

The Palms

Guest edited by William J. Baker and Scott Zona

A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA phylogeny

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Received June 2005; accepted for publication November 2005

Published phylogeny reconstructions of the palm family (Arecaceae) are based on plastid DNA sequences or restriction fragment length polymorphisms (RFLPs), nuclear DNA sequences, morphological characters or a combination thereof, and include between 33 and 90 palm species. The present study represents all previously recognized subfamilies, tribes and subtribes of palms and 161 of the 189 genera. The plastid DNA region *matK* was sequenced for 178 palm species and ten commelinid monocot outgroup species, and was combined with new and previously published plastid DNA sequences of *trnL-trnF*, *rps16* intron and *rbcL*. The addition of *matK* sequences and more taxa resulted in a highly resolved and largely well-supported phylogeny. Most importantly, critical basal nodes are now fully resolved and, in most cases, strongly supported. On the basis of this phylogeny, we have established a new subfamilial classification of the palms, in which five subfamilies are recognized, rather than the six that were included in the previous classification. The circumscriptions of the subfamilies Calamoideae and Nypoideae were corroborated. The phylogeny supported a new circumscription for the subfamily Coryphoideae, including all taxa previously recognized in Coryphoideae with the addition of the tribe Caryoteae, formerly of the subfamily Arecoideae. The phylogenetic analysis also supported a new delimitation for the subfamily Ceroxyloideae that contains the tribes Cyclospatheae and Ceroxyloae, and all genera formerly included in the subfamily Phytelephantoideae, but excludes the tribe Hyophorbeae. Finally, the subfamily Arecoideae was modified to exclude the tribe Caryoteae and to include the tribe Hyophorbeae. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, 151, 15–38.

ADDITIONAL KEYWORDS: *matK* – Palmae – *rbcL* – *rps16* intron – *trnL-trnF*.

INTRODUCTION

The palm family (Arecaceae, Palmae) is resolved as a monophyletic group in all higher-level molecular studies of monocots (e.g. Chase *et al.*, 2000; Asmusen & Chase, 2001). During the last 10 years, sub-

stantial progress has been made in the understanding of the relationships within the family. Many estimates of palm phylogeny have been published at various taxonomic levels. Nevertheless, numerous ambiguities have persisted, hindering any attempt to rearrange the formal classification of the family, such as, for example, the placements of the tribes Cyclospatheae and Phoeniceae, and of the sub-

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family Phytelephantoideae. In this paper, which is focused strictly on the circumscription of palm subfamilies, we shall refer primarily to those phylogeny reconstructions that explore the systematics of the family at the highest level (Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen, Baker & Dransfield, 2000; Asmussen & Chase, 2001; Hahn, 2002a; Lewis & Doyle, 2002). We use the formal subfamily, tribal and subtribal names in the sense of Dransfield & Uhl (1998), who divided the family into six subfamilies varying in size from one genus (subfamily Nypoideae) to 112 genera (subfamily Arecoideae; see Appendix). For the subfamily Calamoideae, however, we use the classification of Baker, Dransfield & Hedderson (2000a). This study provides part of the justification for a forthcoming new classification of palms based on phylogenetic data (Dransfield *et al.*, 2005); we make references to the new classification, where appropriate, within the figures and in the discussion section below.

CURRENT STATUS OF PALM FAMILY PHYLOGENETICS

Subfamilies Calamoideae and Nypoideae

The subfamily Calamoideae is resolved as monophyletic in all palm family phylogenies (Uhl *et al.*, 1995; Baker *et al.*, 1999, 2000a; Baker, Hedderson & Dransfield, 2000b, c; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Lewis & Doyle, 2001; Hahn, 2002a). Baker *et al.* (2000a, b, c) explored the relationships within this subfamily and proposed a new classification for the Calamoideae with three tribes and nine subtribes based on a combination of molecular and morphological data.

Nypa, the sole representative of the subfamily Nypoideae, is always resolved on an isolated branch when maximum parsimony is employed as the optimality criterion (Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Lewis & Doyle, 2001; Hahn, 2002a). In a few analyses using maximum likelihood, *Nypa* is nested in various positions among members of the subfamily Calamoideae or the subfamily Coryphoideae (Hahn, 2002a), but these relationships have received scant support in other systematic studies.

The Calamoideae and the Nypoideae are the principal candidates for the position as the sister taxon to the remaining members of Arecaceae. In two recent papers with extensive taxon and nucleotide character sampling, the subfamily Calamoideae was resolved as sister to all other members of the palm family in total evidence analyses based on parsimony (Asmussen & Chase, 2001; Hahn, 2002a). This finding contrasts markedly with the first phylogenetic study of palms based on restriction fragment length polymorphisms (RFLPs) and morphology, in which *Nypa* resolved as

sister to the remaining members of Arecoideae, with the Calamoideae sister to all palms excluding *Nypa* (Uhl *et al.*, 1995). However, this result was probably influenced by the use of only one taxon as an outgroup, *Dioscorea* (Dioscoreaceae), which is only distantly related to palms and commelinid monocots as a whole (Chase *et al.*, 2000), thereby increasing the potential for a spurious rooting. In subsequent studies, Baker *et al.* (1999) and Asmussen *et al.* (2000) did not include nonpalm outgroups, due to alignment problems, rooting their phylogenies internally on *Nypa* following Uhl *et al.* (1995). Although their methods were explicit, the results are prone to misinterpretation. However, another study, which included nonpalm outgroups, supports *Nypa* as sister to all other palms (Lewis & Doyle, 2001). Unfortunately, in none of these studies are the relative positions of *Nypa* or the Calamoideae strongly supported by bootstrap analysis, rendering the results effectively equivocal.

Subfamily Coryphoideae

More than half the phylogenetic analyses of the palm family based on DNA sequences do not resolve the subfamily Coryphoideae as monophyletic (Baker *et al.*, 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Hahn, 2002a). However, the plastid RFLP phylogeny of Uhl *et al.* (1995), in which the taxonomic sampling was heavily biased towards coryphoids, resolved subfamily Coryphoideae including the tribe Caryoteae from the subfamily Arecoideae as a monophyletic group. The study of Lewis & Doyle (2001), based on DNA sequences of the nuclear gene, malate synthase, and that of Hahn (2002a), based on a combined, reduced data set, resolved the Coryphoideae as monophyletic. It should be noted, however, that the sample size was small in both cases. Many data sets group the tribe Caryoteae of the subfamily Arecoideae together with members of the subfamily Coryphoideae, often with close relationships to the subtribe Coryphinae or the tribe Borasseae (Uhl *et al.*, 1995; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Hahn, 2002a).

Subfamilies Ceroxyloideae and Phytelephantoideae

It is clear from most phylogenetic analyses that the subfamily Ceroxyloideae (*sensu* Dransfield & Uhl, 1998) is not monophyletic (Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Lewis & Doyle, 2001; Hahn, 2002a, b). One tribe, the Hyophorbeae, is consistently resolved with members of the subfamily Arecoideae. The exact relationships and positions of the tribes Ceroxyleae and Cyclospatheae are not yet clear, however. In contrast, the subfamily Phytelephantoideae is always resolved as monophyletic (Uhl *et al.*, 1995; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Hahn, 2002a)

with the exception of Baker *et al.* (1999), where the two included species are unresolved in a polytomy at the base of the Arecoideae line (Moore, 1973).

Recent studies provide modest support for a clade of Phytelephantoideae, Ceroxyloideae, and Arecoideae, a group that is equivalent to the Arecoideae line *sensu* Moore (1973; Asmussen & Chase, 2001; Hahn, 2002a, b). Various studies give indications of potential relationships between the Ceroxyloideae, Cyclospatheae, and Phytelephantoideae, or between at least two of the three groups (Uhl *et al.*, 1995; Asmussen & Chase, 2001; Hahn, 2002a, b). Most strikingly, Asmussen & Chase (2001) provided evidence, albeit weakly supported, that Phytelephantoideae, Cyclospatheae and Ceroxyloideae form a monophyletic sister group to the subfamily Arecoideae.

Subfamily Arecoideae

Most studies point towards a broadly monophyletic subfamily Arecoideae, with the majority including the tribe Hyophorbeae (subfamily Ceroxyloideae) and excluding the tribe Caryoteae (Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Hahn, 2002a, b).

POTENTIAL FOR REVISION OF THE CURRENT CLASSIFICATION

Although much progress has been made towards a robust phylogeny of the palm family, a major revision of the prevailing classification based on published phylogenetic hypotheses is premature. At the highest level in particular, the lack of resolution and bootstrap support at the basal nodes forming the backbone of the phylogeny seriously hinders the production of a robust, lasting, circumscription of subfamilies. For reasons outlined above, three of the current subfamilies are in particular need of clarification, namely Coryphoideae, Ceroxyloideae and Phytelephantoideae. The objectives of this study were to explore further the phylogeny of the palm family by building on previous studies (Baker *et al.*, 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001) with substantially expanded taxon sampling and by adding the plastid DNA region *matK* to the pre-existing selection of plastid DNA regions (*trnL-trnF*, *rps16* intron and *rbcL*) used in these studies, and to use our findings to propose a formal revision of the subfamily classification of the Arecoideae.

MATERIAL AND METHODS

SAMPLING

This study included 178 palm species, representing 162 of the 189 genera recognized in the 1998 treatment of Arecoideae (Dransfield & Uhl, 1998). All 36

subtribes, 14 tribes and six subfamilies in the classification of Uhl & Dransfield (1987) and all 36 subtribes, 14 tribes and six subfamilies of Dransfield & Uhl (1998; see Appendix) were represented. All tribes and subtribes of the revised classification of the Calamoideae of Baker *et al.* (2000a) were also represented. The *matK* region was chosen as an additional plastid DNA region because it has provided many parsimony-informative characters in other monocot studies. Other plastid DNA regions (*rpl16*, *rpoC*, and *ndhF*) were tested on a small sample of species as potential new plastid DNA markers, but these regions showed amplification difficulties, whereas *matK* amplified readily in all palm test samples. All *matK* sequences were produced for this study and are published here for the first time. In addition, *rbcL*, *rps16*, and *trnL-trnF* sequences for taxa not previously included in our data sets were generated; all other data were recycled from three previous studies (Baker *et al.*, 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; see Appendix). Ten monocot outgroup species were selected from among the clades most closely related to the palm family (Chase *et al.*, 2000; see Appendix).

DNA EXTRACTION, POLYMERASE CHAIN REACTION (PCR) AND NUCLEOTIDE SEQUENCING

Total genomic DNA was extracted from fresh or silica gel-dried plant material using the 2× CTAB method of Doyle & Doyle (1987) or the DNeasy Plant Mini Kit (Qiagen). Some of the 2× CTAB extractions were followed by purification on caesium chloride/ethidium bromide gradients (1.55 g ml⁻¹) or with the QIAquick PCR purification kit (Qiagen) with 35% guanidinium chloride ((NH₂)₂C:NH.HCl). The DNA concentrations were measured on a biophotometer (Eppendorf). All samples were vouchered with herbarium specimens (see Appendix).

The *matK* sequences were amplified from total genomic DNA using the primer *matK*-19F with *trnK*-2R (Table 1; Steele & Vilgalys, 1994). If amplification was unsuccessful, reactions were repeated using *matK*-19F with *matK*-1862R or in two pieces with any combination of the available primers (Table 1). PCR reactions (100 µl) were prepared on ice by combining 65 µl ddH₂O, 10 µl 10× DNA polymerase buffer, 8 µl 20 µmol l⁻¹ MgCl₂, 4 µl 10 mmol l⁻¹ each dNTP, 1 µl 10 mg ml⁻¹ bovine serum albumin, 5 µl of each primer (10 µmol l⁻¹), 1 µl 5 µl⁻¹ Supertaq DNA polymerase (HT Biotechnology), and 25 ng of template DNA. The amplifications were conducted on an MJ Research PTC-200 thermocycler programmed as follows: one cycle at 94 °C for 3 min, 28 cycles of 94 °C for 1 min, 50 °C (or up to 60 °C for problematic DNA samples) for 1 min, and 72 °C for 2 min, and a final cycle at 72 °C

Table 1. Primer sequences designed for this project and not previously published

Primer name	Primer sequence
<i>MatK</i> -300F	5'-AGT TCA GTA CTT GTR AAA CG-3'
<i>MatK</i> -445R	5'-GGG AAG ATA CTA ATC GCA GC-3'
<i>MatK</i> -809F	5'-CGA TTA ACA TCT TCT GGA GC-3'
<i>MatK</i> -971R	5'-ATG CAT GAA GGG ATC CTT GA-3'
<i>MatK</i> -1315F	5'-TCG TGT GCT AGA ACT TTG GC-3'
<i>MatK</i> -1334R	5'-GCC AAA GTT CTA GCA CAC GA-3'
<i>MatK</i> -1862R	5'-CAT TGC ACA CGA CTT TAC C-3'
<i>RbcL</i> -1407R	5'-CCA GCT TAT CTA CTG GTT CG-3'

for 5 min. The resulting PCR products were checked on a 0.8% agarose gel with ethidium bromide and purified using the QIAquick PCR purification kit (Qiagen) with 35% guanidinium chloride ((NH₂)₂C:NH.HCl). The amplification primers and protocols for the *rbcL* region were those described in Asmussen & Chase (2001); a new primer, *rbcL*-1407R was designed and used for DNAs that would not amplify with *rbcL*-reverse (Fay *et al.*, 1998). The *rps16* intron region was amplified using the primers of Oxelman, Lidén & Berglund (1997) and the protocols of Asmussen *et al.* (2000). The *trnL-trnF* region was amplified using the primers of Taberlet *et al.* (1991) and the protocols for amplification followed Asmussen *et al.* (2000) and Baker *et al.* (1999).

The concentrations of purified PCR products were measured on a biophotometer and the products were sequenced using the ABI PRISM BigDye terminator cycle sequencing ready reaction kit (Perkin-Elmer, AB Applied Biosystems). For *matK*, the PCR amplification primers, *matK*-19F and *trnK*-2R, performed poorly as sequencing primers and therefore six new primers were designed as sequencing primers (Table 1). The sequencing primers for *rbcL*, *rps16* and *trnL-trnF* were those described in Asmussen & Chase (2001), Asmussen *et al.* (2000) and Baker *et al.* (1999) in addition to the new *rbcL*-1407R (Table 1). Cycle-sequencing reactions (10 µl) were prepared by combining 1 µl terminator mix, 3 µl 5× cycle-sequencing buffer (200 mmol l⁻¹ trizma base, 5 mmol l⁻¹ MgCl₂, pH 9.0, from the BigDye terminator kit), 1 µl primer (1 µmol l⁻¹), 25 ng DNA from the cleaned PCR product and ddH₂O up to 10 µl. Cycle sequencing was conducted on an MJ Research PTC-200 thermocycler programmed as follows: 25 cycles of 96 °C for 30 s, 50 °C for 15 s and 60 °C for 4 min.

Cycle-sequencing products were cleaned using Dye-Ex Spin columns (Qiagen) or Sephadex G-50 (Roche) following the protocol of the manufacturer. The cleaned cycle-sequencing products were analysed on a PE Applied Biosystems 377 automated DNA

sequencer (Perkin-Elmer) or a PE Applied Biosystems 3100 capillary automated DNA sequencer (Perkin-Elmer). Each base position in the forward and reverse sequences was checked and assembled using the program SEQUENCHER 3.0 (Gene Codes Corp.).

SEQUENCE ALIGNMENT

Initial automated alignments of consensus sequences were performed with the MegAlign program (Lasergene software package, DNASTAR Inc.) and followed by refinement by hand. The alignment of *rbcL* sequences was straightforward due to the absence of length variation. The alignment of *matK* was also relatively straightforward except for a number of indels at the 3' end. For the length-variable *rps16* intron and *trnL-trnF* sequences, the alignments included numerous indels, but they were not recoded as additional characters. The aligned *matK*, *rbcL*, *rps16* intron and *trnL-trnF* sequence matrices were combined and analysed together. For separate analyses of *rbcL*, *rps16* intron and *trnL-trnF*, see Asmussen & Chase (2001), Asmussen *et al.* (2000) and Baker *et al.* (1999).

CLADISTIC ANALYSES

The four data sets were readily combined because they all originated from plastid DNA and therefore have identical evolutionary history, which makes congruence tests superfluous. However, the tree statistics indicate that the individual data sets are compatible, because the number of nodes, the number of supported nodes and the number of highly supported nodes increase in the result of the analysis of the combined data set (Table 2). The data sets were analysed by Fitch parsimony (Fitch, 1971; unordered, equally weighted characters) using PAUP* version 4.0 Beta 10 (Swofford, 2002). The analyses yielded many trees, principally because of zero-length branches resulting from an inadequate number of informative characters. Thus, heuristic searches could not be run to completion. Therefore, the following search strategy was used. One thousand random replicate searches were conducted using the tree-bisection-reconnection (TBR) branch-swapping algorithm with steepest descent and MULPARS in effect, but holding five trees per step to minimize the time spent swapping on sub-optimal trees. A round of TBR swapping was performed on the trees collected during the 1000 random replicates, collecting 30 000 optimal trees, and these trees were swapped to completion. Support for clades was calculated by conducting 1000 bootstrap replicates, each with five random replicates, subtree pruning-regrafting (SPR) swapping, and saving no more than five trees each replicate. Only groups that appeared in > 50% of the trees were retained. Jack-

Table 2. Tree statistics for each of the individual data sets (*rbcL*, *trnL-trnF*, *rps16* intron, *matK*) and for the combined *rbcL*, *trnL-trnF*, *rps16* intron and *matK* data set

	<i>rbcL</i>	<i>TrnL-trnF</i>	<i>rps16</i> intron	<i>matK</i>	Combined
Length of alignment	1 306	1 842	1 569	2 385	7 102
Number of parsimony-informative characters	192	219	248	553	1 212
Tree lengths	762	655	754	1 809	4 176
Number of trees	> 30 000	> 30 000	> 30 000	> 30 000	> 30 000
Consistency index	0.33	0.53	0.53	0.47	0.44
Retention index	0.65	0.70	0.71	0.74	0.69
Number of nodes in strict consensus tree	65	35	54	90	125
Number of nodes with > 50% bootstrap support	16	30	45	75	99
Number of nodes with > 90% bootstrap support	4	4	9	28	40

knife percentages and Bremer support values were calculated for the subfamily clades and the major nodes connecting the subfamilies. A 10 000 replicate jackknife analysis was conducted with collapse branches if the minimum length was zero, jackknife with 36.79% deletion, emulate 'Jac' resampling in effect, and a full heuristic search of five replicates, saving a maximum of five trees each replicate and nearest-neighbour interchange swapping. Bremer support was calculated using the 'load constraint' option, and for each node conducting 1000 random replicate searches using the TBR branch-swapping algorithm with steepest descent and MULPARS in effect and holding five trees per step. All parsimony analyses were performed under DELTRAN due to the malfunction of ACCTRAN in PAUP* 4b version 10.

RESULTS

SEQUENCE VARIATION

The length of sequences from the *matK* region (amplification product of *matK*-19F and *trnK*-2R) in palms ranged from 1800 (*Mauritia flexuosa*) to 1847 base pairs (*Kerriodoxa elegans*). Most of *matK* and part of the spacer between *matK* and the 3' end of the split gene *trnK* were included in the alignment. The beginning of *matK* could not be identified and the last c. 100 base pairs of the spacer before the 3' end of *trnK* were excluded from the alignment and analyses because many sequences lacked these positions due to differences in the reverse primer used to obtain the PCR product. The data matrix thus consisted of 2385 positions, of which 553 (23.19%) were potentially parsimony informative (Table 2). Approximately 50 gap areas varying from 1 to 204 bases in length were introduced. The larger gaps were distributed in the intergenic spacer between *matK* and the 3' end of *trnK*.

Only the coding region of the *rbcL* amplification product was included in the alignment (1434 base

pairs), and the first 57 and the last 71 base pairs of the *rbcL* gene were excluded from the analysis because most sequences lacked these positions (primer annealing regions). The data matrix thus consisted of 1306 positions, of which 192 (14.7%) were potentially parsimony informative (Table 2). No gaps were introduced.

The length of the *rps16* intron sequences in palms ranged from 686 (*Kerriodoxa elegans*) to 954 (*Maxburretia rupicola*) bases. This is the entire intron except for the first 31 and the last 5 base pairs. The alignment consisted of 1569 positions (Table 2). There were 248 (15.81%) potentially parsimony-informative characters. Sixty gaps varying from 1 to 341 bases in length were introduced.

The length of the *trnL-trnF* sequences in palms ranged from 776 (*Hedyscepe canterburyana*) to 884 base pairs (*Wettinia hirsuta*). The alignment consisted of 1842 positions and no characters were excluded on the grounds of problematic alignment areas (Table 2). There were 219 (11.89%) potentially parsimony-informative characters. Fifty-five gaps varying from 1 to 166 base pairs in length were introduced in the alignment.

The combined matrix of *matK*, *rbcL*, *rps16* intron and *trnL-trnF* consisted of 7102 characters, all included in the analyses (Table 2). There were 1212 (17.07%) potentially parsimony-informative characters. No characters were excluded on the grounds of problematic alignment areas. The 1212 potentially parsimony-informative characters included 844 characters without any gap positions and 368 characters with at least one gap position among the 188 included taxa.

The 30 000 equally most-parsimonious trees collected in the Fitch parsimony analysis were 4176 steps long and had a consistency index of 0.44 (excluding autapomorphies) and a retention index of 0.69 (Table 2). The tree lengths of the cladograms resulting

from the combined analyses were longer than the combined lengths of the four individual data sets (762 + 655 + 754 + 1809 = 3980), indicating that the combined analysis recovered homoplasy not present in each of the individual analyses.

PHYLOGENETIC ANALYSES

The strict consensus tree of the combined data set was well resolved and included many well-supported clades (Fig. 1). The palm family was resolved as monophyletic with a bootstrap support of 100%. The most resolved individual tree had seven polytomies of three taxa each (Fig. 2). Five of these seven polytomies of the most resolved individual tree were present in all individual trees (Fig. 2, arrows 1–5). Polytoomy 6, including four coryphoid taxa, and polytoomy 7, comprising three large clades in the subfamily Arecoideae, were present only in a subgroup of the 30 000 most-parsimonious trees (Fig. 2, arrows 6 and 7). Five of the seven polytomies were positioned in the subfamily Arecoideae, where particularly backbone branch lengths were short compared with backbone branch lengths within the other four subfamilies (Fig. 2).

In the strict consensus tree, the monophyletic (100% bootstrap) subfamily Calamoideae (Fig. 1, clade 1) was resolved as sister to the rest of the palms. Within Calamoideae, *Eugeissona* (tribe Eugeissonae) was sister to the rest of the Calamoideae (59% bootstrap support). Additionally, Calamoideae were divided into two large monophyletic groups corresponding to the two tribes Lepidocaryeae (91% bootstrap support) and Calameae (70% bootstrap support). The Lepidocaryeae clade consisted of the African and American taxa *Mauritia* (subtribe Mauritiinae), *Raphia* (subtribe Raphiinae) and *Oncocalamus*, *Laccosperma* and *Eremospatha* (all three from the subtribe Ancistrophyllinae). The Calameae clade consisted of the largely South-east Asian taxa *Korthalsia* (Korthalsiinae), *Salacca* (Salaccinae), *Calamus* (Calaminae), *Pigafetta* (Pigafettinae), *Plectocomia* (Plectocomiinae) and *Metroxylon* (Metroxylinae).

Nypa fruticans, from the monospecific subfamily Nypoideae, was sister to the remaining palms (namely Calamoideae not included) with a bootstrap support of 97% (Fig. 1, clade 2).

The subfamily Coryphoideae, including Caryoteae from the subfamily Arecoideae, formed a monophyletic lineage with bootstrap support of 97% (Fig. 1, clade 3). All taxa in this clade have induplicate leaves, except for the anomalous coryphoid genus *Guihaia*. Three major clades received high bootstrap support. The first of these, with bootstrap support of 98%, consisted entirely of the New World taxa: the genus *Sabal* (100% bootstrap support; Fig. 1, clade a), sole member of the subtribe Sabalinae (tribe Corypheae), and the New

World genera of the subtribe Thrinacinae (tribe Corypheae; 100% bootstrap support; Fig. 1, clade b). The second major clade, which was weakly supported (61% bootstrap support) as sister to the third (described below), was resolved with 99% bootstrap support and consisted of exclusively Old World taxa: a highly corroborated (100% bootstrap support) monophyletic group of three members of the subtribe Coryphinae (*Nannorrhops*, *Kerriodoxa* and *Chuniophoenix*; Fig. 1, clade c), a highly supported (100% bootstrap support) tribe Caryoteae (subfamily Arecoideae, Fig. 1, clade d), the genus *Corypha* (subtribe Coryphinae; 100% bootstrap support; Fig. 1, clade e) and a highly supported (100% bootstrap support) tribe Borasseae (Fig. 1, clade f). The clade comprising Caryoteae, *Corypha* and the Borasseae was monophyletic with bootstrap support of 91%, whereas the support for *Corypha* as sister to the Borasseae was low (66% bootstrap support). The third major clade received 86% bootstrap support and consisted of the monogeneric tribe Phoeniceae (100% bootstrap support; Fig. 1, clade g) and a highly supported (99% bootstrap support) clade composed of a paraphyletic subtribe Livistoninae (tribe Corypheae) within which a monophyletic, well-supported (86% bootstrap support) clade of all Old World genera of Thrinacinae (tribe Corypheae) was embedded (Fig. 1, clade h).

There was 85% bootstrap support for the clade corresponding to Moore's (1973) Arecoid Line comprising the subfamilies Ceroxyloideae, Phytelephantoideae and Arecoideae, excluding Caryoteae (Fig. 1, clades 4 and 5). The subfamily Phytelephantoideae was monophyletic (99% bootstrap support) and together with two monophyletic tribes, Cyclospatheae (100% bootstrap support) and Ceroxyleae (99% bootstrap support) of the subfamily Ceroxyloideae is denoted as clade 4 on Figure 1 (63% bootstrap support).

The remaining large clade (Fig. 1, clade 5) was weakly supported (70% bootstrap support) and consisted of all genera from the subfamily Arecoideae, except for Caryoteae, with the addition of the tribe Hyophorbeae (subfamily Ceroxyloideae). The tribe Iriarteae was monophyletic (98% bootstrap support) and sister to a clade (76% bootstrap support) of the remaining members of clade 5. Within this latter clade, the base of which is highly unresolved, *Sommieria* and *Pelagodoxa* (subtribe Iguanurinae) formed a monophyletic group (94% bootstrap support). The monophyly of the tribe Hyophorbeae (subfamily Ceroxyloideae) was highly supported by bootstrap (100%). The tribe Geonomeae was resolved as non-monophyletic, *Welfia* and *Pholidostachys* forming a clade with *Manicaria* (subtribe Manicariinae; 89% bootstrap support), whereas a clade of *Asterogyne*, *Geonoma*, *Calyptronoma* and *Calyptrogyne* (80% bootstrap support) resolved elsewhere. The latter group of

Geonomeae was sister to a monophyletic subtribe Euterpeinae (56% bootstrap support). The tribe Cocoeae was not supported as monophyletic: *Beccariophoenix* (subtribe Beccariophoenicinae) was sister to *Sclerosperma* (Sclerospermatinae) with less than 50% bootstrap support. The remaining members of Cocoeae formed an unsupported monophyletic group with *Reinhardtia* as the sister group, again without support. The subtribe Elaeidinae (*Elaeis*) was included in a monophyletic group with the subtribe Bactridinae (*Desmoncus*, *Bactris*, *Aiphanes* and *Acrocomia*; 73% bootstrap support); and the subtribes Butiinae (*Allagoptera*, *Syagrus*, *Cocos*, *Voanioala*, *Jubaeopsis*) and Attaleinae (*Attalea*) formed a well-supported monophyletic group (91% bootstrap). Most of the species representing Indo-Pacific pseudomonomerous genera from the tribe Areceae resolved in an unsupported and highly unresolved clade, with some notable exceptions (*Pelagodoxa*, *Sommieria*, *Iguanura*). However, numerous smaller groups were resolved within this clade. Two subtribe Arecinae species pairs, *Areca triandra* and *Nenga pumila*, and *Hydriastele microspadix* and *H. chaunostachys*, the latter representing the recently synonymized genus *Gronophyllum* (Baker & Loo, 2004) constituted monophyletic lineages with 84 and 78% bootstrap support, respectively, but were not resolved as sister groups. Further clades resolved within the Indo-Pacific pseudomonomerous Areceae clade and supported by bootstrap include: *Rhopalostylis baueri* and *Hedyscepe canterburyana* (subtribe Archontophoenicinae; 53% bootstrap support), *Masoala* (subtribe Masoalinae; 82% bootstrap support), *Marojejya* (subtribe Masoalinae; 93% bootstrap support), *Basselinia* and *Alloschmidia* (subtribe Iguanurinae; 87% bootstrap support), *Acanthophoenix*, *Tectiphiala* and *Oncosperma* (subtribe Oncospermatinae; 50% bootstrap support), *Heterospathe* and *Alsmithia* (subtribe Iguanurinae; 80% bootstrap support), *Laccospadix* and *Linospadix* (subtribe Lino-spadicinae; 99% bootstrap support), *Cyphokentia*, *Moratia*, *Lavoixia*, *Brongniartikentia* and *Clinosperma* (subtribe Iguanurinae; 63% bootstrap support), and *Ptychosperma*, *Ponapea*, *Balaka*, *Veitchia*, *Carpentaria*, *Wodyetia*, *Brassiophoenix* and *Ptychococcus* (subtribe Ptychospermatinae; 62% bootstrap support).

DISCUSSION

THE SEQUENCES

The *matK* sequences produced more than twice the number of parsimony-informative characters (553) for the same taxon sample when compared with the other regions: *rbcL* (192), *trnL-trnF* (219) and *rps16* intron (248; Table 2). This is in agreement with the results from other studies where two or more of these plastid

DNA areas were used (Shaw *et al.*, 2005). The *rbcL* gene produced the fewest parsimony-informative characters (192), but these variable characters resulted in 65 resolved nodes in the palm family, whereas the *trnL-trnF* region and the *rps16* intron produced only 35 and 54 resolved nodes, respectively, despite supplying more informative characters (219 and 248; Table 2). The number of clades with more than 90% bootstrap support was relatively low in each of the individual data sets (four, four and nine), except for *matK* (28), but the combined data set produced the largest number of highly supported (> 90%) clades (40; Table 2).

THE NEW SUBFAMILY CLASSIFICATION

The dense taxon sampling and the large number of nucleotide characters included in this study and the high levels of resolution and support in the resulting trees are unprecedented in higher-level palm phylogenetic research. Our results are sufficiently robust to justify a formal reclassification of palm subfamilies and are equally convincing at lower taxonomic levels in some areas (Fig. 3). Herein, we describe the rationale for recognizing five subfamilies in a forthcoming formal reclassification of the palms (Dransfield *et al.*, 2005).

Subfamily placements for most genera of palms remain unchanged in the majority of cases with respect to the previous classification (Uhl & Dransfield, 1987; Dransfield & Uhl, 1998; see Appendix). Nevertheless, the new subfamily classification requires three major rearrangements (Figs 1, 2): (1) the tribe Caryoteae from the subfamily Arecoideae *sensu* Dransfield & Uhl (1998) is moved to a revised subfamily Coryphoideae; (2) subfamily Phytelephantoideae changes rank to tribe Phytelephanteae and is included within the new circumscription of the subfamily Ceroxyloideae; and (3) the tribe Hyophorbeae from the subfamily Ceroxyloideae (*sensu* Dransfield & Uhl, 1998) is moved to the subfamily Arecoideae.

SUBFAMILIES CALAMOIDEAE AND NYPOIDEAE

This study strongly supports the monophyly of the subfamily Calamoideae and firmly positions it as sister to the rest of the palms (Fig. 1, clade 1). Moreover, our results corroborate those of Asmussen & Chase (2001) and the total evidence analyses of Hahn (2002a). The tribal and subtribal classification of Calamoideae (Baker *et al.*, 2000a) is also corroborated in this study. The position of the subfamily Nypoideae as sister to all palms excluding Calamoideae is strongly supported and its status as a monogeneric subfamily is confirmed, in accordance with all previous studies (Fig. 1, clade 2; Uhl *et al.*, 1995; Baker

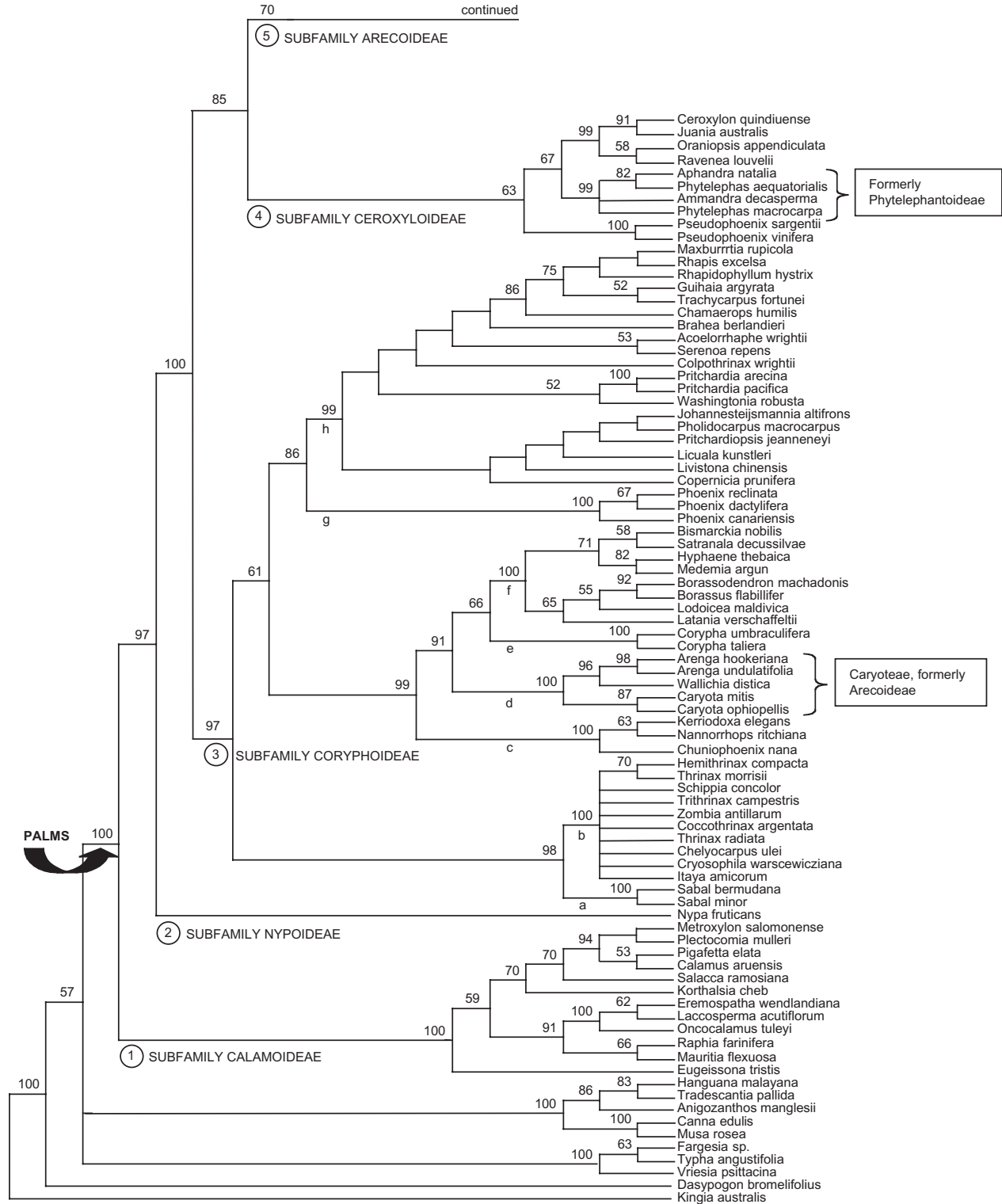


Figure 1. The strict consensus tree of 30 000 equally most-parsimonious cladograms resulting from Fitch parsimony analyses of combined *matK*, *rbcL*, *rps16* intron and *trnL-trnF* data sets. Bootstrap percentages for the clades are given above the branches. Five clades are labelled 1–5 for the discussion of the new subfamily classification in the text. The clades corresponding to the five subfamilies of the new classification are labelled with the subfamily name. Another eight clades are labelled a–h for the discussion of the new tribal classification within the subfamily Coryphoideae. The changes to the classification of Dransfield & Uhl (1998) are indicated with boxes to the right.

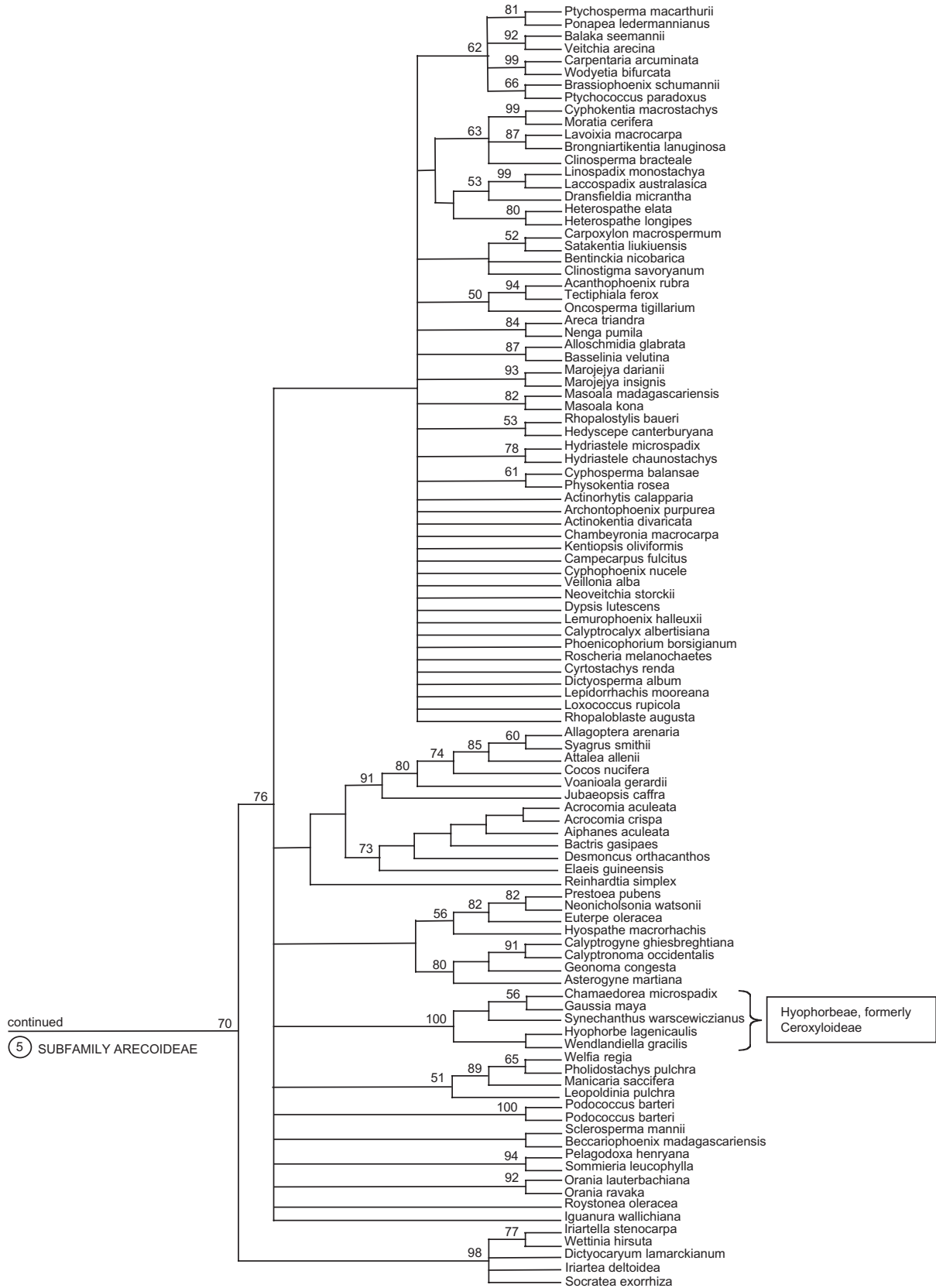


Figure 1. Continued

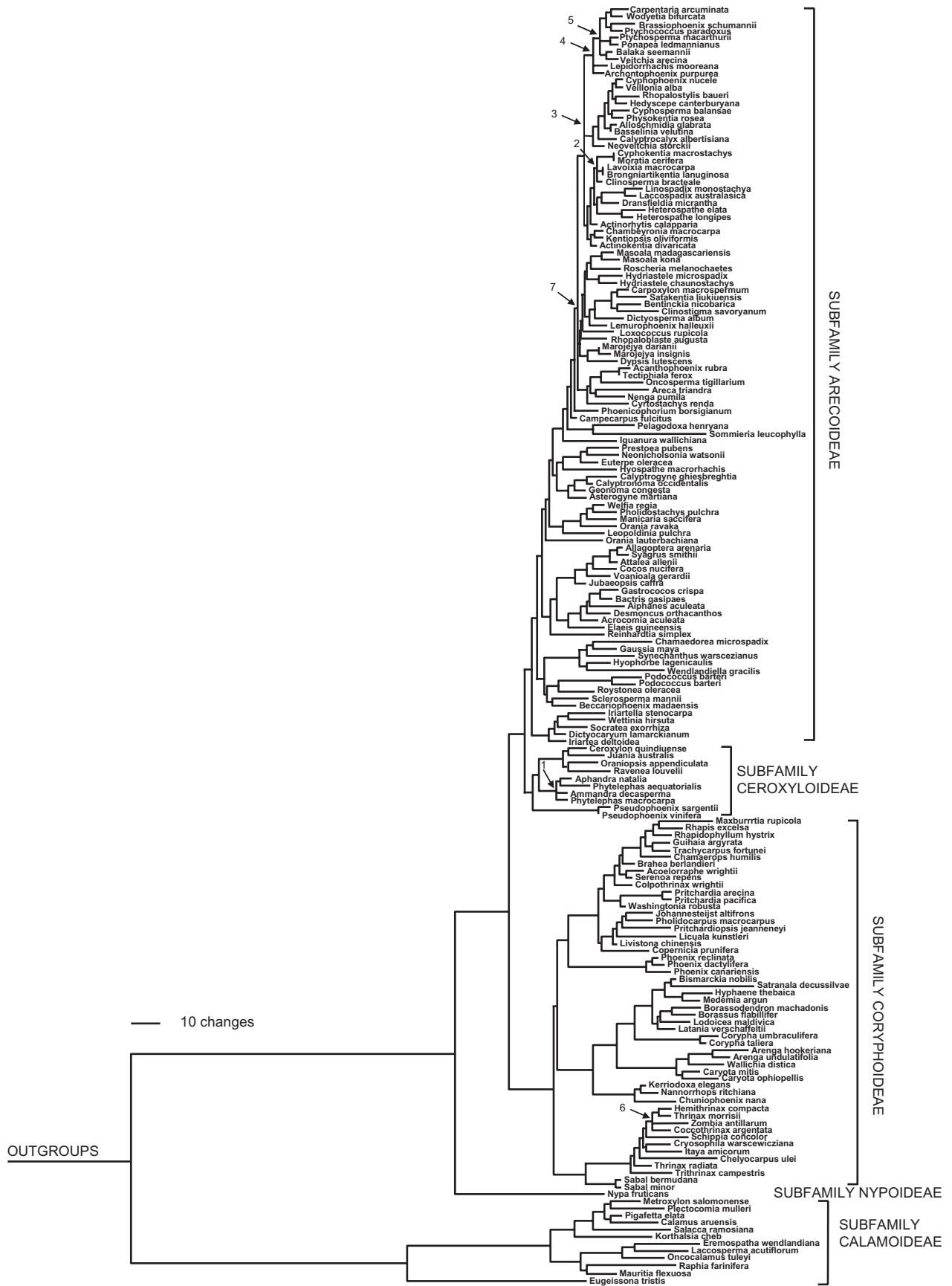


Figure 2. One cladogram with branch lengths of the 30 000 equally most-parsimonious cladograms resulting from Fitch analyses of the combined *matK*, *rbcL*, *rps16* intron and *trnL-trnF* data sets. A representative of the most resolved cladograms was chosen. Outgroups were excluded to make the cladogram fit one page. The cladogram is fully resolved except for seven polytomies, which are labelled 1–7. The polytomies labelled 1–5 were present in all 30 000 most-parsimonious cladograms. The clades corresponding to the five subfamilies of the new classification are indicated to the right.

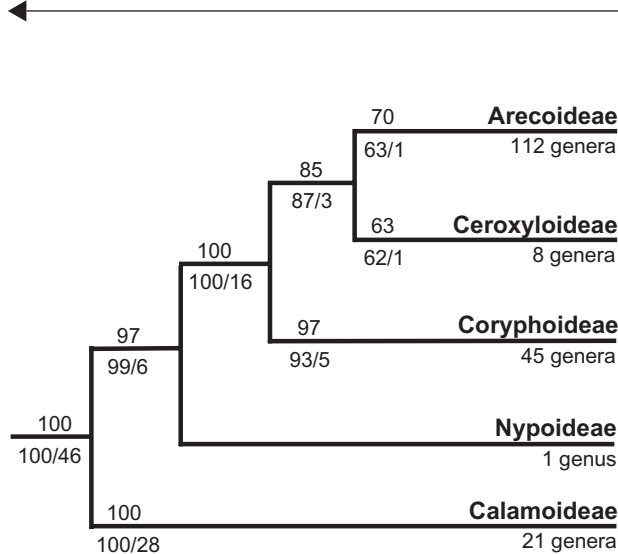


Figure 3. A summary tree showing the relationship of the five subfamilies in the new classification. The number of genera in each subfamily is given below the branches for each subfamily. Bootstrap percentages that support the subfamilies are given above the branches and jackknife percentages and Bremer support values are given below the branches.

et al., 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Lewis & Doyle, 2001; Hahn, 2002a), notwithstanding a few unusual maximum likelihood topologies presented by Hahn (2002a).

SUBFAMILY CORYPHOIDEAE

The *matK* sequences were particularly useful for the resolution of the subfamily Coryphoideae. However, the addition of more genera probably also contributed to the improved resolution of the relationships compared with previous studies (Asmussen & Chase, 2001). The new subfamily Coryphoideae (Fig. 1, clade 3) is modified only by the inclusion of the tribe Caryoteae, a relationship that can also be found among the most-parsimonious solutions emerging from many other phylogenetic analyses of molecular data in the palm family (Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Hahn, 2002a). However, until now, a robust monophyletic group consisting of the subfamily Coryphoideae and the tribe Caryoteae had only been recovered by Uhl *et al.* (1995) and Hahn (2002a).

The position of Coryphoideae as sister to all palms except the Calamoideae and *Nypa* had only previously been recovered by Hahn (2002a) in a highly reduced taxon sample.

The relationship between the Coryphoid genera is well resolved, and there are high bootstrap values for many of the subclades (Fig. 1, clade 3). Two of the three tribes in Dransfield & Uhl's (1998) classification of the subfamily Coryphoideae are resolved as monophyletic: the tribes Borasseae (Fig. 1, clade f) and Phoeniceae (Fig. 1, clade g). The third tribe, Corypheae, is not monophyletic, and just one of the four constituent subtribes, Sabalinae, is monophyletic (Fig. 1, clade a). The significance of these relationships for classification depends on which nodes are recognized and the ranks that they are allocated. In the interests of nomenclatural stability, we propose that as many as possible of the current tribes and subtribes are maintained, but major rearrangements of the tribe Corypheae and three of its four subtribes are needed to satisfy the criterion of monophyly (Fig. 1, clade 3). Such a reorganization (Dransfield *et al.*, 2005) results in eight tribes (Fig. 1, clades a–h) and a number of subtribes, all of which find support among other studies (Uhl *et al.*, 1995; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Hahn, 2002a).

SUBFAMILIES CEROXYLOIDEAE AND ARECOIDEAE

The bootstrap support for the subfamilies Ceroxyloideae and Arecoideae is low (63 and 70%, respectively). However, the monophyly of both subfamilies is strongly supported by data from low copy nuclear DNA genes (W. J. Baker, unpubl. data). Furthermore, the Arecoideae is well defined by the floral triad, notwithstanding the floral cluster of the Hyophorbeae and the presence of triads in Caryoteae. Although the Ceroxyloideae is morphologically heterogeneous, it is defined by all taxa having solitary flowers. The subfamily Phytelephantoideae (*sensu* Dransfield & Uhl, 1998) is highly supported as monophyletic (99% bootstrap support), which is in agreement with other studies (Barfod, 1991; Uhl *et al.*, 1995; Asmussen *et al.*, 2000; Asmussen & Chase, 2001; Hahn, 2002a, b). However, given that Phytelephantoideae is nested between two tribes of Ceroxyloideae, Ceroxyloideae and

Cyclospatheae, as sister to the former, the subfamily can no longer be recognized at the same rank and is placed as a tribe within the new concept of the subfamily Ceroxyloideae (Fig. 1, clade 4). In the studies of Hahn (2002a, b), the Phytelephantoideae and the tribe Ceroxyleae were similarly resolved, but the Cyclospatheae had a different position. The remaining studies on palm family phylogenies placed the Phytelephantoideae unresolved as a member of a polytomy (Uhl *et al.*, 1995; Baker *et al.*, 1999; Asmussen *et al.*, 2000; Lewis & Doyle, 2002). The inclusion of the tribe Hyophorbeae, formerly of the subfamily Ceroxyloideae (*sensu* Dransfield & Uhl, 1998), in the subfamily Arecoideae, as well as the exclusion of the tribe Caryoteae, is in accordance with all previous molecular phylogenies of the palm family (Fig. 1, clade 5). The limits of the subfamily Arecoideae require no further alterations.

CONCLUSION AND FUTURE PLANS

The addition of *matK* sequences and more taxa to the previous palm data sets of Asmussen & Chase (2001) provided the resolution and support required to refine the subfamily classification of the palm family (Fig. 3). Five subfamilies, all monophyletic, rather than six, are now recognized (Dransfield *et al.*, 2005): (1) the subfamily Calamoideae, as circumscribed in Dransfield & Uhl (1998); (2) the subfamily Nypoideae, with just one species, *Nypa fruticans*; (3) the subfamily Coryphoideae, comprising those genera included by Dransfield & Uhl (1998), with the addition of the tribe Caryoteae; (4) the subfamily Ceroxyloideae, including the tribes Cyclospatheae and Ceroxyleae, and the three phytelephantoid genera; (5) the subfamily Arecoideae, following the concept of Dransfield & Uhl (1998), but with the addition of the tribe Hyophorbeae and the exclusion of the tribe Caryoteae. This new subfamily classification will form the backbone of a new edition of *Genera Palmarum* (Uhl & Dransfield, 1987; J. Dransfield, N. W. Uhl, C. B. Asmussen, W. J. Baker, M. M. Harley & C. E. Lewis, unpubl. data).

Within the new subfamilies, high resolution and bootstrap support are recovered in the Calamoideae, Nypoideae, Coryphoideae and, to some extent, the Ceroxyloideae. The subfamily Arecoideae is, however, poorly resolved, and the internal nodes generally receive low bootstrap support. The low resolution and bootstrap support in Arecoideae are principally a result of a relatively low number of parsimony-informative characters in this portion of the tree. The most significant phylogenetic ambiguities remain in three areas: (1) poorly supported nodes for and some within the Ceroxyloideae; (2) poor resolution and support for and within the subfamily Arecoideae; (3) poor support and resolution in the clades of coryphoid gen-

era formerly referred to the subtribes Livistoninae and Thrinacinae. To address these problems and to consolidate further our findings, we plan to add low copy nuclear DNA sequences and additional plastid DNA sequences to this data set and expand the taxon sample to include all genera of palms. Despite these shortcomings, however, we are confident that the well-supported relationships presented here will be robust to the addition of new data and that our revised subfamily circumscriptions represent significant steps towards a natural and stable classification of palms that will stand the test of time.

ACKNOWLEDGEMENTS

This project was supported by grants from the Danish Research Council to Conny Asmussen and Anders Barfod. We thank Charlotte Hansen, University of Copenhagen and Hans Hjort, University of Aarhus for performing the automated sequencing. We are extremely grateful to all those individuals and institutions who have supported our work by providing material for DNA extraction, especially Fairchild Tropical Botanic Garden, the Montgomery Botanical Centre, the Royal Botanic Gardens, Kew, Dr Finn Borchsenius and Phillipp Trénel, University of Aarhus, Dr Carl Lewis, Fairchild Tropical Botanic Garden, and Dr Natalie Uhl, Bailey Hortorium. We also wish to thank an anonymous reviewer for helpful comments.

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APPENDIX

Voucher and database information (EMBL/GenBank/DBJ databases) for the taxa used in this study. Herbarium acronyms are given in parentheses. The first column gives the subfamily classification of Dransfield & Uhl (1998) and the second column gives the new subfamily, tribal and subtribal classification of Dransfield *et al.* (in press)

Subfamily classification (1998)	SUBFAMILY, tribe, subtribe	Species	Voucher information	<i>rbcL</i>	<i>rps16</i> intron	<i>trnL-trnF</i>	<i>matK</i>
CALAMOIDEAE	CALAMOIDEAE						
	Eugeissoneae	<i>Eugeissona tristis</i> Griff.	Baker 501 (KEP)	AJ404774	AJ240869	AJ241278	AM114540
	Lepidocaryeae	<i>Oncocalamus tuleyi</i> Sunderl.	Sunderland 1759 (K)	AJ404776	AJ240871	AJ241376	AM114541
	Ancistrophyllinae	<i>Eremospatha wendlandiana</i> Becc.	Dransfield JD 7004 (K)	AM117812	AJ240868	AJ241277	AM114542
		<i>Laccosperma acutiflorum</i> (Becc.) J.Dransf.	Dransfield JD 7006 (K)	AJ404772	AJ240867	AJ241276	AM114543
	Raphiinae	<i>Raphia farinifera</i> (Gaertn.) Hylander	Rutherford 156 (K)	AJ829907	AJ242184	AM113612	AM114544
	Mauritiinae	<i>Mauritia flexuosa</i> L.f.	<i>Ely et al.</i> 17 (K)	AJ404777	AJ240872	AJ241281	AM114545
	Calameae						
	Korthalsiinae	<i>Korthalsia cheb</i> Becc.	Baker 513 (K)	AM110188	AJ242175	AM113613	AM114546
	Salaccinae	<i>Salacca ramosiana</i> Moge	1979-4409 (K)	AM110189	AJ242176	AM113614	AM114547
	Metroxylinae	<i>Metroxylon salomonense</i> (Warb.) Becc.	Zona 651 (FTG)	AM110190	AM116769	AM113615	AM114548
	Pigafettinae	<i>Pigafetta elata</i> (Mart.) H.Wendl.	Baker 508 (K)	AJ829897	AJ242171	AM113616	AM114549
	Plectocomiinae	<i>Plectocomia mulleri</i> Blume	Baker 563 (K)	AJ829899	AJ242168	AM113617	AM114550
	Calamineae	<i>Calamus aruensis</i> Becc.	Dransfield JD 7571 (K)	AJ404775	AJ240870	AJ241279	AM114551
NYPOIDEAE	NYPOIDEAE	<i>Nypa fruticans</i> Wurrmb	N.W. Uhl s.n. (BH)	AJ404778	AJ240873	AJ241282	AM114552
CORYPHOIDEAE	CORYPHOIDEAE						
	Sabaleae	<i>Sabal bermudana</i> L.H.Bailey	1982-5602 (K)	AJ404766	AJ240862	AJ241271	AM114553
		<i>Sabal minor</i> (N.J.Jacquin) Persoon	1964-4540 (K)	AM110191	AM116770	AM113618	AM114554

Cryosophileae	<i>Schippia concolor</i> Burret	Baher 995 (FTG)	AJ404749	AJ404924	AJ404891	AM114555
	<i>Trithrinax campestris</i> (Burmeist.) Drude & Griseb.	1938–27003 (K)	AJ404745	AJ240844	AJ241253	AM114556
	<i>Zombia antillarum</i> (Desc.) L.H.Bailey	<i>R. Sanders 1763</i> (FTG)	AM110192	AM116771	AM113619	AM114557
	<i>Coccothrinax argentata</i> (Jacq.) L.H.Bailey	1973–12608 (K)	AJ404751	AJ240848	AJ241257	AM114558
	<i>Hemithrinax compacta</i> (Griseb. & H. Wendl.) Hook. f.	<i>C.E. Lewis 02-072</i> (HAJB)	AJ829869	AM116772	AM113620	AM114559
	<i>Thrinax morrisii</i> H. Wendl.	<i>J. Roncal 043</i> (FTG)	AM110193	AM116773	AM113621	AM114560
	<i>Thrinax radiata</i> Lodd. ex Schult. & Schult. f.	1933–047031 (K)	AJ404750	AM116774	AJ241256	AM114561
	<i>Chelyocarpus ulei</i> Dammer <i>Cryosophilla</i> <i>warsewicziana</i> Bartlett	<i>Balslev 6407</i> (AAU) 1991–1092 (K)	AJ404746 AJ404747	AJ240845 AJ240846	AJ241254 AJ241255	AM114562 AM114563
	<i>Itaya amicornum</i> H.E. Moore	<i>Baker 990</i> (FTG)	AJ404748	AJ404923	AJ404890	AM114564
	<i>Phoenix reclinata</i> Jacq.	<i>Goyder et al. 3928</i> (K)	AJ404767	AJ240863	AJ241272	AM114565
	<i>Phoenix canariensis</i> Chabaud	<i>Barrow 75</i> (K)	AM110194	AM116775	AM113622	AM114566
	<i>Phoenix dactylifera</i> L.	<i>Barrow 77</i> (K)	AM110195	AM116776	AM113623	AM114567
	<i>Chamaerops humilis</i> L.	<i>Barrow 76</i> (K)	AJ404754	AM116777	AJ241260	AM114568
	<i>Guihaia argyrata</i> (S.K.Lee & F.N.Wei) S.K.Lee, F.N.Wei & J.Dransf.	1984–4470 (K)	AJ404755	AJ240852	AJ241261	AM114569
	<i>Trachycarpus fortunei</i> (Hook.) H. Wendl.	<i>Dransfeld s.n.</i> (K)	AJ404752	AJ404925	AJ404892	AM114570
<i>Rhapidothyllum hystrix</i> (Pursh) H. Wendl. & Drude	013–6701301 (K)	AJ404753	AM116778	AJ241259	AM114571	
<i>Maxburretia rupicola</i> (Ridley) Furtado	<i>C.E. Lewis 02-080</i> (FTG)	AJ829884	AM116779	AM113624	AM114572	
<i>Rhapis excelsa</i> Henry ex Rehder	1987–2573 (K)	AJ404756	AJ240853	AJ241262	AM114573	
Phoenixaceae						
Livistoneae						
Rhapidiaceae						

Appendix Continued

Subfamily classification (1998)	SUBFAMILY, tribe, subtribe	Species	Voucher information	<i>rbcL</i>	<i>rps16</i> intron	<i>trnL-trnF</i>	<i>matK</i>
	Livistoninae	<i>Livistona chinensis</i> (Jacq.) R.Br. ex Mart.	1982-5601 (K)	AJ404757	AJ240854	AJ241263	AM114574
		<i>Licuala kunstleri</i> Becc.	1985-1497 (K)	AJ404759	AJ240856	AJ241265	AM114575
		<i>Johannesteijsmannia altifrons</i> (Reichb.f. & Zoll.) H.E.Moore	1985-1515 (K)	AJ404758	AJ240855	AJ241264	AM114576
		<i>Pholidocarpus macrocarpus</i> Becc.	<i>B. Chee 47332</i> (KEP)	AJ829894	AM116780	AM113625	AM114577
		<i>Pritchardiopsis jeanneneyi</i> Becc.	<i>Pintaud 315</i> (P)	AM110196	AM116781	AM113626	AM114578
	Unplaced genera in Livistoneae	<i>Acoelorrhaphe wrightii</i> H.Wendl.	<i>D. Bogler 1247</i> (FTG)	AM110197	AM116782	AM113627	AM114579
		<i>Brahea berlandieri</i> Bartlett	<i>C.E. Lewis 03-011</i> (FTG)	AM110198	AM116783	AM113628	AM114580
		<i>Colpothrinax wrightii</i> H. Wendl.	<i>R. Racine 41</i> (FTG)	AJ829862	AM116784	AM113629	AM114581
		<i>Copernicia prunifera</i> (Mill.) H.E.Moore	<i>C.E. Lewis 03-012</i> (FTG)	AM110199	AM116785	AM113630	AM114582
		<i>Pritchardia arecina</i> Becc.	<i>Baker 1183</i> (K)	AJ829905	AM116786	AM113631	AM114583
		<i>Pritchardia pacifica</i> Seem. & H.Wendl.	1952-35501 (K)	AM110200	AM116787	AM113632	AM114584
		<i>Serenoa repens</i> (Bartram) J.K.Small	1958-66102 (K)	AJ404760	AM116788	AJ241266	AM114585
		<i>Washingtonia robusta</i> H.Wendl.	<i>C.E. Lewis 03-013</i> (FTG)	AM110201	AM116789	AM113633	AM114586
	Chuniophoeniceae	<i>Chuniophoenix nana</i> Burret	1986-3018 (K)	AJ404764	AJ240860	AJ241269	AM114587
		<i>Kerriodoxa elegans</i> J.Dransf.	1987-2685 (K)	AJ404765	AJ240861	AJ241270	AM114588
		<i>Nannorrhops richiana</i> H.Wendl.	1990-1132 (K)	AJ404763	AJ240859	AJ241268	AM114589
	Caryoteae	<i>Caryota mitis</i> Lour.	464-85.05037 (K)	AJ404790	AJ240883	AJ241292	AM114590
		<i>Caryota ophiopellis</i> Dowe	<i>Baker 989</i> (FTG)	AJ404791	AJ404930	AJ404897	AM114591
		<i>Arenga hookeriana</i> (Becc.) Whitmore	085-85.01492 (K)	AJ404788	AJ240882	AJ241291	AM114592
	ARECOIDEAE	<i>Arenga undulatifolia</i> Becc.	<i>Baker 987</i> (FTG)	AJ404789	AJ404929	AJ404896	AM114593
		<i>Wallichia disticha</i> T.Anders.	L-80.0770 (BH)	AJ404792	AJ240884	AJ241293	AM114594

CORYPHOIDEAE	Corypheae	<i>Corypha umbraculifera</i> L. <i>Corypha taliera</i> Roxb.	1954–35301 (K) <i>Baker 984</i> (FTG)	AJ404761 AJ404762	AJ240858 AJ404926	AJ241267 AJ404893	AM114595 AM114596
	Borasseae Hyphaeninae	<i>Bismarckia nobilis</i> Hildebr. & H. Wendl. <i>Satranala decussilvae</i> Beentje & J. Dransf. <i>Hyphaene thebaica</i> Mart. <i>Medemia argun</i> Wuert. ex H. Wendl. <i>Latania verschaffeltii</i> Lem. <i>Lodoicea maldivica</i> (J.F. Gmel.) Pers. <i>Borassodendron</i> <i>machadonis</i> (Ridl.) Becc. <i>Borassus flabellifer</i> L.	<i>Bayton R.P. 43</i> (K) <i>Beentje & Dransfield 4810</i> (K) 1994–3803 (K) <i>Baker 986</i> (FTG) <i>J. Roncal 64</i> (FTG) 1994–3231 (K) 1989–3394 (K) <i>Wilkin, Suddee & Thapayai</i> <i>1160</i> (K)	AJ829852 AJ404771 AJ404770 AJ829885 AF829878 AJ404769 AJ404768 AM110202	AM116790 AJ240866 AJ240865 AM116791 AM116792 AJ240864 AJ404927 AM116793	AM113634 AJ241275 AJ241274 AM113635 AM113636 AJ241273 AJ404894 AM113637	AM114597 AM114598 AM114599 AM114600 AM114601 AM114602 AM114603 AM114604
	Latamiinae						
CEROXYLOIDEAE	CEROXYLOIDEAE Cyclospatheae	<i>Pseudophoenix sargenitii</i> H. Wendl. <i>Pseudophoenix vinifera</i> (Mart.) Becc. <i>Ceroxylon quindiuense</i> (H. Karst) H. Wendl. <i>Juania australis</i> Drude ex Hook. f. <i>Oraniopsis appendiculata</i> (F.M. Bailey) J. Dransf., A. K. Irvine & N. W. Uhl <i>Ravenea lowelii</i> Beentje	FTG 82–441C (BH) <i>Baker 1002</i> (FTG) 1976–1160 (K) <i>P. Trénel 4</i> (AAU) 1988–227 (K) 1988–2369 (K)	AJ404779 AJ404780 AJ404781 AJ829874 AJ404782 AJ404783	AJ240874 AJ404928 AJ240875 AM116794 AJ240876 AJ240877	AJ241283 AJ404895 AJ241284 AM113638 AJ241285 AJ241286	AM114605 AM114606 AM114607 AM114608 AM114609 AM114610

Appendix Continued

Subfamily classification (1998)	SUBFAMILY, tribe, subtribe	Species	Voucher information	<i>rbcL</i>	<i>rps16</i> intron	<i>trnL-trnF</i>	<i>matK</i>
PHYTELEPHANT-OIDEAE	Phytelepheae	<i>Ammandra decasperma</i> O.F.Cook	L-77.08309 (BH)	AJ404838	AJ404955	AJ404922	AM114611
		<i>Aphandra natalia</i> (A.J. Henderson & Balslev) Barfod	<i>Baker</i> 985 (K)	AJ404837	AJ404954	AJ404921	AM114612
		<i>Phytelephas aequatorialis</i> Spruce	1993–94 (K)	AJ404835	AJ240908	AJ241317	AM114613
		<i>Phytelephas macrocarpa</i> Ruiz & Pav.	1992–2480 (K)	AJ404836	AJ240907	AJ241316	AM114614
ARECOIDEAE	ARECOIDEAE						
	Iriarteae	<i>Iriartella stenocarpa</i> Burret	<i>B.Millán, J.C.Pintaud, C.Vegas</i> 728 (UNMSM)	AM110203	AM116795	AM113639	AM114615
		<i>Dictyocaryum lamarchianum</i> (Mart.) H.Wendl.	<i>Asmussen III</i> (CP)	AM110204	AM116796	AM113640	AM114616
		<i>Iriartea deltoidea</i> Ruiz & Pav.	<i>Henderson</i> 042 (BH)	AJ404793	AJ240885	AJ241294	AM114617
		<i>Socratea exorrhiza</i> H.Wendl.	<i>Baker</i> 992 (FTG)	AM110205	AM116797	AM113641	AM114618
		<i>Wettinia hirsuta</i> Burret	<i>Baker</i> 991 (FTG)	AJ404794	AJ404931	AJ404898	AM114619
CEROXYLOIDEAE	Chamaedoreae	<i>Hyophorbe lagenicaulis</i> (L.H.Bailey) H.E.Moore	1983–674 (K)	AJ404785	AJ240879	AJ241288	AM114620
		<i>Wendlandiella gracilis</i> Damm, var. <i>polyclada</i> (Burret) A.Henderson	<i>Zona</i> 754 (FTG)	AM110206	AM116798	AM113642	AM114621
		<i>Synechanthus warszewitzianus</i> H.Wendl.	<i>Knudsen & Asmussen</i> 640 (AAU)	AJ404786	AJ240880	AJ241787	AM114622
		<i>Chamaedorea microspadix</i> Burret	BH 60–811 (BH)	AJ404787	AJ240881	AJ241290	AM114623
		<i>Gaussia maya</i> (O.F.Cook) H.J.Quero & Read	1958–80101 (K)	AJ404784	AJ240878	AJ241287	AM114624
ARECOIDEAE	Podococceae	<i>Podococcus barteri</i> G.Mann & H.Wendl.	<i>Reitsma</i> 2840 (BH)	AM110207	AJ240886	AJ241295	AM114625
		<i>Podococcus barteri</i> G.Mann & H.Wendl.	<i>Sunderland</i> 1803 (K)	AM110208	AM116799	AM113643	AM114626

Oranieae	<i>Orania lauterbachiana</i> Becc.	L-78.0662 (BH)	AJ404796	AJ240887	AJ241296	AM114627
Sclerospermeae	<i>Orania ravaka</i> H.Beentje	<i>Dransfeld JD 7731</i> (K)	AM110209	AM116800	AM113644	AM114628
	<i>Sclerosperma mannii</i> H.Wendl.	<i>Sunderland TCHS 1794</i> (K)	AJ404823	AJ404948	AJ404915	AM114629
Roystoneae	<i>Roystonea oleracea</i> (Jacq.) O.F.Cook	1963-57401 (K)	AJ404805	AJ404936	AJ404903	AM114630
Reinhardtieae	<i>Reinhardtia simplex</i> (H.Wendl.) Drude ex Dammer	1988-366 (K)	AJ404799	AJ404933	AJ404900	AM114631
Cocoseae	<i>Beccariophoenix</i> <i>madagascariensis</i> Jum. et H.Perrier	1989-3532 (K)	AJ404826	AJ404951	AJ404918	AM114632
Attaleinae	<i>Jubaeopsis caffra</i> Becc.	<i>T.B. Sikkahane 139</i> (NH)	AJ829876	AM116801	AM113645	AM114633
	<i>Voanioala gerardii</i> J. Dransf.	<i>Dransfeld JD 6389</i> (K)	AM110210	AM116802	AM113646	AM114634
Bactridinae	<i>Allagoptera arenaria</i> (Gomes) Kuntze	BH 79.312 (BH)	AJ404828	AJ240902	AJ241311	AM114635
	<i>Attalea allenii</i> H.E.Moore	<i>Knudsen & Asmussen</i> 612 (AAU)	AJ404829	AJ240903	AJ241312	AM114636
Bactridinae	<i>Cocos nucifera</i> L.	1968-4480 (K)	AM110211	AM116803	AM113647	AM114637
	<i>Syagrus smithii</i> (H.E.Moore) Glassm.	<i>Balslev 6404</i> (AAU)	AJ404827	AJ240901	AJ241310	AM114638
Bactridinae	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	<i>Baker 1000</i> (FTG)	AM110212	AM116804	AM113648	AM114639
	<i>Acrocomia crispa</i> (Kunth) C.F.Baker ex Becc.	<i>J. Roncal 79</i> (FTG)	AM110213	AM116805	AM113649	AM114640
Elaeidinae	<i>Aiphanes aculeata</i> Willd.	<i>Borchsenius 599</i> (AAU)	AJ404831	AJ404953	AJ404920	AM114641
	<i>Bactris gasipaes</i> Kunth	<i>C.E. Lewis 02-027</i> (FTG)	AM110214	AM116806	AM113650	AM114642
Manicarieae	<i>Desmoncus orthacanthos</i> Mart.	<i>Zona 620</i> (FTG)	AM110215	AM116807	AM113651	AM114643
	<i>Elaeis guineensis</i> Jacq.	1987-216 (K)	AJ404830	AJ404952	AJ404919	AM114644
Manicarieae	<i>Manicaria saccifera</i> Gaertn.	<i>C.E. Lewis 03-010</i> (FTG)	AJ404797	AJ240888	AJ241297	AM114645

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Subfamily classification (1998)	SUBFAMILY, tribe, subtribe	Species	Voucher information	<i>rbcL</i>	<i>rps16</i> intron	<i>trnL-trnF</i>	<i>matK</i>	
Euterpeae	Hyospathe macrorrhachis Burret	<i>Hyospathe macrorrhachis</i>	Balslev 6421 (AAU)	AJ404804	AJ240891	AJ241300	AM114646	
		<i>Euterpe oleracea</i> Mart.	L-70.0017 (BH)	AJ404802	AJ240889	AJ241298	AM114647	
		<i>Prestoea pubens</i> H.E.Moore	Knudsen & Asmussen 619 (AAU)	AM110216	AM116808	AM113652	AM114648	
		<i>Neonicholsonia watsonii</i> Dammer	L-81.0303 (BH)	AJ404803	AJ240890	AJ241299	AM114649	
		<i>Welfia regia</i> H. Wendl.	Knudsen & Asmussen 607 (AAU)	AJ829917	AM116809	AM113653	AM114650	
		<i>Pholidostachys pulchra</i> H.Wendl. ex Burret	Knudsen & Asmussen 613 (AAU)	AM110217	AM116810	AM113654	AM114651	
		<i>Calyptrogyne ghiesbreghtiana</i> (Linden & H.Wendl.) H.Wendl.	Knudsen & Asmussen 627 (AAU)	AM110218	AM116811	AM113655	AM114652	
		<i>Calyptronoma occidentalis</i> (Sw.) H.E.Moore	FTG 71375 D (FTG)	AJ404832	AJ240904	AJ241313	AM114653	
		<i>Asterogyne martiana</i> (H.Wendl.) H.Wendl. ex Drude	L-81.0284 (BH)	AJ404833	AJ240905	AJ241314	AM114654	
		<i>Geonoma congesta</i> H.Wendl. ex Spruce	Borchsenius 348 (AAU)	AM110219	AJ240906	AJ241315	AM114655	
Leopoldinieae Pelagodoxeae	<i>Leopoldinia pulchra</i> Mart. <i>Pelagodoxa henryana</i> Becc. <i>Sommieria leucophylla</i> Becc.		Romero 3060 (VEN) 1988-2935 (K) 1992-3477 (K)	AJ404798 AJ829892 AM110220	AJ404932 AM116812 AM116813	AJ404899 AM113656 AM113657	AM114656 AM114657 AM114658	
		Areceae Archontophoenicinae	<i>Actinorhynchus calapparia</i> H.Wendl. & Drude	C.E. Lewis 97-011 (FTG)	AJ829847	AM116814	AM113658	AM114659
			<i>Archontophoenix purpurea</i> Hodel & Dowe	Pintaud 492 (TL)	AJ404806	AJ404937	AJ404904	AM114660
Areceae Archontophoenicinae	<i>Actinokentia divaricata</i> (Brongn.) Dammer <i>Chambeyronia macrocarpa</i> (Brongn. Vieill. ex Becc. <i>Kentiopsis oliviformis</i> (Brongn. & Gris) Brongn.		Pintaud 351 (K)	AM110221	AM116815	AM113659	AM114661	
			Pintaud 361 (K, NY)	AM110222	AM116816	AM113660	AM114662	
			Pintaud 358 (K, NOU, NY)	AJ404809	AJ240892	AJ241788	AM114663	

Arecinae	<i>Areca triandra</i> Roxb. <i>Nenga pumila</i> (Mart.) H.Wendl. var. <i>pachystachys</i> (Blume) Fernando <i>Alloschmidia glabrata</i> (Becc.) H.E.Moore <i>Basselinia velutina</i> Becc. <i>Campecarpus fulcitus</i> (Brongn.) H.Wendl. ex Becc. <i>Cyphophoenix nucele</i> H.E.Moore <i>Cyphosperma balansae</i> (Brongn.) H.Wendl. ex Salomon <i>Physokentia rosea</i> H.E.Moore <i>Veillonita alba</i> H.E.Moore <i>Carpoxylon</i> <i>macrosperrum</i> H.Wendl. & Drude <i>Satakentia iukuiensis</i> (Hatusima) H.E.Moore <i>Neoveitchia storckii</i> Becc. <i>Cyphokentia macrostachya</i> Brongn. <i>Moraita cerifera</i> H.E.Moore <i>Lavoixia macrocarpa</i> H.E.Moore <i>Brongniartikentia</i> <i>lanuginosa</i> H.E.Moore <i>Clinosperma bracteale</i> (Brongn.) Becc.	1984–2295 (K) <i>Baker 994</i> (FTG) <i>Pintaud 468</i> (K) <i>Pintaud 365</i> (P) <i>Pintaud 483</i> (TL) <i>Pintaud 372</i> (K, NOU, NY, P) <i>Pintaud 491</i> (TL) <i>Pintaud 452</i> (TL) <i>Pintaud 470</i> (TL) <i>Zona 722</i> (FTG) <i>Pintaud 446</i> (K) <i>Roncal 73</i> <i>Pintaud 482</i> (TL) <i>Pintaud 469</i> (TL) <i>Pintaud 364</i> (P) <i>Pintaud 368</i> (P) <i>Pintaud 349</i> (K, NY)	AJ404819 AJ404818 AJ829849 AM110223 AM110224 AJ404821 AM110225 AJ829896 AM110226 AJ829859 AM110227 AJ829888 AJ829864 AM110228 AJ829879 AJ829854 AJ829861	AJ404912 AJ404911 AM113661 AM113662 AM113663 AJ241309 AM113664 AM113665 AM113666 AM113667 AM113668 AM113669 AM113670 AM113671 AM113672 AM113673 AM113674	AM114664 AM114665 AM114666 AM114667 AM114668 AM114669 AM114670 AM114671 AM114672 AM114673 AM114674 AM114675 AM114676 AM114677 AM114678 AM114679 AM114680
Basseliniinae					
Carpoxylinae					
Clinospermatinae					

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Subfamily classification (1998)	SUBFAMILY, tribe, subtribe	Species	Voucher information	<i>rbcL</i>	<i>rps16</i> intron	<i>trnL-trnF</i>	<i>matK</i>
Dypsidinae		<i>Dyopsis lutescens</i> (H. Wendl.) Beentje & J. Dransf.	1978–1196 (K)	AJ404800	AJ404934	AJ404901	AM114681
		<i>Lemurophoenix halleuxii</i> J. Dransf.	Baker 1008 (K)	AM110229	AJ404935	AJ404902	AM114682
		<i>Marojejya darianii</i> J. Dransf. & N. Uhl	Baker 998 (K)	AJ404825	AJ404950	AJ404917	AM114683
		<i>Marojejya insignis</i> Humbert	Baker 1016 (K)	AM110230	AM116832	AM113675	AM114684
		<i>Masoala madagascariensis</i> Jum.	1992–3552 (K)	AJ404824	AJ404949	AJ404916	AM114685
		<i>Masoala kona</i> Beentje	Baker 1038 (K)	AM110231	AM116833	AM113676	AM114686
		<i>Calypstrocalyx albertianus</i> Becc.	Baker 1109 (K)	AM110232	AM116834	AM113677	AM114687
		<i>Linospadix monostachya</i> (Mart.) H. Wendl.	Fredriksen et al. C-210 (C)	AJ404811	AJ404941	AJ404908	AM114688
		<i>Laccospadix australasica</i> H. Wendl. & Drude	L-79.0850 (BH)	AJ404812	AJ240895	AJ241304	AM114689
		<i>Oncosperma tigillarum</i> (Jack) Ridl.	R. Sanders 1768 (FTG)	AM110233	AM116835	AM113678	AM114690
Oncospermatinae		<i>Acanthophoenix rubra</i> (Bory) H. Wendl.	C.E. Lewis 98–067 (BH)	AM110234	AM116836	AM113679	AM114691
		<i>Tectiphiala ferox</i> H.E. Moore	C.E. Lewis 98–070 (BH)	AJ829914	AM116837	AM113680	AM114692
		<i>Ptychosperma macarthurii</i> (H. Wendl. ex H.J. Veitch)	Zona 869 (FTG)	AM110235	AM116838	AM113681	AM114693
		<i>Ponapea ledermanniana</i> Becc.	Zona 878 (FTG)	AJ829903	AM116839	AM113682	AM114694
Ptychospermatinae		<i>Balaka seemannii</i> Becc.	L-69.0404 (BH)	AJ404814	AJ240896	AJ241305	AM114695
		<i>Veitchia arecina</i> Becc.	Baker 1003 (FTG)	AJ404813	AJ404942	AJ404909	AM114696
		<i>Carpentaria arcuminata</i> (H. Wendl. & Drude) Becc.	Baker 999 (FTG)	AJ829858	AM116840	AM113683	AM114697
		<i>Wodyetia bifurcata</i> A.K. Irvine	FTG 85–11113 (FTG)	AM110236	AM116841	AM113684	AM114698
		<i>Brassiophoenix schumannii</i> (Becc.) Essig	L-72.0031 (BH)	AJ404815	AJ240897	AJ241306	AM114699
		<i>Ptychococcus paradoxus</i> (Scheff.) Becc.	Baker 572 (K)	AJ829906	AM116842	AM113685	AM114700

Rhopalostylidinae	<i>Rhopalostylis baueri</i> H.Wendl. & Drude var. <i>baueri</i> <i>Hedyospe canterburyana</i> (C.Moore & F.Muell.) H. Wendl. & Drude	<i>Pintaud 384</i> (NY)	AJ404808	AJ404939	AJ404906	AM114701
Verschaffeltiinae	<i>Phoenicophorium</i> <i>borsigianum</i> (K.Koch) Stuntz <i>Roscheria melanochaetes</i> (H.Wendl.) H.Wendl. <i>Beninckia nicobarica</i> Becc. <i>Clinostigma savoryanum</i> (Rehder & E.H.Wilson) H.E.Moore & Fosberg <i>Cyrtostachys renda</i> Blume <i>Dictyosperma album</i> H.Wendl. & Drude <i>Dransfieldia micrantha</i> (Becc.) W.J. Baker & Zona <i>Heterospatha elata</i> (Becc.) F.B.Essig & B.E.Young <i>Heterospatha longipes</i> (H.E.Moore) Norup <i>Hydriastele microspadix</i> (Becc.) Burret <i>Hydriastele chaunostachys</i> (Burret) H.E.Moore <i>Iguanura wallichiana</i> (Mart.) Bentham et Hook.f. ex Becc. <i>Lepidorrhachis mooreana</i> (F.Muell.) O.F.Cook <i>Loxococcus rupicola</i> H.Wendl. <i>Rhopaloblaste augusta</i> (Kurz) H.E.Moore	1986–2346 (K) 1985–1825 (K) <i>Pintaud 457</i> (TL) <i>Pintaud 442</i> (MAK) 1982–5882 (K) <i>C.E. Lewis 98-061</i> (BH) <i>C.E. Lewis s.n.</i> (FTG) <i>C.E. Lewis 99-034</i> (GUAM) <i>Pintaud 461</i> (TL) <i>Baker 573</i> (K) L-72.0359 (BH) 1985–1488 (K) <i>Baker 1167</i> (K) 1990–2497 (K) <i>C.E. Lewis 99-044</i> (FTG)	AM110237 AM110238 AM110239 AM110240 AJ404810 AM110241 AM110242 AM110243 AJ829850 AJ404817 AJ404816 AJ404820 AJ829881 AJ829882 AM110244	AJ404938 AM116843 AJ404947 AM116844 AM116845 AJ404940 AM116846 AM116847 AM116848 AM116849 AJ404943 AJ240898 AJ404946 AM116850 AM116851 AM116852	AJ404905 AM113686 AJ404914 AM113687 AM113688 AJ404907 AM113689 AM113690 AM113691 AM113692 AJ404910 AJ241307 AJ404913 AM113693 AM113694 AM113695	AM114702 AM114703 AM114704 AM114705 AM114706 AM114707 AM114708 AM114709 AM114710 AM114711 AM114712 AM114713 AM114714 AM114715 AM114716 AM114717
Unplaced genera in Areceae						

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Subfamily classification (1998)	SUBFAMILY, tribe, subtribe	Species	Voucher information	<i>rbcL</i>	<i>rps16</i> intron	<i>trnL-trnF</i>	<i>matK</i>
	Outgroups (family)						
	Dasyopogonaceae	<i>Kingia australis</i> R.Br.	Chase 2230 (K)	AM110245	AM116853	AM113696	AM114718
	Dasyopogonaceae	<i>Dasyopogon bromeliifolius</i> R.Br.	Chase 2229 (K)	AM110246	AM116854	AM113697	AM114719
	Hanguanaceae	<i>Hanguana malayana</i> Merr.	1998–1475 (K)	AM110247	AM116855	AM113698	AM114720
	Haemodoraceae	<i>Anigozanthos manglesii</i> D.Don	Asmussen 109 (CP)	AM110248	AM116856	AM113699	AM114721
	Poaceae	<i>Fargesia</i> sp.	Asmussen 105 (CP)	AM110249	AM116857	AM113700	AM114722
	Typhaceae	<i>Typha angustifolia</i> L.	Asmussen 107 (CP)	AM110250	AM116858	AM113701	AM114723
	Cannaceae	<i>Canna edulis</i> Ker-Gawl.	Asmussen 104 (CP)	AM110251	AM116859	AM113702	AM114724
	Musaceae	<i>Musa rosea</i> Baker	Asmussen 101 (CP)	AM110252	AM116860	AM113703	AM114725
	Bromeliaceae	<i>Vriesia psittacina</i> Lindl.	Asmussen 102 (CP)	AM110253	AM116861	AM113704	AM114726
	Commelinaceae	<i>Tradescantia pallida</i> (Rose) D.R.Hunt	Asmussen 103 (CP)	AM110254	AM116862	AM113705	AM114727