis 98-093 [BH]; RPB2, TCMK 21 [K]): AF453333/AY543109; ***Areca concinna*** (Baker 1146 [K]): AY348907/AY543110; ***Areca triandra*** (1984-2295 [K]): AY348912/AY543115; ***Asterogyne martiana*** (Baker 89021 [BISH]): AF453334/AJ830154; ***Astrocaryum mexicanum*** (Cuenca *et al*., 2008): EF491113/EF491154; ***Attalea allenii*** (Knudsen & Asmussen 612 [AAU]): AJ831346/AJ830207; ***Bactris maraja*** (Gunn, 2004): AY601214/–; ***Balaka burretiana*** (Zona 713 [FTG]): AJ831228/AJ830194; ***Balaka longirostris*** (Pintaud 463 [SUVA]): AJ831229/AJ830029; ***Barcella odora*** (Cuenca *et al*., 2008): EF491112/EF491158; ***Basselinia glabrata*** (Pintaud 468 [K]): AJ831225/AJ830026; ***Basselinia gracilis*** (Pintaud 560 [P]): AJ831230/–; ***Basselinia humboldtiana*** (Pintaud 532 [K]): AJ831231/AJ830030; ***Basselinia tomentosa*** (Pintaud 542 [K]): AJ831232/–; ***Basselinia velutina*** (Pintaud 553 [P]): AJ831233/AJ830031; ***Beccariophoenix madagascariensis*** (Baker 993 [FTG]): AF453335/AJ830155; ***Bentinckia condapanna*** (1993-2989 [K]): AF453336/AJ830032; ***Brassiophoenix drymophloeoides*** (Coons 1398 [FTG]): AJ831235/AJ830195; ***Burretiokentia grandiflora*** (Pintaud 438 [K]): AJ831242/AJ830035[1], AJ830036[2], AJ830037[3], AJ830038[4]; ***Burretiokentia vieillardii*** (Pintaud 197 [NY]): AJ831243/AJ830039; ***Butia capitata*** (Gunn, 2004; Cuenca *et al*., 2008): AY601251/EF491157; ***Calyptrocalyx albertisianus*** (Baker 1109 [K]): AJ831244/AJ830040; ***Calyptrocalyx awa*** (Dowe 721 [JCT]): AJ831249/AJ830045; ***Calyptrocalyx elegans*** (Dowe 731 [JCT]): AJ831257/AJ830053; ***Calyptrocalyx forbesii*** (Baker 1179 [K]): AJ831246/AJ830042; ***Calyptrocalyx hollrungii*** (Baker 1176 [K]): AJ831251/AJ830043; ***Calyptrocalyx lauterbachianus*** (Banka 2009 [K]): AJ831245/AJ830041; ***Calyptrocalyx multifidus*** (Dowe 724 [JCT]): AJ831252/AJ830048; ***Calyptrocalyx polyphyllus*** (Baker 1177 [K]): AJ831250/AJ830044; ***Calyptrocalyx sessiliflorus*** (Dowe 725 [JCT]): AJ831253/AJ830049; ***Calyptrocalyx yamutumene*** (Dowe 730 [JCT]): AJ971821/AJ971832; ***Calyptrogyne costatifrons*** (Knudsen & Asmussen 603 [AAU]): AJ831347/AJ830208; ***Calyptrogyne ghiesbreghtiana*** (Roncal *et al*., 2005): AY772764/AY779364; ***Calyptronoma occidentalis*** (Roncal *et al*., 2005): AY772765/AY779365; ***Carpentaria acuminata*** (Zona 827 [FTG]): AJ831259/AJ830196; ***Carpoxylon macrospermum*** (Zona 722 [FTG]): AF453337/AJ830055; ***Caryota mitis*** (Lewis 99-013 [BH]): AF453338/AJ830156; ***Ceroxylon quindiuense*** (1976-1160 [K]): AJ831349/AJ830157[1], AJ830158[2], AJ830159[3], AJ830160[4], AJ830162[5], AJ830161[6]; ***Chamaedorea microspadix*** (Henderson 391 [FTG]): AJ831352/AJ830166; ***Chamaerops humilis*** (Lewis 99-012 [BH]): AF453339/AY543097; ***Chambeyronia macrocarpa*** (Pintaud 512 [P]): AJ831260/AJ830056; ***Clinosperma bracteale*** (Pintaud 349 [K]): AJ831261/AJ830057; ***Clinosperma lanuginosa*** (Pintaud 368 [P]): AJ831236[1], AJ831237[2], AJ831238[3], AJ831239[4], AJ831240[5]/AJ830033; ***Clinosperma***

macrocarpa (Pintaud 364 [P]): AJ831302/AJ830110; ***Clinosperma vaginata*** (Pintaud 484 [TL]): AJ831241/AJ830034; ***Clinostigma exorrhizum*** (Pintaud 451 [SUVA]): AJ831262/FR729728; ***Clinostigma savoryanum*** (Pintaud 442 [MAK]): AJ831263/AJ830059; ***Cocos nucifera*** (Gunn, 2004; Cuenca *et al.*, 2008): AY601232/EF491150; ***Cyphokentia cerifera*** (Pintaud 347 [K]): AJ831318/AJ830129; ***Cyphokentia macrostachya*** (Pintaud 558 [P]): AJ831264/AJ830060; ***Cyphophoenix alba*** (Pintaud 277 [K]): AJ831336[1], AJ831337[2], AJ831338[3], AJ831339[4], AJ831340[5], AJ831341[6]/AJ830149; ***Cyphophoenix elegans*** (Pintaud 216 [P]): AJ831265/–; ***Cyphophoenix fulcita*** (Pintaud 524 [P]): AJ831258/AJ830054; ***Cyphophoenix nucele*** (Pintaud 372 [K]): AJ831266/AJ830061; ***Cyphosperma balansae*** (Baker 89-030 [BISH]): AF453340/AY543098; ***Cyrtostachys renda*** (1982-5882 [K]): AF453341/AJ830062; ***Deckenia nobilis*** (Lewis 98-031 [BH]): AF453342/AJ830063; ***Desmoncus chinantlensis*** (Gunn, 2004): AY601212/–; ***Desmoncus orthacanthos*** (Cuenca *et al.*, 2008): –/EF491156; ***Dictyosperma album*** (Lewis 98-031 [BH]): AF453343/AJ830064; ***Dransfieldia micrantha*** (Baker 1066 [K]): AJ831326/AJ830139; ***Drymophloeus litigiosus*** (Barrow 125 [K]): AJ831267/AJ830197; ***Dypsis ambilaensis*** (Dransfield 6496 [K]): AJ831268/AJ830065[1], AJ830066[2], AJ830067[3], AJ830068[4], AJ830069[5]; ***Dypsis fibrosa*** (Yesilyurt 803 [K]): AJ831269/AJ830070; ***Dypsis heterophylla*** (Lewis 99-047 [BH]): AF453344/–; ***Dypsis hiarakae*** (Beentje 4578 [K]): AJ831270/AJ830071[1], AJ830072[2], AJ830073[3], AJ830074[4], AJ830075[5]; ***Dypsis lanceolata*** (Yesilyurt 804 [K]): AJ831271/AJ830076; ***Dypsis leptocheilos*** (PRK: Baker 988 [FTG]; RPB2: Yesilyurt 802 [K]): AF453345/AJ830077; ***Dypsis lutescens*** (Lewis 00-004 [BH]): AF453346/AJ830078; ***Dypsis mananjarensis*** (Beentje 4796 [K]): AJ831273/AJ830079; ***Dypsis pilulifera*** (Beentje 4574 [K]): AJ831274/AJ830080; ***Dypsis scottiana*** (Beentje 4608 [K]): AJ831275/–; ***Elaeis guineensis*** (Gunn, 2004; Roncal *et al.*, 2005): AY601219/AY779380; ***Elaeis oleifera*** (Yesilyurt 805 [K]): AJ831350/AJ830163; ***Eremospatha wendlandiana*** (Dransfield JD 7004 [K]): FR729730/FR729729; ***Euterpe precatoria*** (Zona 751 [FTG]): AF453347/–; ***Gaussia maya*** (Lewis 00-001 [FTG]): AF453348/AJ830165; ***Geonoma congesta*** (Roncal *et al.*, 2005): AY772745/AY779345; ***Geonoma deversa*** (Roncal 19 [FTG]): AJ831354/AJ830210; ***Hedyscepe canterburyana*** (Baker 1170 [K]): AJ971823/AJ971844; ***Heterospathe cagayanensis*** (Kyburz s.n. [no voucher]): AJ831277/AJ830082; ***Heterospathe delicatula*** (Baker 1190 [K]): AJ831278/AJ830083; ***Heterospathe elata*** (Lewis 99-034 [GUAM]): AF453350/AJ830085; ***Heterospathe humilis*** (Banka 2011 [K]): AJ831280/AJ830086; ***Heterospathe longipes*** (Baker 1180 [FTG]): AJ831226/AJ830027; ***Heterospathe macgregorii*** (Baker 651 [K]): AJ831281/AJ830087; ***Heterospathe philippinensis*** (Fernando 1623 [LBC]): AJ831282/AJ833634; ***Heterospathe phillipsii*** (Pintaud 454 [SUVA]): AJ831283/AJ830088; ***Heterospathe scitula*** (Fernando 1625 [LBC]): AJ831284/AJ830089; ***Heterospathe sibuyanensis*** (Zona 1050 [FTG]): AJ831285/AJ830090; ***Heterospathe versteegiana*** (Baker 1117 [K]): AJ831293/–; ***Howea belmoreana*** (Baker 1154 [K]): AJ831294/AJ830098; ***Howea forsteriana*** (Baker 1156 [K]): AJ971828/AJ971838; ***Hydriastele beguinii*** (Zona 799 [FTG]): AY348951/AY543163; ***Hydriastele brassii*** (Baker 823 [K]): AY348916/AY543116; ***Hydriastele chaunostachys*** (Baker 89028 [BISH]): AF453349/AJ833635; ***Hydriastele costata*** (Baker 836 [K]): AY348925/AY543127; ***Hydriastele microspadix*** (Baker 573 [K]): AY348932/AY543136; ***Hyophorbe lagenicaulis*** (Fantz 3297 [FTG]): AF453351/AJ830168; ***Hyospathe macrorhachis*** (Balslev 6421 [AAU]): –/AJ830169; ***Iguanura wallichiana*** (Lewis 99-049 [BISH]): AF453352/AY543099; ***Iriartea deltoidea*** (Cuenca *et al.*, 2008): EF491109/EF491149; ***Jubaea chilensis*** (Gunn, 2004): AY601255/–; ***Jubaeopsis caffra*** (Gunn, 2004; Cuenca *et al.*, 2008): AY601272/EF491152; ***Kentiopsis magnifica*** (Pintaud 346 [NY]): AJ831299/AJ830103[1], AJ830104[2], AJ830106[3]; ***Kentiopsis oliviformis*** (Pintaud 358 [K]): AF453353/AY543100; ***Laccospadix australasicus*** (Baker 1172 [K]): AJ831300/AJ830108; ***Laccospadix australasicus*** (Baker 1173 [K]): AJ831301/AJ830109; ***Lemurophoenix halleuxii*** (Lewis 98-073 [BH]): AF453354/AJ830112[1], AJ830113[2], AJ830114[3], AJ830115[4], AJ830116[5]; ***Leopoldinia pulchra*** (Romero 3060 [VEN]): AF453355/AY543102; ***Lepidorrhachis mooreana*** (Baker 1167 [K]): AJ831303/AJ830117; ***Linospadix albertisiana*** (Dowe 720 [JCT]): AJ831305/AJ830119; ***Linospadix minor*** (1988-2450 [K]): AJ971831/AJ971841; ***Linospadix palmeriana*** (Dowe 726 [JCT]): AJ831306/AJ830120; ***Lodoicea maldivica*** (Lewis 98-020 [BH]): AF453357/AJ830171; ***Loxococcus rupicola*** (1990-2497 [K]): AY348942/AY543151; ***Lytocaryum weddellianum*** (Gunn, 2004): AY601249/–; ***Manicaria saccifera*** (Henderson s.n. [NY]): AF453358/AJ830173; ***Marojejya darianii*** (Lewis 99-037 [BISH]): AF453359/AJ830121; ***Marojejya insignis*** (Baker 1016 [K]): AJ831307/AJ830122[2], AJ830123[3], AJ830124[4]; ***Masoala kona*** (Baker 1038 [K]): AJ831308[1], AJ831309[2], AJ831310[3], AJ831311[4], AJ831312[5]/AJ830126; ***Masoala madagascariensis*** (1992-3552 [K]): AJ831313[1], AJ831314[2], AJ831315[3], AJ831316[4], AJ831317[5], AF453360 (Lewis and Doyle, 2002)/AJ830128; ***Nenga gajah*** (Dransfield 6352 [K]): AY348913/AY543153; ***Nenga pumila*** **var** ***pachystachya*** (Baker 994 [FTG]): AY348914/AY543154; ***Neonicholsonia watsonii*** (Lewis 99-052 [BISH]): AJ831356/AJ830172; ***Neoveitchia storckii*** (Roncal 73 [FTG]): AJ831319/AJ830130; ***Nephrosperma vanhoutteanum*** (Lewis 98-006 [BH]): AF453362/AJ830131; ***Normanbya normanbyi*** (Zona 876 [FTG]): AF453363/AJ830198; ***Nypa fruticans*** (PRK: Noblick 5197 [K]; RPB2: Baker 512 [SAR]): AJ831357/AJ830174; ***Oncosperma horridum*** (Lewis 99-024 [BH]): AJ831320/AJ830133; ***Oncosperma tigillarium*** (Lewis 98-051 [BH]): AF453364/AJ830134; ***Orania lauterbachiana*** (Lewis 99-038 [BISH]): AF453365/AJ830175; ***Orania ravaka*** (Dransfield 7731 [K]): AJ831358/–; ***Orania trispatha*** (Lewis 98-098 [BH]): AF453366/AJ830176; ***Oraniopsis appendiculata*** (1988-227 [K]): AJ831359/AJ830177; ***Parajubaea torallyi*** (Gunn, 2004): AY601264/–; ***Pelagodoxa henryana*** (1988-2933 [K]): AJ831321/AJ830135; ***Phoenicophorium borsigianum*** (Lewis 98-024 [K]): AF453368/AJ830136; ***Pholidostachys pulchra*** (Roncal 26 [FTG]): AJ831360/AJ830211; ***Physokentia dennisii*** (88-4170 [K]): AF453369/AJ830137; ***Physokentia rosea*** (Pintaud 452 [TL]): AJ831322/AJ830138; ***Phytelephas aequatorialis*** (1993-94 [K]): AJ831361/AJ830178; ***Phytelephas macrocarpa*** (Ely 9 [K]): AJ831362/AJ830179; ***Pinanga coronata*** (Baker 1145 [K]):

AY348944/AY543156; ***Pinanga simplicifrons*** (Loo 314 [K]): AY348949/AY543161; ***Podococcus barteri*** (Reitsma 2840 [BH]): AF453370/AJ830180; ***Ponapea ledermanniana*** (Zona 878 [FTG]): AJ831323/AJ830199; ***Ponapea palauensis*** (Lewis 99-055 [BISH]): AJ831328/AJ830203; ***Pseudophoenix vinifera*** (Baker 1002 [FTG]): AJ831363[1], AJ831364[2], AJ831365[3], AJ831366[4]/AJ830181; ***Ptychococcus paradoxus*** (Baker 572 [K]): AJ831324/AJ830200; ***Ptychosperma macarthurii*** (Zona 869 [FTG]): AJ831325/AJ830201; ***Ptychosperma microcarpum*** (Zona 965 [FTG]): AJ831327/AJ830202; ***Ptychosperma salomonense*** (Houghton 1300 [FTG]): AF453371/AY543105; ***Reinhardtia gracilis*** (Fisher 95-9 [FTG]): AF453372/AJ830182; ***Reinhardtia simplex*** (1988-366 [K]): AJ831371/AJ830183; ***Rhopaloblaste augusta*** (Lewis 99-004 [FTG]): AF453373/AY543107; ***Rhopaloblaste ceramica*** (Banka 2050 [LAE]): AJ831329/AJ830141; ***Rhopaloblaste ledermanniana*** (Heatubun 191 [K]): AJ831331/AJ830144; ***Rhopaloblaste singaporensis*** (Baker 1174 [K]): AJ831330/AJ830142; ***Rhopalostylis baueri*** (Pintaud 384 [NY]): AJ831333/AJ830145; ***Roscheria melanochaetes*** (Lewis 98-036 [BH]): AF453374/AJ830140; ***Roystonea oleracea*** (1963-57401 [K]): AJ831372/AJ830184; ***Roystonea regia*** (Baker 996 [K]): AF453375/AJ830185[1], AJ830186[2], AJ830187[3], AJ830188[4], AJ830189[5]; ***Satakentia liukiuensis*** (Lewis 99-051 [BISH]): AF453376/AJ830146; ***Sclerosperma mannii*** (Sunderland 1794 [K]): AF453377/AJ830190; ***Socratea exorrhiza*** (Baker 992 [FTG]): AF453378/AY543108; ***Solfia samoensis*** (Tipama'a 001 [FTG]): AJ831334/AJ830204; ***Sommieria leucophylla*** (1992-3571 [K]): AJ831335/AJ830147; ***Syagrus smithii*** (Gunn, 2004; Roncal *et al.*, 2005): AY601263/AY779378; ***Synechanthus fibrosus*** (Cuenca *et al.*, 2008): EF491103/EF491143; ***Synechanthus warscewiczianus*** (Cuenca *et al.*, 2008): –/EF491144; ***Tectiphiala ferox*** (Lewis 98-070 [BH]): AF453380/AJ830148; ***Veitchia spiralis*** (Zona 724 [FTG]): AJ831342/AJ830205; ***Verschaffeltia splendida*** (Lewis 98-039 [BH]): AF453381/AJ830150; ***Voanioala gerardii*** (Gunn, 2004; Cuenca *et al.*, 2008): AY601266/EF491153; ***Welfia regia*** (Borgardt 1032 [BH]): AF453382/–; ***Wendlandiella gracilis*** (Henderson 390 [FTG]): AJ831353/AJ830167; ***Wettinia hirsuta*** (Baker 991 [FTG]): AJ831373/AJ830191[1], AJ830192[2]; ***Wodyetia bifurcata*** (Zona 906 [FTG]): AJ831343/AJ830206.