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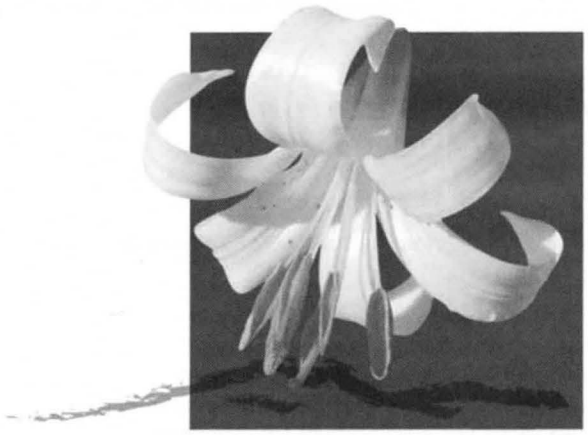

MONOCOTS

Comparative Biology and Evolution

Excluding Poales

Arecales

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A PHYLOGENETIC STUDY OF ARECACEAE BASED ON SEEDLING MORPHOLOGICAL AND ANATOMICAL DATA

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ABSTRACT

A morphological and anatomical survey was carried out of seedlings of 62 taxa of palms representing all major groups. The data were analyzed using cladistic parsimony analysis. Seedling data were analyzed independently and combined with adult morphological data. Outgroup selection was made within the family using the calamoids and *Nypa fruticans*; outside the family, the monocot family Dasypogonaceae were used. The analysis with the calamoids and *Nypa fruticans* as outgroups resolved some of the major groups. The combined analysis, using both seedling and adult data and Dasypogonaceae as the outgroup, provided better resolution. Most of the major groups were monophyletic although the coryphoids and arecoids appeared paraphyletic.

Key words: anatomy, Arecaceae, cladistics, germination, palms, phylogeny, seedlings.

INTRODUCTION

The palm family Arecaceae (Palmae) is one of the largest families of monocotyledons. The most recent estimate is that it contains 189 genera (Uhl and Dransfield 1999) and approximately 2000 species. These are widespread in tropical areas throughout the world, with the greatest concentration of species in tropical America and Southeast Asia. Few palms are found outside the tropics. Individuals are usually abundant in tropical ecosystems, especially in lowland and montane moist forests.

Arecaceae are also one of the most economically important families of plants to man, ranking after grasses and, in the tropics, equal with legumes. Apart from the well-known crops, coconut (*Cocos nucifera* L.), oil palm (*Elaeis oleifera* [Kunth] Cortés ex Prain), and date palm (*Phoenix dactylifera* L.), other species of palm provide numerous useful products such as foodstuffs, fibers, and medicines (Balick and Beck 1990).

Because of their economic importance, and because of their abundance in tropical ecosystems, palms have received much attention from botanists. Numerous aspects of the family have been extensively studied, such as systematics, reproductive biology, economic uses, and biogeography. Nevertheless, some important aspects of palm biology remain to be investigated, including seedling biology.

As a starting point, this study recognized that there has been no recent survey of germination and seedlings in the palm family, and that the subject remains poorly understood. In this study, the seedling morphology and eophyll anatomy of 62 genera in 15 major groups were used for a cladistic analysis of the family. Although this study was carried out against an academic background, it is envisioned that it will have some practical consequences for understanding the germination of palms. Because almost all palms are propagated by seed, the subject of germination is clearly an important one.

Palm seedling morphology has had sporadic attention over the past century and a half through the works of Martius (1823–1850), Gatin (1906), Zurawska (1912), Tomlinson (1960*b*, 1990), and Basu and Basu (1978). None of these studies was designed as an extensive survey of palm seedling morphology and anatomy and at the time there was no overview of monocot seedling anatomy and morphology for a context within which to place the observations. More recently, Tillich (1995) has reviewed seedling morphology in all monocotyledons and demonstrated the usefulness of seedling characters in monocot systematics. In Tillich's review, the palm family formed an isolated group with basal characters. He also standardized germination terminology throughout the monocotyledons. Tillich (2000) stressed the importance of the cotyledon morphology and the nature of the first cataphyll vs. the eophyll to define seedling types and evolutionary levels. He concluded that the ancestral seedling type in monocots is characterized by a compact cotyledon, one to several cataphylls, a short hypocotyl with inconspicuous collar, and a vigorously growing, branched primary root. He considered the seedling structure as a key character to detect phylogenetic relationships.

Anatomical studies have been oriented mainly to understanding the germination process and the structure of the seedling, but little is known about the anatomy of seedling leaves. Tomlinson (1960*b*, 1990) studied the nature of young leaves, introducing the term "eophyll" (from the Greek *eos*—early, *phyllon*—leaf) to describe the first expanded, photosynthetic leaf of the seedling. His aim was to differentiate the first laminar leaf from succeeding leaves. He discussed the ontogeny of seedling leaves, suggesting that palm leaves go through a gradual transition from small, simple leaves to large compound leaves.

Current Classification and Phylogenetic Analyses

Palms form a distinct group among the monocotyledons. Their monophyly is strongly supported by both molecular

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and morphological data analyses. Palms are resolved as an isolated group, the sister to Poales within Commelinidae (Stevenson and Loconte 1995). Chase et al. (2000) placed the palms within the commelinoids as sister group to Dasypogonaceae, Commelinales, Poales, and Zingiberales. In Stevenson et al. (2000), the palms were resolved as a monophyletic branch with *Dioscorea* L. (Dioscoreaceae) as the sister group.

Uhl and Dransfield (1987) divided the family into 6 subfamilies, 13 tribes, and 38 subtribes. This traditional approach used morphological descriptions of adult individuals, flower and leaf anatomy, fossil record, and phytogeography to establish relationships among the taxa. This work was written before cladistic methodology became widespread, and is therefore pre-cladistic in outlook. However, it was the starting point for all subsequent phylogenetic studies of the family.

Later Uhl et al. (1995) used morphological and chloroplast DNA restriction site variation to analyze the relationships among the members of the family, using cladistic methodology. Fifty-nine genera and 67 species representing all subfamilies and tribes were analyzed, using *Dioscorea* as an outgroup. The combined analysis of morphological and molecular data showed more resolution than the analysis of the independent data sets. These results were supported by Baker et al. (1999) who used DNA sequences from the *trn*L–*trn*F region, which appear to be highly conserved in palms with few informative sites and a high level of ambiguity.

Asmussen et al. (2000) used *rps*16 intron and *trn*L–*trn*F cDNA sequences. Sixty-five taxa were tested to determine the monophyly of the currently accepted subfamilies, tribes, and subtribes of the family. Their results support the monophyly of Calamoideae. The remaining subfamilies were not resolved as monophyletic but a major clade comprising all Arecoideae, Ceroxyloideae, Coryphoideae, and Phytelephantoideae was highly supported. The position of the tribe Caryoteae supported Uhl et al.'s (1995) results, including the subtribes of Coryphinae and tribe Borasseae in Coryphoideae.

Subsequently, Asmussen and Chase (2001) used coding and noncoding plastid DNA. They concentrated on finding the root of the family, and used, in addition to 94 palm taxa, 24 monocot outgroups. The results showed that the family was monophyletic and highly divergent in comparison to other monocot clades. *Nypa* Steck was sister to all other palms and the second branch, the subfamily Calamoideae, was resolved as sister to the rest of the palms, but this result was poorly supported (jackknife support value 50%).

Lewis and Doyle (2001), using 428 base pairs (bp) of the malate synthase exon region, corroborated Asmussen and Chase's (2001) results. However, subfamilies Arecoideae, Ceroxyloideae, Coryphoideae, and Phytelephantoideae remained unresolved as a large clade that included 45 palm taxa and 5 outgroups. A second analysis was run with a sample size of 16 taxa and two outgroups. The use of 1002 bp increased bootstrap values, and placed *Nypa* as sister to the rest of the palms. Hahn (2002), using *atp*B, *rbc*L, and 18S nuclear ribosomal DNA (nrDNA) sequences, reported incongruence between data sets and between molecular and morphological data. He identified four main groups of palms: Calamoideae, sister to all other palms; Arecoideae (excluding Caryoteae, Ceroxyloideae, and Phytelephantoideae); Coryphoideae (including Caryotoideae); and Nypoideae. It is clear from the preceding that different data sets give different results. This disparity makes sampling strategies difficult. Thus, in order to effectively sample as many proposed palm groups as possible, we decided to use the system of Moore (1973) because it had the most number of groups, which also were recognized at different levels (i.e., subfamily and tribes) by Uhl and Dransfield (1987). This gave us maximum effective sampling short of doing all palms.

Objectives

The present study had two major objectives. First, to analyze morphological and anatomical characters using cladistic methodology and to see if the data supported previous phylogenies based on morphological and molecular data. Secondly, to perform a combined analysis of the seedling data with morphological data from adults using a previously published data set (Uhl et al. 1995). Our goal was to provide a data set to combine eventually with molecular data so that the disparate results from the numerous previous analyses could be resolved.

MATERIALS AND METHODS

Plant Material

This study is at the generic level using the 15 major groups of palms as delimited by Moore (1973) (Table 1). Seedlings representing all the major groups were fixed in FPA (formalin:propionic acid:alcohol—5:5:90) and stored in 70% EtOH (ethanol). Seedling morphology was studied by direct observation. Anatomy of the lamina and petiole was studied by observation of transverse sections, epidermal peels, and leaf clearings using an Olympus Differential Interface Contrast Attachment model BH2-NIC microscope. Anatomical procedures followed Martens and Uhl (1980) and Chávez (2003). Photographs of anatomical features were taken using a Nikon FX-35 camera attached to the microscope. For morphological features a Nikon Coolpix 990 digital camera was used. Images were stored as JPEG files in Adobe PhotoShop.

Sampling and Outgroup Selection

Sixty-three taxa (62 genera including two species of *Phytelephas* Ruiz & Pav.) were used. Seedling data for 19 morphological (characters 0–18) and 31 anatomical characters (19–49) were scored. Thirty-seven adult characters (50–86 in Table 2 of this paper) were provided by Dr. Natalie Uhl (Uhl et al. 1995) for the combined analysis; discussion of these characters may be found in that work. Twenty-seven taxa in the present study were not included in Uhl's matrix; therefore, the adult morphological information for these taxa was completed primarily using *Genera Palmarum* (Uhl and Dransfield 1987), Palmae in *The Families and Genera of Vascular Plants* (Dransfield and Uhl 1998), and literature cited therein.

Choice of an outgroup was guided by the studies of Uhl et al. (1995), Baker et al. (1999), Asmussen and Chase (2001), and Lewis and Doyle (2001). Dasypogonaceae were

Table 1. List of material examined (classifications as per Moore 1973). All voucher specimens deposited at NY.

Taxon	Voucher #
1. CORYPHOID PALMS	
Acoelorraphe wrightii (Griseb. & H. Wendl.) H. Wendl. ex Becc.	Chávez 909
Chamaerops humilis L.	Chávez 910
Chuniophoenix hainanensis Burret	Chávez 964
Colpothrinax cookii Read	Chávez 965
Copernicia baileyana León	Chávez 918
Corypha L. sp.	Chávez 911
Cryosophila grayumi R. Evans	Chávez 920
Itaya amicorum H. E. Moore	Chávez 955
Livistona chinensis R. Br.	Chávez 966
Nannorrhops ritchiana (Griff.) Aitchson	Chávez 915
Pritchardia remota (Kuntze) Becc.	Chávez 917
Rhapidophyllum hystrix (Pursh) H. Wendl. & Drude	Chávez 963
Sabal minor (Jacq.) Pers.	Chávez 912
Serenoa repens (Bartram) Small	Chávez 959
Thrinax excelsa Lodd. ex Griseb.	Chávez 903
Trithrinax brasiliensis Mart.	Chávez 967
Trachycarpus H. Wendl. sp.	Chávez 902
Washingtonia filifera (Linden) H. Wendl.	Chávez 930
2. PHOENICOID PALMS	
Phoenix roebelinii O'Brien	Chávez 904
3. BORASSOID PALMS	
Borassus L. sp.	Chávez 968
Hyphaene coriacea Gaertn.	Chávez 969
Latania loddegesii Mart.	Chávez 957
4. CALAMOID (= Lepidocaryoid) PALMS	
Calamus flagelum Griff.	Chávez 945
Mauritia flexuosa L. f.	Chávez 948
Pigafetta filaris (Giseke) Becc.	Chávez 944
Plectocomia Mart. & Blume sp.	Chávez 946
5. NYPOID PALMS	
Hypa fruticans Wurmb	Chávez 949
6. CARYOTOID PALMS	
Arenga hookeriana (Becc.) Whitmore	Chávez 907
Caryota mitis Lour.	Chávez 916
Wallichia densiflora Mart.	Chávez 905
7. PSEUDOPHOENICOID PALMS	
Pseudophoenix sargentii H. Wendl.	Chávez 971
8. CEROXYLOID PALMS	
Ceroxylon Humb. & Bonpl. sp.	Henderson 3019
Oraniopsis appendiculata (F. M. Bailey) J. Dransf., A. K. Irvine & N. W. Uhl	Henderson 3070
Ravenea rivularis Jum. & H. Perrier	Chávez 972
9. CHAMAEDOREOID PALMS	
Chaemaedorea microspadix Burret	Chávez 937
Gaussia maya (O. F. Cook) Quero & Read	Chávez 978
Synechanthus fibrosus (H. Wendl.) H. Wendl.	Chávez 938
10. IRIARTEOID PALMS	
Irartea deltoidea Ruiz & Pav.	Henderson 3015
Iriartella setigera (Mart.) H. Wendl.	Henderson 647
Socratea exorrhiza (Mart.) H. Wendl.	Chávez 935
11. PODOCOCCOID PALMS	
Podococcus barteri Mann & H. Wendl.	Reitsma 2840
12. ARECOID PALMS	
Archontophoenix alexandrae (F. Muell.) H. Wendl. & Drude	Chávez 932
Dictyosperma album (Bory) H. Wendl. & Drude	Chávez 934
Dypsis lutescens (H. Wendl.) Beentje & J. Dransf.	Chávez 931
Euterpe precatoria Mart.	Balslev 4813
Hyospathe elegans Mart.	Chávez 929
Neonicholsonia watsonii Dammer	Chávez 928
Nephrosperma vanhoutteanum (H. Wendl.) Balfour	Chávez 939
Orania regalis Zipp.	Chávez 985
Phoenicophorium borsigianum (K. Koch) Stuntz	Henderson 2063
Roystonea borinquena O. F. Cook	Chávez 927
Veitchia montgomeryana H. E. Moore	Chávez 977
13. COCOSOID PALMS	
Allagoptera leucocalyx (Mart.) Kuntze	Chávez 941
Astrocaryum alatum Loomis	Stevenson 1200
Bactris killippii Burret	Henderson 2015
Elaeis guineensis Jacq.	Chávez 942
Jubaea chilensis (Molina) Baillon	Chávez 975
Syagrus coronata (Mart.) Becc.	Chávez 947
Voanioala gerardii J. Dransf.	Chávez 976
14. GEONOMOID PALMS	
Geonoma interrupta (Ruiz & Pav.) Mart.	Henderson 30
Welfia regia H. Wendl.	Henderson 301
15. PHYTELEPHANTOID PALMS	
Phytelephas seemanii O. F. Cook	Chávez 950
P. tenuicaulis (Barfod) Henderson	Chávez 951

used as an outgroup. Character information for this taxon was obtained from Clifford et al. (1998), Rudall et al. (1999), Tillich (2000), and pers. obs. (Table 2).

Heuristic searches were run on 1000 random taxon entry sequences, 100 replications and holding 10 trees in each case, followed by tree-bisection-reconnection (TBR) branch swapping (max*). Multistate characters were nonadditive. Uninformative characters were excluded from all the analyses.

The data was edited in WinClada (Nixon 2000). Initial parsimony analyses were run using NONA (Goloboff 1993), using the Mult* algorithm. Character distribution and calculation of the strict consensus tree were carried out using WinClada (Nixon 2000).

Discussion of Characters

Morphological characters of seedlings.—The description and rationale for each of the 19 morphological characters and their states found in the seedlings are discussed below:

0. Plumular/radicular axis: straight = 0; oblique = 1; angular = 2. These three states represent the axis formed by

Table 2. Matrix with seedling and adult morphological data. * = polymorphic, ? = unknown, $ = subset polymorphism, - = inapplicable.

	Character																	
	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85
Dasypogonaceae	00000	00000	*--*0	0--00	0**00	00001	??00*	**00?	?00-?	1?0?-	0-000	---00	00000	00-00	00110	00000	000?0	00
Nypa	---0-	01141	00111	0?001	?1001	10111	$1100	2-$00	00101	0111*	10001	04100	00110	02010	-0100	-0000	00000	02
Calamus	1010-	01111	00111	01202	21000	01001	2*010	2-201	0011-	1000*	00001	04101	00101	42100	01110	00110	00000	01
Mauritia	1010-	01111	00100	00102	21000	01101	2*010	2-20*	10111	1000*	00000	04100	00101	42100	01110	00110	00000	10
Pigafetta	1010-	01111	00111	01201	100-0	01000	-1110	2-201	10111	1000*	00001	04100	00101	42100	01110	00110	00001	00
Plectocomia	1010-	01100	1??11	00202	200-0	01000	-*?10	2-201	10111	1000*	00001	04100	10101	42100	01110	00110	00000	01
Acoelorraphe	00000	11000	1??00	00000	000-0	11010	-0110	0-000	0010-	10000	00100	00000	00100	10-00	0-110	10000	00011	00
Chamaerops	00000	10-00	14000	00000	000-1	11010	-0110	0-000	00101	10000	00100	00000	000-0	02100	0-100	01000	00??1	00
Chuniophoenix	00100	11000	1??00	00001	11011	10000	-1-11	-0000	0010-	20000	00000	00010	00101	10-00	1-110	00000	00000	00
Colpotrinax	00100	11100	1??00	000$0	010*1	10011	$1001	-0200	00111	1000*	00100	00000	00100	00-00	0-110	10000	00001	00
Copernicia	00001	10-00	1??00	00000	01010	11010	-1010	0-000	0000-	1000*	00100	00000	00111	10-00	0-110	10000	00000	00
Corypha	00011	10-00	1??10	10001	01011	11010	-1000	1-101	01100	0000*	01100	00000	10100	10-00	0-110	01000	00102	00
Cryosophila	00000	10-00	15000	00000	01001	01000	-0101	-0201	0010-	0000*	00100	00100	00100	00-00	0-100	-2000	00011	00
Itaya	00000	10-00	1??00	00001	11001	01000	-0000	2-200	0010-	11---	01100	00100	00100	00-00	0-0--	-1000	00000	00
Livistona	00001	11000	13010	00001	11000	11001	$1010	0-000	0010-	1000*	00100	00000	00100	10-00	0-110	10000	00011	00
Nannorrhops	00000	01000	1??00	00000	01001	10110	-0-01	-0000	10010	20000	11000	00010	10101	10-00	1-110	00000	00100	00
Pritchiardia	00002	01020	0??10	00001	11010	11110	-1110	0-000	1010-	1000*	00100	00000	00100	00-00	0-110	10000	00000	00
Rhapidophyllum	00102	11100	1??00	00000	01011	11010	-1110	0-000	0010-	10000	00110	03000	00100	11200	00100	-1000	00011	00
Sabal	00000	11000	19010	00000	01001	10010	-1101	-2101	0100*	2000*	01100	00110	00100	00-00	0-110	00000	00111	00
Serenoa	00000	11100	17000	00000	01010	11110	-1110	2-000	00001	10000	00100	00010	00110	10-00	0-110	10000	00011	00
Thrinax	00002	10-00	14000	00000	01000	11000	-100-	--000	0000-	00000	01100	00000	00100	00-00	0-0--	-3000	00011	00
Trithrinax	00100	10-00	1??00	00000	000-1	00010	-0-01	-2201	0100-	01000	00110	00110	00100	00-00	0-100	-1000	00011	00
Trachycarpus	00000	10-00	1??10	00000	01001	11000	-1101	-2000	0010-	10000	00100	00000	00100	11200	00100	-1000	00011	00
Washingtonia	00100	01000	18000	00000	000-1	10010	-1-10	2-000	00011	10000	01100	00000	00100	10-00	0-110	10000	00011	00
Borassus	00011	10-00	1??10	100$0	000-1	11111	$1101	-0111	0110*	20000	01100	00010	00100	12100	11110	03001	01002	00
Hyphaene	00011	10-00	0??10	000$0	01001	10111	$1101	-2$11	0111*	20000	11100	00010	00100	12100	11110	03001	00102	00
Latania	00011	10-01	10000	000$0	01001	10111	$1101	-0111	01111	20000	01100	00010	00100	12100	11110	03001	01002	00
Phoenix	00000	10-00	16010	00000	000-1	11011	$1000	0-000	00001	00000	00000	01010	000-0	02100	00100	-0000	00011	00
Arenga	00001	10-00	1??00	10010	01000	10101	00100	0-001	10100	0011*	00001	12100	10100	32000	00110	01000	00001	10
Caryota	00001	10-01	10000	10011	11001	10000	---00	0-001	100-0	0110	00001	12100	10100	32000	00110	01000	00001	10
Wallichia	00001	10-00	1??00	10010	01001	10101	00100	0-001	00100	0011*	00001	12000	10100	32000	00110	01000	00001	10
Pseudophoenix	00000	10-10	0??11	01100	000-1	11110	-0111	-2000	00100	10000	00001	04101	00100	00-00	0-110	02000	00101	00
Ceroxylon	10100	01110	06111	002$1	11010	11000	-0011	-0201	1011-	0*200	00001	04100	01100	02110	00110	01000	00101	00
Oraniopsis	10100	01110	0??11	002$0	01010	11001	$0111	-0201	1011-	0*20*	00001	04100	01100	02110	00110	01000	00101	00
Ravenea	10100	01111	00111	022$0	01000	11000	-0010	0-000	0011-	0*200	00001	04100	01100	02110	00110	01000	00100	0-
Chamaedorea	2010-	01111	00111	00220	000-0	00000	---10	0-001	1011-	01100	00001	04101	00100	02100	00110	00000	00101	00
Gaussia	2010-	01111	00111	002$0	000-0	00000	-0-10	0-001	1011-	01100	00001	04101	00100	22000	00110	02000	00101	00
Synechanthus	2010-	01111	00111	00220	000-0	00000	-0-10	0-000	1011-	01100	00001	04101	00100	22000	00110	00000	00101	00
Iriartea	2110-	01110	0??11	10120	01100	10001	00000	0-000	00111	0*11*	00001	14101	00100	32000	00110	00000	00001	10
Iriartella	21?0-	01??0	-??11	111$0	01100	10001	00000	2-201	00101	0011*	00001	14101	00100	32000	00110	0?000	00102	00
Socratea	2110-	01131	00111	10120	01100	10001	00000	2-000	00111	0*11*	00001	14101	00100	32010	00110	03000	00002	10
Pododoccus	?1??-	01??0	-??11	1?120	01100	00001	0--00	0-001	0010-	0000*	00001	14100	00100	32000	00110	00000	00100	00
Archontophoenix	2100-	01111	00111	10220	01000	10001	00010	0-200	10110	1000*	00001	04101	00110	32000	00111	0?000	00011	00
Dictyosperma	2110-	01111	00111	101$0	01001	00000	-0-10	0-200	10100	10000	00001	04101	00110	32000	00111	01000	00000	00
Dypsis	2110-	01111	00111	00120	01000	00011	01110	0-000	10110	10000	00001	04101	00110	32000	00111	0??00	00101	00
Euterpe	2110-	01111	00111	002$0	11000	01000	-0011	-2001	00110	10000	00001	04101	00110	32000	00111	00000	00000	00
Hyospathe	2110-	01111	00111	101$0	01001	00000	-0-10	0-200	10100	10000	00001	04101	00110	32000	10111	0??00	00100	00
Neonicholsonia	2110-	01111	00111	002$$	$00-0	00001	$0110	0-000	00100	1000*	00001	04100	00110	32000	00111	0??00	00010	00
Nephosperma	2110-	01121	00111	00220	01000	01010	-1010	0-201	10111	10000	00001	04100	00110	32000	00111	0??00	00010	00
Orania	20001	10-11	00111	101??	?1000	00111	01?10	2-210	00110	20000	00001	14100	00110	32000	00110	00000	10101	00
Phoenicophorium	2110-	01110	02111	001$1	11000	01010	-0010	2-200	1010-	1000*	00001	04100	00110	32000	00111	02?00	00110	00
Roystonea	2110-	01110	0??11	001$0	01000	10001	00100	0-000	00100	1010*	00001	04101	00110	32000	01111	0??00	00100	00
Veitchia	2110-	01121	00111	102$$	$1001	10011	$1010	0-000	10110	1*00*	00001	04101	00110	32000	00111	0??00	00000	00
Allagoptera	00000	10-10	0??11	022$0	01001	11010	-0011	-2211	01110	30200	10001	04100	00110	32000	01110	00002	00000	00
Astrocaryum	1000-	01111	00111	00210	01001	10101	$1010	0-200	00110	30101	00011	04100	00110	32000	00110	03?02	00001	00
Bactris	1000-	01111	00111	00210	01000	10001	00010	0-000	00111	30101	00011	04100	00110	32000	00110	03?02	00000	00
Elaeis	1010-	01010	05111	002$0	01001	10001	00100	0-000	1011-	3020*	00001	04100	00110	32000	01110	03?02	00002	00
Jubaea	10000	11010	0??11	02000	01001	11011	11101	-2211	01110	30000	00001	04100	00110	32000	11110	01?02	00000	00
Syagrus	00100	10-10	0??11	02200	01001	11010	-1001	-2211	01100	30200	00001	04100	00110	32000	01110	00?02	00010	00
Voanioala	?0100	10-11	00111	022$0	01001	10101	11110	0-201	0011-	$0200	00001	041?0	00110	32000	01110	0??02	00000	?0
Geonoma	1010-	01011	00111	00220	01000	00001	00-10	0-000	0011-	10100	00001	04100	00110	32000	01110	00?00	00100	00
Welfia	1000-	01011	00111	00220	01000	00001	00-10	0-000	0011-	00200	00001	04100	00110	32000	01110	01?00	00100	00
Phytelephas seemanii	10001	11021	00111	0?200	01000	01010	-1000	0-000	00101	11000	00001	04100	00110	02111	00210	00000	11000	00
P. tenuicaulis	10001	11021	00111	0?200	01000	01010	-0000	0-000	00101	11000	00001	04100	00110	02111	00210	00000	11000	00

the plumule and the primary root. The plumule was similar in all three cases, vertically oriented (negative geotropism). In the first state, the plumule arises in the same plane as the primary root, forming a vertically oriented straight axis. In the second state, the primary root is diagonally oriented with reference to the plumule. In the third state, the primary root is horizontally oriented and the plumule perpendicular to it.

1. Primary root: persistent = 0; ephemeral = 1. Primary roots of palms, and indeed monocots in general, are short lived and are soon replaced by shoot-born roots. During the early stage of seedling development, the primary root was present in all the taxa studied. This character was scored inapplicable for *Nypa* because the radicle of this taxon never develops. Stout primary roots were scored as persistent and primary roots of similar or less thickness than shoot-born roots and short lived were scored as ephemeral.

2. Swollen disk collar: absent = 0; present = 1. The disk collar develops as a distinct structure with swollen doughnut-shaped contour. The primary root emerges in the center of the flat surface.

3. Lenticels: absent = 0; present = 1. Lenticels are portions of periderm with numerous intercellular spaces (Esau 1977). Lenticels occur as creamy-white circular spots on the hyperphyll, sheathing bases, and primary roots.

4. Hyperphylls connection to fruit: flat = 0; swollen = 1; constricted = 2. Morphologically the cotyledon is divided into three portions, the haustorium, the hyperphyll, and the sheath. Tillich (1995) refers to the hyperphyll as the proximal segment of the cotyledon that connects the haustorium with the sheath. This structure varies greatly in size and length. The portion in contact with the seed can be flat, swollen, or constricted.

5. Cotyledonary sheath: absent = 0; present = 1. The presence or absence of the cotyledonary sheath was scored based on the attachment of the hyperphyll to this sheath. When the hyperphyll was attached to the collar, the cotyledonary sheath was scored as absent. When the hyperphyll appeared attached at any point above the collar node, the sheath was scored as present.

6. Coleoptile: absent = 0; present = 1. This structure, also known as the ligule or ocrea in palms, is formed by meristematic activity on the ring-shaped opening of the cotyledonary sheath in some taxa (Tillich 1995).

7. Coleoptile split: nonsplit = 0; split = 1. Coleoptiles are variable in length and they have distinctive opening features. Gatin (1906) divided the coleoptiles into three types, those with an apical opening, those with a lateral split, and those with tongue-like projections. These differences were not sharp enough to discriminate into three stages. Therefore, the coleoptiles were scored based on the nonsplitting and splitting pattern.

8. Cataphylls: one = 0; two = 1; three = 2; four = 3; more than four = 4. Cataphylls, also known as scale leaves, are bladeless leaves that form as the seedling grows and precede the eophyll. One or more cataphylls may be formed before the eophyll is formed.

9. Eophyll shape: entire = 0; segmented = 1. Palm eophylls are often described as having three distinct shapes: entire, pinnate, or palmate. Here the shapes are scored based on their basic structure, either entire or segmented.

10. Third leaf: nonlaminar = 0; laminar = 1. The term "third leaf" was used following a numerical series. The cotyledon is considered the first leaf, the cataphylls are considered as second leaf, third leaf, etc. Therefore, the first laminar leaf or eophyll continues the numerical series. The third leaf was chosen as a character state because it is at this number series that variation mostly occurs. The third leaf falls in the category of either cataphyll or laminar leaf.

11. Split eophyll: first = 0; second = 1; third = 2; fourth = 3; fifth = 4; sixth = 5; seventh = 6; eighth = 7; ninth = 8; tenth = 9. The leaf successional series from the first eophyll follows a distinct pattern in some groups (Tomlinson 1960*a*). In some cases, a plant will produce an entire eophyll and several eophyll-like leaves before the first split leaf appears. The eophylls were numbered and the first that presented evidence of splitting was recorded. There was a high percentage of missing information for this character because most of the material was fixed once the first eophyll was fully expanded.

12. Eophyll splitting side: adaxial = 0; abaxial = 1. In eophylls, as in adult leaves, splitting may occur along adaxial ribs or abaxial ribs (Uhl and Dransfield 1987).

13. Midrib at basal end: reduced = 0; distinct = 1. The proximal section of the eophyll was examined. A distinct axis (midrib) was present in bifid and pinnate leaves. The midrib of entire eophylls can have a major vascular bundle running along the whole length of the lamina, or it can be short and restricted to the basal portion. In some instances, the midrib could not be observed and appeared like a cluster of individual strands; in this case, the midrib was considered reduced.

14. Venation pattern: nonpinnate = 0; pinnate = 1. The non-pinnate state includes those eophylls with reduced axis, where the vascular strands run independently from a common starting point. Pinnate states were associated with eophylls, having either a short or a long midrib.

15. Vascular bundles: convergent = 0; not convergent = 1. In most eophylls, the vascular bundles converge at the apex, forming a distinct cluster of two or more vascular bundles. In others, the vascular bundles diverge toward the lamina margins, forming praemorse (denticulate) margins.

16. Eophyll proximal plication: reduplicate = 0; induplicate = 1; both = 2. Plication refers to the folding of the lamina. Kaplan et al. (1982) and Dengler et al. (1982) showed that plication originates by differential growth. Uhl and Dransfield (1987) classified palm leaves based on the position of the resulting splitting. Palms with an A-shaped blade as viewed adaxially were termed reduplicate and those with a V-shaped blade as viewed adaxially were termed induplicate. For eophylls, in order to standardize information, only the marginal plications were examined. As expected, in most cases both margins of an individual eophyll were identical; i.e., either induplicate or reduplicate. However, for some taxa, a third configuration was observed in which one margin was reduplicate and the other induplicate, this condition is termed "both" for brevity. To corroborate the validity of the character, sections of unexpanded eophylls were obtained and examined. The most salient point is that the eophylls of all species were consistent within each species.

17. Eophyll distal plication: reduplicate = 0; induplicate = 1; both = 2. The same principle for the previous character was applied to the distal part of the eophyll. Entire eophylls

maintain a uniform plication type along length of the lamina and thus the distal end is the same as the plication of the proximal end. In divided eophylls, the outer distal marginal folds remain the same as the basal marginal fold. The distal inner fold directly reflects the splitting pattern; if the splitting occurs in the abaxial side, the margin has a reduplicate fold and if the splitting occurs on the adaxial side, the margin has an induplicate fold.

18. Epidermal cell shape: rectangular = 0; fusiform = 1; rhombohedral = 2. Surface observations of epidermal peels from intercostal areas were used to examine this character. The information is restricted and was obtained only from the adaxial epidermis; information on the abaxial epidermis was not always available.

Anatomical characters of seedlings.—Each of the 31 anatomical characters and their states that were used and scored for the seedlings is discussed below in terms of usage of terminology and applicably and scoring.

19. Adaxial anticlinal walls: linear = 0; sinuous = 1; dentate = 2. Tomlinson (1960*a*) noted that cuticular deposit in the cell wall could give the walls a sinuous appearance. For eophylls, a cuticle layer was not always present and when present it was mostly restricted to the margin or above and below the ribs; nonetheless, there was enough in intercostal areas to score the states. The linear, sinuous, and dentate states were distinct, although some occasional intermediate cells were observed.

20. Abaxial anticlinal walls: linear = 0; sinuous = 1; dentate = 2. This is the same as the previous character and was scored from intercostal areas.

21. Epidermal trichomes: absent = 0; present = 1. Trichomes are usually present at costal and intercostal regions on both surfaces. The character was scored by examining the hair bases, which are persistent.

22. Single conical trichomes: absent = 0; present = 1. Trichomes are variable in structure and form. The most distinct type of hair was a unicellular, conical, filamentous hair.

23. Trichome base: free = 0; associated with fibrous bundles = 1. Although evidence shows that hairs occur in costal and intercostal regions (Tomlinson 1961), in some taxa there was a distinct association with fibrous bundles. The epidermal cells surrounding the hair appear sunken in transverse view.

24. Stomata: superficial-epidermal = 0; sunken = 1. Stomata are restricted to intercostal areas and are more abundant on the abaxial surface. In transverse section, the position of the guard cells with relation to the epidermal layer shows two distinct patterns; stomata with guard cells restricted to the epidermal layer level and stomata with guard cells at the hypodermal layer level. However, in some taxa the guard cells are not completely sunken in the hypodermis and they occupy the epidermal layer and part of the hypodermal layer.

25. Hypodermal layer: absent = 0; present = 1. Usually leaves have a hypodermal layer of cells beneath the epidermis and the hypodermal cells are larger and colorless. Because it has been shown that a hypodermis is usually present in plants exposed to xeric conditions (Esau 1977; Tomlinson 1961, 1990), but may be absent in plants growing in shade conditions, plasticity of the character was tested prior its inclusion in the matrix. For this purpose, samples of adult and seedlings of *Livistona chinensis* and *Pritchardia* Seem. & H. Wendl. ex H. Wendl. sp. were collected from natural populations in both xeric and shade conditions. These samples were examined and compared with seedlings grown under artificial conditions. The results showed that the hypodermis was present in all samples, and thus this character was retained.

26. Hypodermal fibers: absent = 0; present = 1. The colorless cells forming the hypodermis are in some cases replaced by fibers. The fibers occur alone, in bundles, or as a continuous layer. However, only their presence or absence was scored.

27. Palisade layer: absent = 0; present = 1. Palisade parenchyma cells are elongate and may be arranged in several layers. The palisade parenchyma in eophylls is not easy to differentiate but is present, usually as a single layer.

28. Spongy layers: five or fewer = 0; six or more = 1. Although the thickness of the eophylls is relatively similar, the number of layers is variable. Eophylls with large cells tend to have fewer layers than eophylls with smaller cells. This character appears to be constant for certain groups.

29. Mesophyll nonvascular fibers: absent = 0; present = 1. Fibers are a common feature in leaves. These are aggregated into bundles of few to several fiber strands.

30. Fibrous bundle distribution: equidistant bundle = 0; adaxial bundle = 1; abaxial bundle = 2. The distribution of the fibrous strands among the mesophyll layers is distinctive and three different types discriminate.

31. Expansion cells: absent = 0; present = 1. Expansion cells are present in the lamina on most palms. Their main function is to unfold and expand the lamina at maturity (Tomlinson 1961). Expansion cells are larger than the rest of the mesophyll cells. These cells differ from the bulliform epidermal cells of grasses because they are situated beneath the epidermal layer. Their arrangement is usually perpendicular to the surface layer and they are located at the folding regions of the lamina.

32. Fiber lumina size: small = 0; wide = 1. Tomlinson (1961) discussed the shape of the fiber lumen. He describes narrow vs. wide lumina and septate vs. nonseptate lumina. In eophyll fibers, it was not easy to observe the shape or any peculiar characteristic such as septae. However, wide lumina vs. narrow lumina were easily observable.

33. Longitudinal major vascular bundle association with folds: not associated = 0; associated = 1. Three vascular bundle sizes were identified; major vascular bundles, median vascular bundles, and minor vascular bundles. Major vascular bundles are usually situated at the plications and are attached adaxially to the epidermis and abaxially to the expansion cells. In a few taxa, major vascular bundles are situated halfway between two folding regions.

34. Longitudinal median vascular bundle: free = 0; buttressed = 1. Longitudinal median vascular bundles are slightly smaller than major vascular bundles and are not situated at the plications. These vascular bundles can be free or connected to epidermal layer by fibrous buttresses.

35. Free longitudinal median vein distribution: equidistant = 0; adaxial = 1; abaxial = 2. The free vascular bundles are distributed in the mesophyll and are not attached to the epidermal layers. Equidistant between the adaxial and abaxial surfaces is the most common feature.

36. Buttressed longitudinal median vascular bundle distribution: adaxial = 0; abaxial = 1; adaxial and abaxial = 2. The vascular bundles are attached to either the adaxial or abaxial layers by fibrous buttresses and in some cases the vascular bundles are attached to both layers.

37. Longitudinal minor vascular bundle distribution: equidistant = 0; adaxial side = 1; abaxial side = 2. Minor vascular bundles are small and have a single phloem strand. In eophylls, minor vascular bundles occur independently, or are attached to the surfaces.

38. Longitudinal minor vascular bundle associated with fold: not associated = 0; associated = 1. In general, expansion cells occupy the grooved fold, but in some taxa, the groove is occupied by minor vascular bundles.

39. Outer sheath of longitudinal minor vascular bundles: surrounding vascular bundle = 0; u-shaped = 1; lateral sides = 2; cap-shaped = 3. Vascular bundles are surrounded by two bundle sheaths: a parenchymatic colorless outer sheath (OS) and a sclerotic inner sheath (IS). The distribution of the OS can be complete and surround the vascular bundle, or incomplete and cover the vascular bundle partially. In the second case, the adaxial or abaxial sides of the vascular bundle are attached to the epidermal or subepidermal layers, and the OS shields only to the free surfaces.

40. Radial attachment cells associated with outer sheath cells of longitudinal minor vascular bundles: absent = 0; present = 1. A second layer of ellipsoid parenchymatic cells was detected surrounding the first OS. These cells are arranged radially with their narrow extremes toward the first OS.

41. Longitudinal minor vascular bundle buttress: absent = 0; present = 1. Fibers form large buttresses continuous with the lignified or sclerotic IS. These are attached to the adaxial, or abaxial hypodermal, or epidermal layers.

42. Midrib: not prominent = 0; prominent = 1. Midribs were examined from the proximal end of the eophyll. Midribs are usually prominent on either the adaxial or the abaxial surface.

43. Number of bundles composing the midrib: single bundle = 0; group of bundles = 1. Vascular midribs were found for all taxa. The vascular bundles were either solitary or scattered in the ground parenchyma.

44. Marginal rib composition: vascular bundle = 0; nonvascular bundle = 1. The margins can be occupied by vascular bundles or fibrous bundles.

45. Phloem strands: one = 0; two = 1; three = 2; four = 3. Although the single and double strands were the norm, three and four irregular strands also were observed.

46. Large metaxylem: one = 0; two = 1. The metaxylem may have one or two wide vessels.

47. Silica body shape: spherical/ellipsoid = 0; hat-shaped = 1; irregular = 2. Stegmata with silica bodies are found in longitudinal files adjacent to vascular or nonvascular fibers. Silica bodies can be of different shapes, the most common being spherical or ellipsoid. Others look like a flying saucer or a hat, and others do not have a specific shape or exhibit a range of irregular shapes.

48. Silica body surface: spinulose = 0; smooth = 1. The margins of the silica body are generally smooth, but some have spine-like protuberances.

49. Stegmata distribution: around vascular bundle = 0; around nonvascular bundle = 1. Silica bodies were found mostly in association with vascular and nonvascular bundles.

Excluded Characters

The following characters were excluded from current analyses because they represent autapomorphies, but are potentially informative in an expanded taxon matrix.

1. Haustorium: complete = 0; incomplete = 1. Haustorium is defined as the apical part of the cotyledon that develops into an absorbing organ. The complete cotyledon may become the absorbing organ, or only the apical part will develop into an absorbing organ while the remaining part will extend forming the hyperphyll. The structures were not clearly defined.

2. Hyperphyll: absent = 0; present = 1. The elongation of the hyperphyll is not a discrete character. The length describes a continuous range of sizes.

3. Hyperphyll texture: smooth = 0; rugulose = 1. A wide array of textures may appear either smooth or rugulose with distinct single or multiple longitudinal grooves lengthwise, etc.

4. Shoot-born roots: absent = 0; present = 1. Roots that arise endogenously (Tillich 1995), may occur at nodal or internodal regions. All primary roots are replaced by shoot-born roots.

5. Root hairs: absent = 0; present = 1. Root hairs in palms were formerly regarded as absent, but Seubert (1996*a*, *b*, 1997, 1998*a*, *b*) demonstrated that root hairs are a common feature in palm roots.

6. Transverse vascular bundles connections: connecting two vascular bundles = 0; connecting more than two vascular bundles = 1. Longitudinal vascular bundles, although parallel, are not isolated from each other; a complex network of transversal vascular bundles connects them. Some transversal vascular bundles connect several longitudinal vascular bundles one after another. Other vascular bundles connect only a couple of vascular bundles and intercostal regions.

7. Shape of subsidiary cell: rectangular = 0; ellipsoid = 1; reniform = 2. Stomata are similar in most taxa. Rectangular subsidiary cells resemble the adjacent epidermal cells, they occur in most arecoids. Ellipsoid subsidiary cells are uncommon, they occur scattered among all major groups. The kidney-shaped subsidiary cells are characteristic of most coryphoids, *Plectocomia* and *Pigafetta* (Blume) Becc. of the lepidocaryoids, Hyophorbeae, and Phytelephantoideae.

8. Terminal subsidiary cells: overarching = 0; not overarching = 1. In surface view, the arrangement of the terminal subsidiary cells shows two patterns. Some are wide and overreach the guard cells and the lateral subsidiary cells. The second state shows the terminal subsidiary cells restricted to the guard cell region.

9. Inner guard cells striations: absent = 0; present = 1. The inner walls of the guard cell in the caryotoids have distinct striations as observed earlier by Tomlinson (1961).

10. Single globose hair: absent = 0; present = 1. Single globose epidermal hairs were recorded only for the geonomoids.

11. Mesophyll: indistinct palisade = 0; distinct palisade = 1. The mesophyll regions were difficult to discriminate.

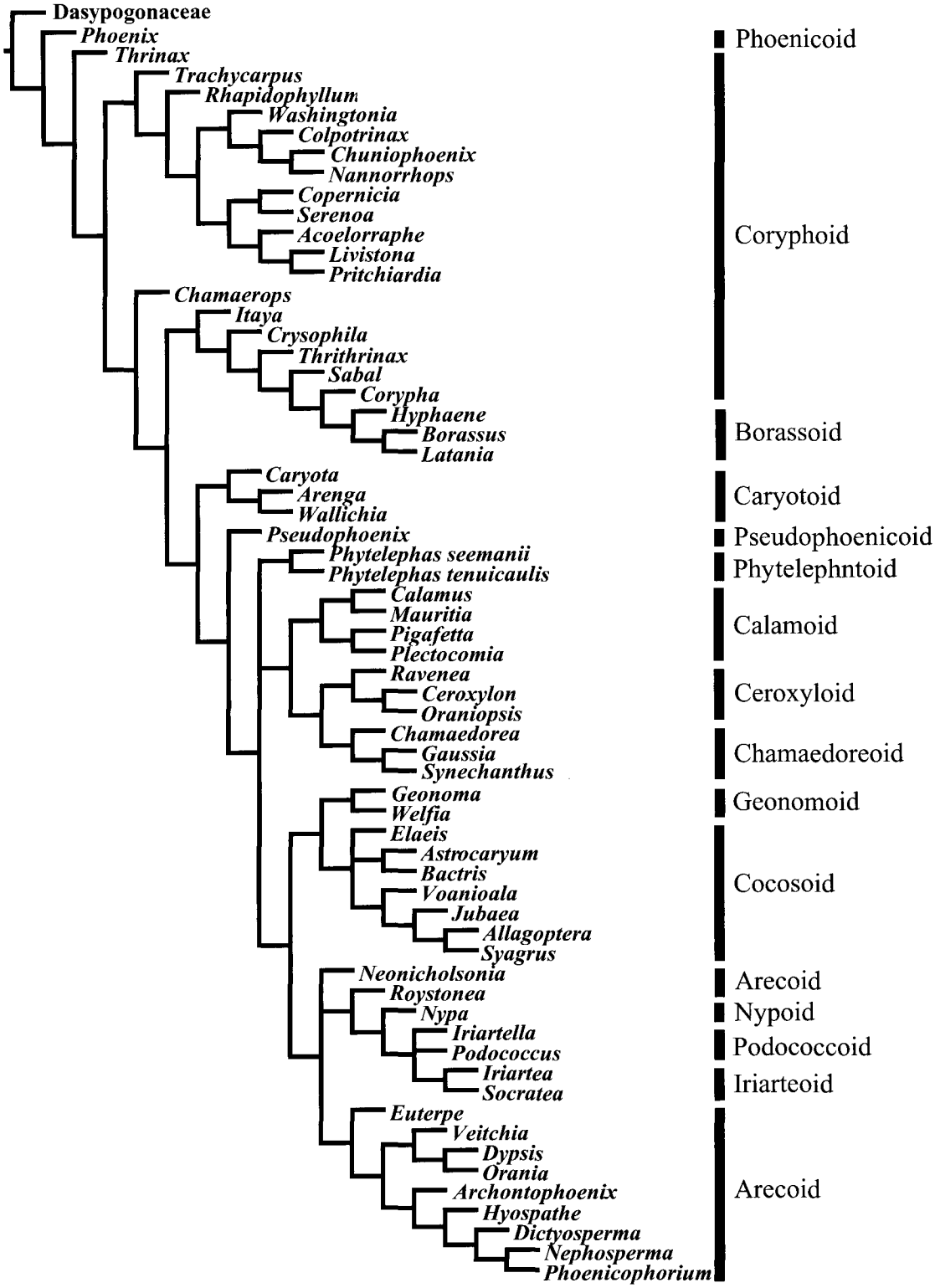

Fig. 1.—Strict consensus tree using Dasypogonaceae as the outgroup. Tree length = 535, CI = 0.20, RI = 0.66.

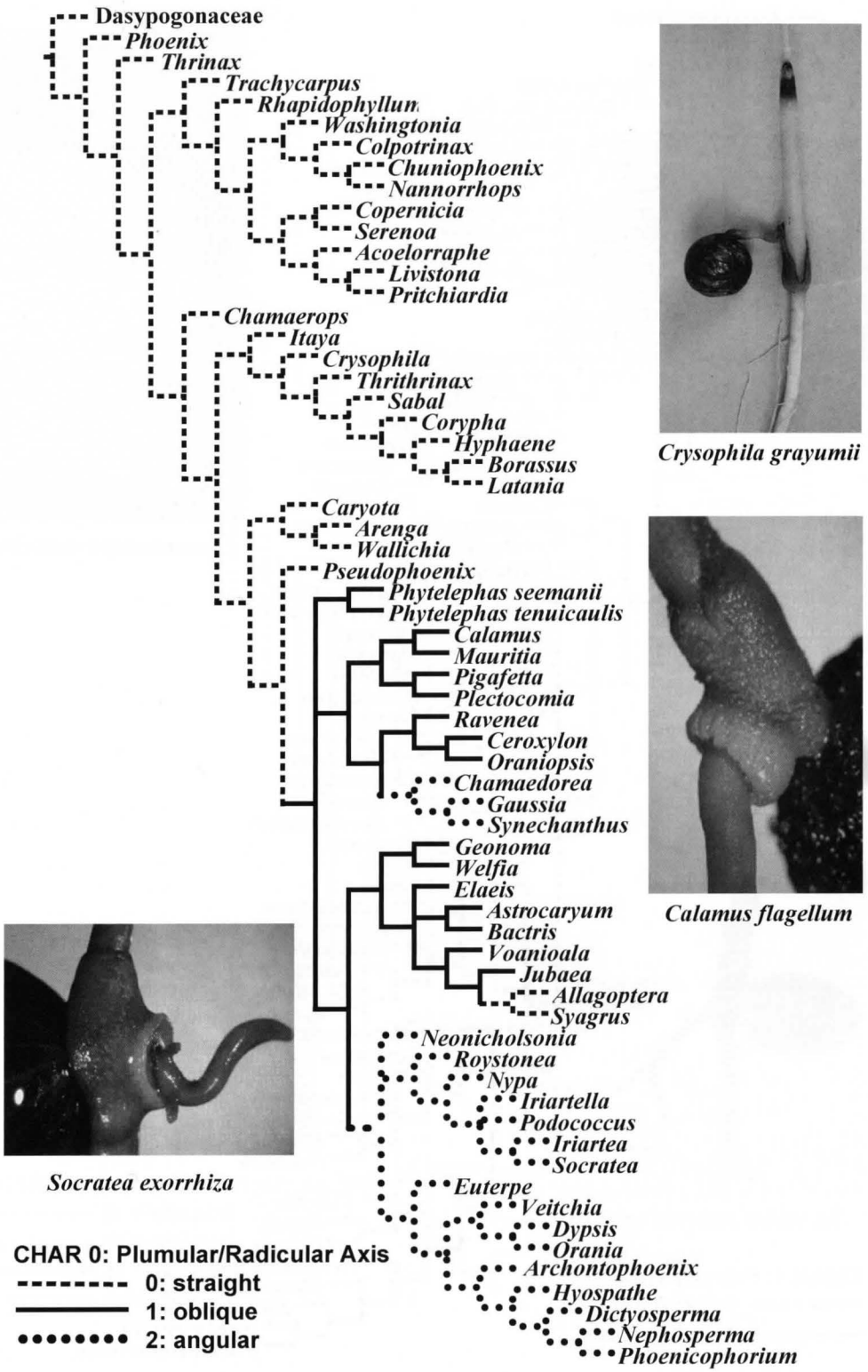

Fig. 2.—Seedling character distribution. Plumular/radicular axis.

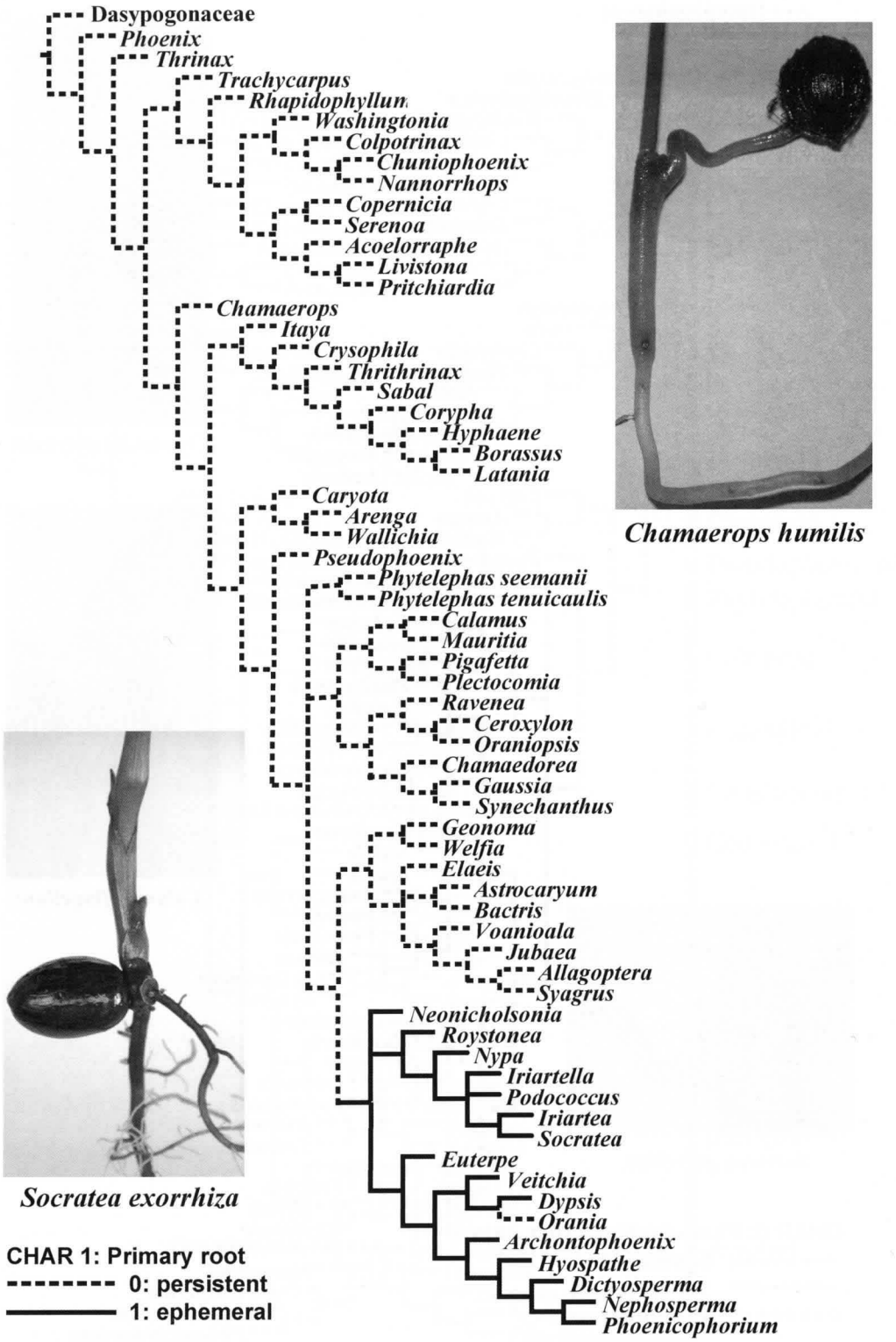

Fig. 3.—Seedling character distribution. Primary root.

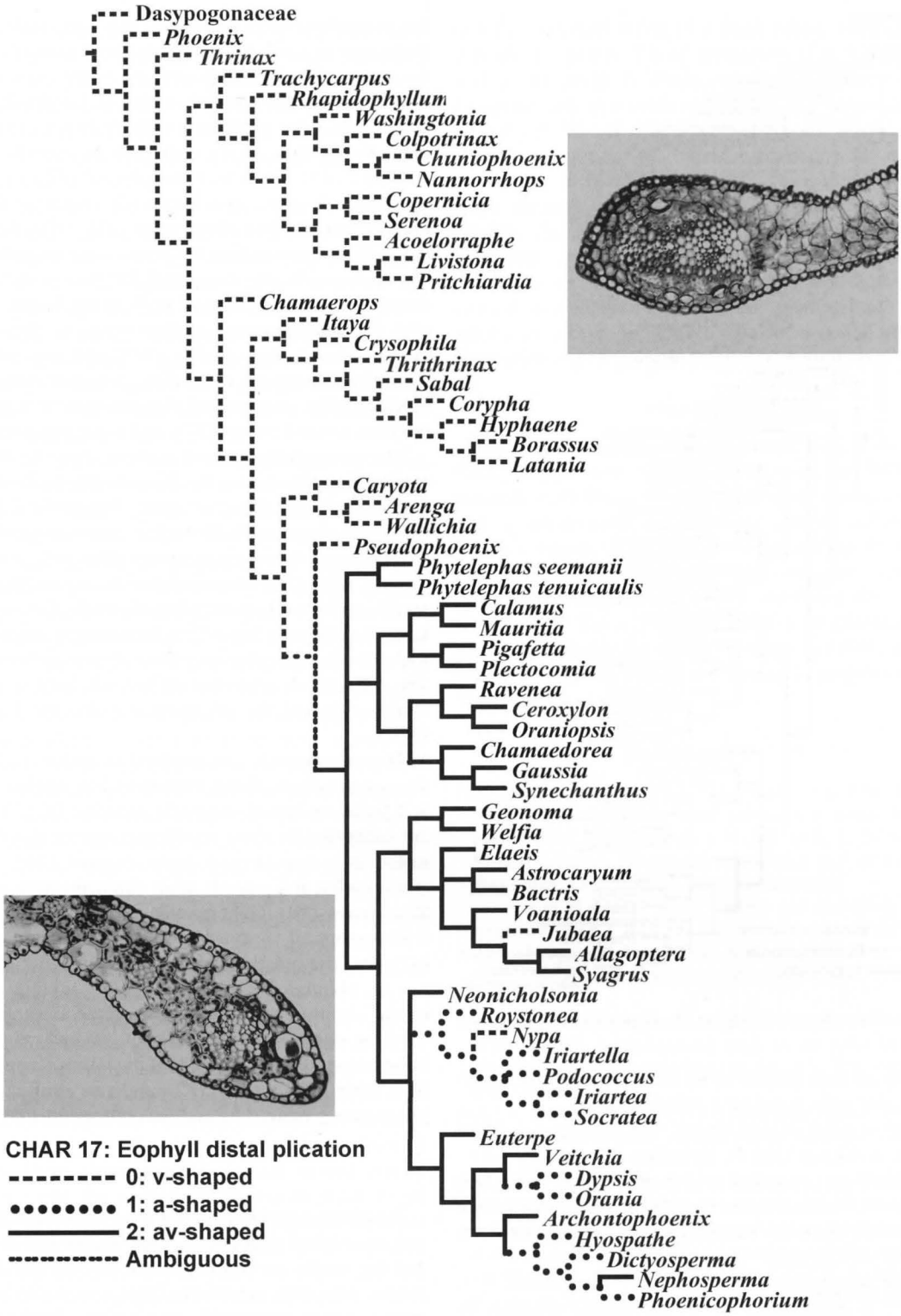

Fig. 4.—Seedling character distribution. Eophyll distal plication.

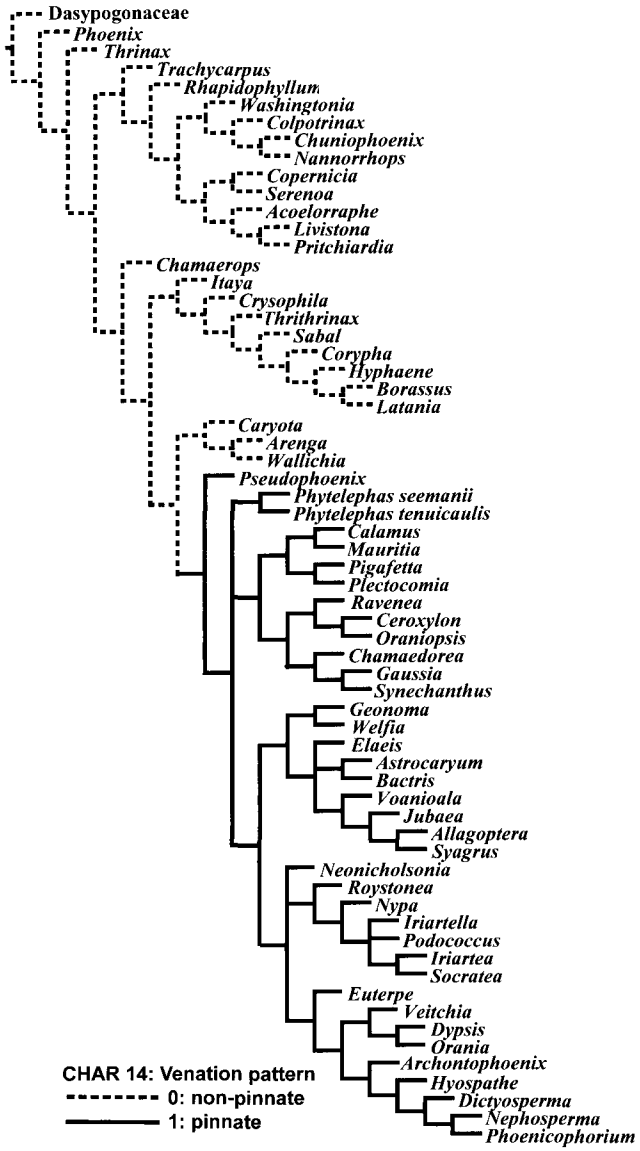

Fig. 5.—Seedling character distribution. Eophyll venation pattern.

The cells may all look similar or be differentiated into slightly perpendicular cells forming a palisade layer.

12. Midrib in adult leaves: absent = 0; present = 1. Most taxa do have a distinct midrib, including *Phoenix* L.

13. Midrib shape: rounded = 0; angular = 1. There was a wide array of midrib shapes: rounded if the contour were curved (rounded, ellipsoid, pear-shape, etc.) or angular if the contours have any straight sides.

14. Petiole transverse section: terete = 0; crescent = 1, pentagonal = 2. Although most of the simple eophylls do not have a distinct petiole, when distinct, some petioles were terete and others crescent shaped. Taxa with bifid eophyll (except *Caryota* L.) had a petiole with a rounded abaxial side and a slightly concave adaxial side. Taxa in the caryotoids have a distinct five-sided petiole (pentagonal).

RESULTS

The analysis resulted in six MPTs (Fig. 1) of 535 steps, with a CI of 0.20 and RI of 0.66. Nine of the major groups are monophyletic. The phoenicoids are resolved as a basal clade next to a paraphyletic coryphoid group. The caryotoids are monophyletic, supported by eight seedling character states: flat hyperphyll connection (4), longitudinal veins nonconvergent (15), epidermal cells fusiform (18), hypodermal cells absent (26), minor veins OS incomplete (39), phloem strands 2 (45), silica body hat-shaped (47), silica body margins smooth (48); and five adult character states: pinnae praemorse (55), flowering hapaxanthic (60), flowers in triads (65), plants monoecious (67), and atectate pollen wall (85). The calamoids are supported by four seedling character states: adaxial and abaxial wall of epidermal cells dentate (19) (20), longitudinal median veins at abaxial side (35), minor vein at abaxial side (37); and five adult character states: tubular bracts subtending flower clusters (64), flowers in diads (65), staminodial ring present (71), micropyle not oriented toward center (77), and scaly pericarp (78).

The ceroxyloids formed a sister clade to the chamaedoreoids. The monophyly of the ceroxyloids is supported by a single seedling character state: hypodermal layer present (25); and three adult character states: prophyll incomplete (61), flowers open precociously (68), and ovules hemianatropous (76). The chamaedoreoids are supported by three seedling character states: plumular/radicular axis angular (0), lack of epidermal hairs (21), hypodermal fibers absent (26); and a single adult character state: developed crownshaft (59). The ceroxyloids and chamaedoreoids have a single phloem strand (59) and the stigmatic remains are basal to lateral (82).

The geonomoids are resolved as sister to the cocosoids. The geonomoids share rhombohedral epidermal cells (18) and basal to lateral stigmatic remains (82). The cocosoids are supported by three seedling character states: sunken stomata (24), hypodermal layer present (25), four phloem strands (45); and a single adult character state: endocarp with three pores (79). Geonomoids and cocosoids share midribs with a group of vascular bundles (43), irregular silica bodies (47), and the presence of a staminodial ring (71). *Podococcus* G. Mann & H. Wendl. is nested among the iriarteoids in the basal arecoid clade. This clade is supported by four seedling character states: nonconvergent veins (15), rhombohedral epidermal cells (18), unicellular, conical trichomes (22), fiber lumina small (32); and two adult character states: praemorse pinnae (55) and several peduncular bracts (63).

DISCUSSION

Seedlings provide few but also consistent morphological and anatomical characters. Some major groups are resolved and the results are similar to the phylogenies based on molecular data. The caryotoids form a monophyletic clade separate from the coryphoids, as found by Asmussen and Chase (2001) and Hahn (2002). The cocosoids are polyphyletic in contrast to all previous studies, which resulted in analyses that showed monophyly for the group. Seedling data alone were not adequate for subdividing this group.

A straight plumular/radicular axis is a common feature for palms in the basal lineages, such as borassoids, coryphoids, phoenicoids, and caryotoids. Oblique axes are present in groups such as calamoids, ceroxyloids, and phytelephantoids. An angular axis is present in the arecoids, geono-

moids, chamaedoreoids, and iriarteoids (Fig. 2). Persistent primary roots (Fig. 3) are present in basal groups including calamoids and ceroxyloids; in intermediate groups such as chamaedoreoids and geonomoids; and two independent taxa, *Orania* Zipp. of the arecoids and *Voanioala* J. Dransf. of the cocosoids. These last two taxa have exceptional morphological features within their groups.

With few exceptions, the cotyledonary sheath separates the basal grade of the calamoids, ceroxyloids, arecoids, chamaedoreoids, iriarteoids, and *Nypa*. *Orania* and *Voanioala*, all of which lack a distinct cotyledonary sheath, form a clade composed of phytelephantoids, pseudophoenicoids, cocosoids, coryphoids, caryotoids, and phoenicoids, all of which have a distinct cotyledonary sheath as a synapomorphy. Cataphyll number per seedling varies; a single cataphyll is found in the basal clades and variable numbers of cataphylls are scattered among the remaining clades.

The reduplicate and induplicate plication types are not as distinct as in adult leaves. Some taxa have induplicate (V-shaped) folding at both margins; others reduplicate (A-shaped) folding at both margins. A third type has induplicate folding at one margin and reduplicate at the other margin (Fig. 4). Venation patterns of eophylls (Fig. 5) are pinnate in all bifid eophylls and in the simple eophylls of cocosoids. All the remaining groups are non-pinnate category because the variation in axis (rachis) length. *Mauritia* L. f. of the calamoids has a palmate eophyll that differs from the palmate eophylls of the coryphoid palms, in that the longitudinal vascular bundles radiate uniformly from a well-defined, but reduced rachis; in contrast, the longitudinal vascular bundles of the coryphoids originate at different points of an obscure rachis or radiate irregularly from an anastomosed major bundle. This character can be subdivided further if the number of taxa is expanded. Hypodermal fibers have a selective distribution; they occur at the mesophyll layer and/or, with some exceptions, among the mesophyll layers.

Phoenix branches first, followed by *Thrinax* Sw. These two taxa have appeared together in most clades, as in previous analyses, e.g., (Hahn 2002). The ceroxyloids appear next to phytelephantoids in molecular studies, but here they form a clade with the chamaedoreoids. Martius (1823–1850) put *Pseudophoenix* H. Wendl. ex Sarg. and *Phytelephas* together, and these two taxa are resolved as sister taxa in most trees. Molecular analyses place the caryotoids as sister to the borassoids. Here, the borassoids appear nested among the coryphoids while the caryotoids appear as sister to all taxa except the coryphoids. *Roystonea* O. F. Cook resolves as sister to the chamaedoreoids in molecular analyses; here it resolves among the arecoids as sister to *Nypa* and the iriarteoids. *Podococcus* appears nested among the iriarteoids sister to *Iriartella* H. Wendl. *Pseudophoenix* has been defined as a "floater" in Uhl et al. (1995) but here it appears consistently as sister to the phytelephantoids, calamoids, ceroxyloids, geonomoids, cocosoids, and arecoids.

Nypa and calamoids are not basal in the morphological analysis as they are in the molecular analyses. Instead, the calamoids form a clade with the ceroxyloids and chamaedoreoids and *Nypa* is nested among the arecoids, sister to the iriarteoids and *Podococcus*.

The seedling and adult characters used in this study show promise in contributing to a more robust phylogenetic analysis of the palms. Those characters that show homoplasy, such as character 0: Plumular/radicular axis, which occurs independently in a clade comprised of *Chamaedorea* Willd., *Gaussia* H. Wendl., and *Synechanthus* H. Wendl. and a clade comprised of arecoid, nypoid, podococcoid, and iriateoid palms may in fact be shown to be derived by different pathways through reciprocal illumination and developmental studies. The next step should be to match terminals across all existing data sets to produce a combined "total evidence" matrix. In our opinion, this approach would go a long way toward producing a more robust phylogenetic tree, based upon a more comprehensive data set that will allow a better understanding of palm biology and evolution.

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