Syst. Biol. 51(1):92–112, 2002

A Molecular Phylogenetic Study of the Palmae (Arecaceae) Based on *atp*B, *rbc*L, and 18S nrDNA Sequences

WILLIAM J. HAHN

Department of Ecology, Evolution, and Environmental Biology, Center for Environmental Research and Conservation, Columbia University, 1200 Amsterdam Ave., New York, New York 10027, USA; E-mail: wh55@columbia.edu

Abstract.—Notoriously slow rates of molecular evolution and convergent evolution among some morphological characters have limited phylogenetic resolution for the palm family (Arecaceae). This study adds nuclear DNA (18S SSU rRNA) and chloroplast DNA (cpDNA; *atp*B and *rbc*L) sequence data for 65 genera of palms and characterizes molecular variation for each molecule. Phylogenetic relationships were estimated with maximum likelihood and maximum parsimony techniques for the new data and for previously published molecular data for 45 palm genera. Maximum parsimony analysis was also used to compare molecular and morphological data for 33 palm genera. Incongruence among datasets was detected between cpDNA and 18S data and between molecular and morphological data. Most conflict between nuclear and cpDNA data was associated with the genus *Nypa*. Several taxa showed relatively long branches with 18S data, but phylogenetic resolution of these taxa was essentially the same for 18S and cpDNA data. Base composition bias for 18S that contributed to erroneous phylogenetic resolution in other taxa did not seem to be present in Palmae. Morphological data were incongruent with all molecular data due to apparent morphological homoplasy for Caryoteae, Ceroxyloideae, Iriarteae, and Thrinacinae. Both cpDNA and nuclear 18S data firmly resolved Caryoteae with Borasseae of Coryphoideae, suggesting that at least some morphological characters used to place Caryoteae in Arecoideae are homoplastic. In this study, increased character sampling seems to be more important than increased taxon sampling; a comparison of the full (65-taxon) and reduced (45- and 33-taxon) datasets suggests little difference in core topology but considerably more nodal support with the increased character sample sizes. These results indicate a general trend toward a stable estimate of phylogenetic relationships for the Palmae. Although the 33-taxon topologies are even better resolved, they lack several critical taxa and are affected by incongruence between molecular and morphological data. As such, a comparison of results from the 45- and 33-taxon trees offers the best available reference for phylogenetic inference on palms.

The Palmae (Arecaceae) include ~2000 species in 189 genera found throughout the tropics and subtropics of the world. Comprehensive taxonomic studies of the family (Dransfield and Uhl, 1998; Uhl and Dransfield, 1987) and several analyses of phylogenetic relationships have been conducted (Wilson et al., 1990; Uhl et al., 1995; Baker et al., 1999; Asmussen et al., 2000; Asmussen and Chase, 2001; Lewis and Doyle, 2001). Although none of these studies completely resolved palm relationships, each offered an enhanced foundation for continued study of palm phylogeny.

A combined phylogenetic analysis of all available palm data has not been performed but a comparison of the trees from the different studies indicates many points of congruence. Studies using chloroplast DNA (cpDNA) are the most extensive and offer the broadest basis for comparison, through nuclear DNA and morphological analyses also make important contributions to phylogenetic understanding of the family.

All palm cpDNA studies (Wilson et al., 1990; Uhl et al., 1995; Baker et al., 1999; Asmussen et al., 2000; Asmussen and Chase, 2001) identify a monophyletic Calamoideae and the monotypic Nypoideae as the first branching elements, but their specific order of branching is not consistent. For the remainder of the family, two poorly supported groups are identified. In the first group, Coryphoideae and the three genera of Caryotoid palms (*Arenga*, *Caryota*, and *Wallichia*) are consistently grouped by cpDNA data but Coryphoideae s.l. is not always monophyletic. The second group contains Arecoideae (minus Caryoteae), Ceroxyloideae, and Phytelephantoideae (the Arecoid Line sensu Moore, 1973). Subfamilies Arecoideae and Ceroxyloideae (sensu Dransfield and Uhl, 1988) are paraphyletic in all morphological and molecular phylogenetic studies published to date.

Nuclear DNA malate synthase intron data (Lewis and Doyle, 2001) identify *Nypa* as the first branching lineage of palms but differ

from cpDNA data in placing *Pseudophoenix* (Ceroxyloideae) as the next branching lineage, followed by a largely unresolved assemblage of the remaining taxa. Several distinct lineages are supported within this latter group, including Calamoideae and tribes Caryoteae and Iriarteae of Arecoideae (sensu Dransfield and Uhl, 1988), but most relationships are either unresolved or not supported. Other studies of nuclear DNA (e.g., Gaut et al., 1996) included few taxa and offer little insight into palm relationships.

Morphological phylogenies of palms (Uhl et al., 1995) are highly unresolved and therefore do not directly contradict molecular phylogenies in most respects. Of the differences that are supported, perhaps the most striking concerns the Caryotoid palms. This group is placed sister to tribe Borasseae of subfamily Coryphoideae in all cpDNA phylogenies but is resolved within subfamily Arecoideae in the morphological analyses. Nuclear DNA data are equivocal on the position of the Caryotoid palms.

These studies provide many points of phylogenetic resolution for palms, but none offers a fully resolved hypothesis of relationship for the family nor are any of the published trees well supported in all areas. Among the proposed reasons for these shortcomings are difficulties in outgroup choice and character polarization, homoplasy in morphological data, and slow rates of molecular evolution for standard DNA markers.

The position of the palms among monocots has been difficult to ascertain, and relationships with groups as varied as the Araceae, Cyclanthaceae, Pandanaceae, and Poaceae have been suggested (see Uhl and Dransfield, 1987, for discussion). More recent morphological (Stevenson and Loconte, 1995) and molecular phylogenetic studies (Chase et al., 2000; Soltis et al., 2000) have resolved Palmae within the Commelinid monocots, but the specific placement of Palmae among Commelinids is unclear. Nonetheless, the use of Commelinid outgroups have reduced difficulties in palm outgroup comparison (e.g., Asmussen and Chase, 2001; Lewis and Doyle, 2001).

Homoplasy for some morphological characters has also contributed to difficulties in palm phylogeny reconstruction. Uhl et al. (1995), using morphological data, were unable to resolve relationships within the family and identified substantial homoplasy among the characters studied. Furthermore, the morphological and molecular phylogenies of Uhl et al. (1995) differed in several ways suggesting that at least one of the data types was improperly coded or was exhibiting patterns unexpected under the evolutionary model. Similar results have been observed in other morphological phylogenetic studies of palms (e.g., Baker et al., 2000, for the Calamoideae), an indication that morphological data alone are insufficient to resolve phylogenetic relationships within the family.

Several authors have used molecular data to explore palm phylogenetic relationships. Unfortunately, the comparatively slow rates of molecular evolution for palms identified in every study to date (e.g., Wilson et al., 1990; Gaut et al., 1992; Eyre-Walker and Gaut, 1997) and the patterns of palm diversification limit the ability of standard molecular markers to resolve phylogenetic relationships. Thus inference of these relationships requires careful consideration of the data and analyses needed to recover palm phylogeny.

Asmussen and Chase (2001) used comparatively large samples of coding (*rbc*L) and noncoding (*rps*16 introns and *trn*L-*trn*F introns and spacers) cpDNA sequence data to resolve palm phylogenetic relationships. Their results demonstrated greater resolution with increased sample sizes, but the phylogenetic signal in their data was still inadequate for complete resolution. MP searches were terminated at 5,000 shortest trees, and consensus trees were only partly resolved, indicating that additional data are required to resolve palm relationships.

Although uncertain outgroup relations, morphological homoplasy, and slow rates of molecular evolution have contributed to the limited phylogenetic resolution of palms, a more general problem may be responsible for the lack of success (Hahn, 1999). The palm fossil record suggests an early origin for the family and comparatively rapid radiation into many of the main lineages (see Harley and Baker, 2001, for a recent review). Since the initial diversification, relatively few new major groups of palms have emerged, but considerable time has passed in which additional uninformative changes could have accumulated along the long terminal branches. If any of these changes are convergent or parallel, difficulties in phylogenetic reconstruction can result among

the critical deep branches (Felsenstein, 1978; Hendy and Penny, 1989; Donoghue and Sanderson, 1992; Cooper and Fortey, 1998).

The observed patterns of palm morphological homoplasy seem to fit the deep branch phylogeny scenario. Morphological synapomorphies are not defined for most major groups in the family, and no morphological synapomorphy has been identified for the family overall. Furthermore, only 8 of the 40 informative morphological characters used by Uhl et al. (1995) are completely consistent within the family.

Molecular data for palms also fit the pattern of a deep branch phylogeny and are further limited by their slow rates of evolution (Gaut et al., 1992; Eyre-Walker and Gaut, 1997). With such rates, the number of substitutions that might have occurred along the internal edges of the true underlying tree would probably be very small and easily obscured by any parallel changes along the comparatively long terminal branches. This is observed in the molecular data available, where relatively few sites are variable and many of those exhibit homoplasy (e.g., Asmussen and Chase, 2001).

Several approaches have been suggested for reconstructing phylogenies of apparently deep and rapid evolutionary radiations and phylogenies with comparatively long terminal branches. These include (1) the use of less variable (and presumably less homoplastic) characters (Swofford et al., 1996), (2) the use of larger and more comprehensive datasets (e.g., the "total evidence" approach of Kluge, 1989; but see Bremer et al., 1999; Halanych, 1998), (3) the inclusion of more taxa and balanced selection of ingroup taxa to help break up long branches (e.g., Kim, 1996; Graybeal, 1998; Poe, 1998; Poe and Swofford, 1999), (4) careful attention to outgroup choice (e.g., Maddison et al., 1984), and (5) the use of methods of analysis that are less sensitive to the effects of long branch attraction (e.g., Huelsenbeck and Hillis, 1993; Huelsenbeck, 1995).

In the present study, palm phylogenetic relationships were estimated by a combination of these strategies. Comparatively large samples of cpDNA and nuclear rDNA sequences were generated to complement existing noncoding cpDNA data and to explore patterns of evolution for each of these different data types. A broad array of ingroup and outgroup taxa were analyzed to help break up long branches thought to exist among some palm lineages. Finally, the relative quality of the different data types was evaluated by way of combined and partitioned analyses, and by using methods of analysis considered to be less sensitive to deep branch problems or homoplastic data.

Methods and Materials

Taxon sampling.—Sixty-five palm genera were sampled, representing all six subfamilies and 14 tribes recognized in the family. Members of all but 6 of the 36 subtribes (sensu Dransfield and Uhl, 1998) were included.

Monophyly of Palmae has been supported in all phylogenetic studies to date (e.g., Stevenson and Loconte, 1995; Chase et al., 2000; Soltis et al., 2000), but sister group relationships of the palms to other monocots are less certain. For the present study, outgroup taxa were restricted to *Calectasia* and *Dasypogon* of Dasypogonaceae and *Hanguana* of Hanguanaceae, as indicated in the studies of Soltis et al. (2000) and Chase et al. (2000).

DNA extraction, amplification, and sequencing.—Leaf tissue was collected from wild or cultivated material (Table 1). Total nucleic acids were extracted by using a modified hexadecyl trimethyl ammonium bromide (CTAB) method (Taylor and Powell, 1982; Hahn and Sytsma, 2000) and the same isolate was used to generate all new sequences.

Three gene regions were sampled: *atp*B and *rbc*L from the plastid genome, and the 18S small subunit of the 45S nuclear rDNA cistron. These regions were amplified with primer pairs S2 and S1494R (Hoot et al., 1995), Z1 and rbcL 3′ (Zurawski et al., 1981; Olmstead et al., 1992), and NS1 and C18L (Bult et al., 1992), respectively. Sequencing primers were used as listed by these authors.

Polymerase chain reaction (PCR) conditions were as described by Bult et al. (1992). Some amplifications used the FailSafe® amplification premix (Epicentre Technologies, Madison, WI). PCR products were cleaned by using the polyethylene glycol/NaCl precipitation method of Kusukawa et al. (1990).

Sequencing was performed on Applied Biosystems 373a or 377 automated sequencers by using dye terminator cycle sequencing chemistry with ~100 ng of DNA template, 4.0 μL of DyeDeoxy® FS Terminator or BigDye® premix (PE Biosystems, Inc., Foster

TABLE 1. Taxa sampled in this study. Taxonomy from DransField and Uhl (1998); FTG, Fairchild Tropical Garden; H, Hahn; MONT, Montgomery Botanical Center; NYBG, New York Botanical Garden; WIS, University of Wisconsin, Madison.

SUBFAMILY	Species	Voucher and origin	GenBank accession nos.		
			*atp*B	*rbc*L	18S
TRIBE, Subtribe					
CORYPHOIDEAE					
CORYPHEAE					
Thrinacinae	*Chelyocarpus repens* Kahn and Mejia	H7070, WIS; cult. FTG 88 559	AY012400	AY012457	AY012343
	Chamaerops humilis L.	H7044, WIS; cult. FTG s.n.	AY012399	AY012456	AY012342
	Rhapis subtilis Becc.	H7094, WIS; cult. FTG 71 239	AY012401	AY012458	AY012344
	Thrinax radiata Lodd. ex Schult. & Schult. f.	H7600, WIS; Florida, USA	AY012402	AY012459	AY012345
	Trachycarpus fortunei (W. J. Hook.) H. Wendl.	H7074, WIS; cult. FTG 92 202	AY012403	AY012460	AY012346
	Trithrinax campestris (Burmeister) Drude and Grieseb. ex Drude	H7104, WIS; cult. FTG 91 273	AY012404	AY012461	AY012347
Livistoninae	*Licuala grandis* H. A. Wendl.	H6394, WIS; cult. FTG 61 45B	AY012405	AY012462	AY012348
	Livistona speciosa Kurz	H5918, WIS; Thailand	AY012406	AY012463	AY012349
	Pritchardiopsis jeanneneyi Becc.	H s.n., WIS; New Caledonia	AY012407	AY012464	AY012350
	Washingtonia fillifera (Linden) H. Wendl.	H6941, WIS; cult. Univ. Wisc.	AY012408	AY012465	AY012351
Coryphinae	*Corypha utan* Lamarck	H7053, WIS; cult. FTG RM1006	AY012409	AY012466	AY012352
Sabalinae	*Sabal dominguensis* Becc.	H7733, MONT; Dominican Republic	AY012410	AY012467	AY012353
PHOENICEAE	*Phoenix dactylifera* L.	H6899, WIS; cult. Univ. Wisc.	AY012411	AY012468	AY012354
BORASSEAE	*Borassus flabellifera* L.	H7059, WIS; cult. FTG 74 201	AY012412	AY012469	AY012355
Lataniinae	*Hyphaene coriacea* Gaertn.	H7080, WIS; cult. FTG 86 208	AY012413	AY012470	AY012356
Hyphaeninae					
CALAMOIDEAE					
CALAMEAE					
Metroxylinae	*Metroxylon vitiense* (H. A. Wendl.) Benth. and J. D. Hook.	H6373, WIS; cult. FTG 89 197	AF233086	AF233089	AF168860
Calamineae	*Salacca zalacca* (J. Gaertn.) Voss ex Bilmorin	H6377, WIS; cult. FTG 64 661	AY012415	AY012472	AY012358
	Calamus caesius Blume	H6390, WIS; cult. FTG 64 129C	AF233081	AY044619	AF168828
LEPIDOCARYEAE	*Mauritia flexuosa* L. f.	H7087, WIS; cult. FTG 88 576	AY012416	AY012473	AY012359
NYPOIDEAE	*Nypa fruticans* Wurmb.	H7106, WIS; cult. FTG s.n.	AY012414	AY012471	AY012357
CEROXYLOIDEAE					
CYCLOSPATHEAE	*Pseudophoenix vinifera* (Mart.) Becc.	H7732, MONT; Dominican Republic	AY012417	AY012474	AY012360
CEROXYLEAE	*Ravenea hildebrandii* C. D. Bouché	H6392, WIS; cult. FTG 71A	AY012418	AY012475	AY012361
HYOPHORBEAE	*Chamaedorea seifrizii* Burret	H s.n., WIS; cult. Univ. Wisc.	AF233083	AF206748	AF069209
	Hyophorbe lagenocaulis (L. H. Bailey) H. E. Moore	H7109, WIS; cult. FTG 80 509	AY012419	AY012476	AY012362
	Wendlandiella polyclada Burret	H6377, WIS; cult. FTG 77 248	AY012420	AY012477	AY012363
ARECOIDEAE					
CARYOTEAE	*Arenga pinnata* (Wurmb.) Merrill	H6431, WIS; cult. FTG 80 756	AY012421	AY012478	AY012364
	Caryota mitis Lour.	H6627, WIS; Thailand	AF233082	AY044620	AF168831

IRIARTEAE					
	Dictyocaryum lamarckianum (Mart.) H. Wendl.	H6339, WIS; cult. NYBG	AY012422	AY012479	AY012365
	Iriartea deltoidea Ruíz and Pav.	H6340, WIS; cult. NYBG	AF233084	AF233088	AF168854
	Socratea exorrhiza (Mart.) H. Wendl.	H6341, WIS; cult. NYBG	AY012423	AY012480	AY012366
	Wettinia hirsuta Burret	H6381, WIS; cult. FTG 86 409	AY012424	AY012481	AY012367
PODOCOCCEAE	*Podococcus barteri* G. Mann and J. Wendl.	H7110, WIS; cult. FTG 88 480	AF233086	AF233090	AF168870
ARECEAE					
Oraniinae	*Orania trispatha* (J. Dransf. and N. W. Uhl) Beentje and J. Dransf.	H7095, WIS; cult. FTG 92 313	AY012425	AY012482	AY012368
Manicariinae	*Manicaria sacchifera* J. Gaertn.	H7641, WIS; Amazonas, Brasil	AY012426	AY012483	AY012369
Leopoldiniinae	*Leopoldinia pulchra* Mart.	H7642, WIS; Amazonas, Brasil	AY012427	AY012484	AY012370
Malortieinae	*Reinhardtia simplex* (H. Wendl.) Drude ex Dammer	H7811, WIS; cult. NYBG	AY012428	AY012485	AY012371
Dypsidinae	*Dypsis lastelliana* (Baill.) Beentje and J. Dransf.	H6371, WIS; cult. FTG 88 171	AY012429	AY012486	AY012372
Euterpeinae	*Prestoea acuminata* (Willd.) H. E. Moore	H7650, MONT; Guadeloupe, France	AY012430	AY012487	AY012373
Roystoneinae	*Roystonea regia* (Kunth) O. F. Cook	H7100, WIS; cult. FTG 92 386	AY012431	AY012488	AY012374
Archontophoenicinae	*Chambeyronia macrocarpa* (Brongn.) Vieill. ex Becc.	H6366, WIS; cult. FTG 77 147	AY012432	AY012489	AY012375
	Kentiopsis oliviformis (Brongn. and Gris.) Brongn.	H6382, WIS; cult. FTG 71 146	AY012433	AY012490	AY012376
Cyrtostachydinae	*Cyrtostachys renda* Blume	H6365, WIS; cult. FTG 87 688	AY012434	AY012491	AY012377
Linospadicinae	*Calyptrocalyx sp.*	H6378, WIS; cult. FTG 86 331	AY012444	AY012501	AY012387
	Howea belmoreana (C. Moore and F. v. Mueller) Becc.	H6440, WIS; cult. FTG 73 337	AY012435	AY012492	AY012378
Ptychospermatinae	*Balaka seemanni* Becc.	H6368, WIS; cult. FTG 75 43N	AY012436	AY012493	AY012379
	Drymophloeus beguinii (Burret) H. E. Moore	H6370, WIS; cult. FTG 91 31A	AY012437	AY012494	AY012380
	Ptychosperma burretianum Essig	H6375, WIS; cult. FTG 81 592	AY012438	AY012495	AY012381
	Veitchia sessilifolia (Burret) H. E. Moore	H6382, WIS; cult. FTG 85 188	AY012439	AY012496	AY012382
Arecinae	*Areca vestiaria* Giseke	H6363, WIS; cult. FTG 73 451	AY012440	AY012497	AY012383
	Gronophyllum pinangoides (Becc.) Essig and B. E. Young	H6437, WIS; cult. FTG 81 618	AY012441	AY012498	AY012384
	Hydriastele wendlandiana (F. v Mueller) H. A. Wendl. & Drude	H6438, WIS; cult. FTG 57 793	AY012447	AY012504	AY012390
Iguanurinae	*Bentinckia nicobarica* (Kurz) Becc.	H6374, WIS; cult. FTG 88 107	AY012442	AY012499	AY012385
	Burretokentia hapala H. E. Moore	H6364, WIS; cult. FTG 89 689	AY012443	AY012500	AY012386
	Cyphopheonix nucele H. E. Moore	H6391, WIS; cult. FTG 74 344	AY012445	AY012502	AY012388
	Dictyosperma album (Bory) H. Wendl. and Drude	H6369, WIS; cult. FTG 88 207	AY012446	AY012503	AY012389
Oncospermatinae	*Oncosperma tigillarum* (Jack) Ridley	H6362, WIS; cult. FTG 152	AY012448	AY012505	AY012391
COCOEAE					
Beccariophoenicinae	*Beccariophoenix madagascariensis* Jum. and H. Perrier	H7077, WIS; cult. FTG 91 308	AY012449	AY012506	AY012392
Butiinae	*Cocos nucifera* L.	H7042, WIS; cult. FTG 80 798	AY012450	AY012507	AY012393
Attaleinae	*Orbignya barbosiana* Burret	H6379, WIS; cult. FTG 75 644	AY012451	AY012508	AY012394
Elaeidinae	*Elaeis oleifera* (Kunth) Cortés	H7085, WIS; cult. FTG 87 117	AY012452	AY012509	AY012395
Bactridinae	*Astrocaryum alatum* Loomis	H6386, WIS; cult. FTG 78 424	AY012453	AY012510	AY012396
GEONOMEAE	*Calyptronoma occidentalis* (Sw.) H. E. Moore	H6380, WIS; cult. FTG 75 159	AY044459	AY044622	AF406630
	Geonoma oxycarpa Mart.	H7907, WIS; cult. FTG 86 408	AY044460	AY044623	AF406631
PHYTELEPHANTOIDEAE	*Aphandra natalia* (Balslev & Henderson) Barfod	Pintaud 20; Ecuador	AY044458	AY044619	AF406632
	Phytelephas aequatorialis Spruce	H6247, WIS; cult. Lyon Arboretum, Hawaii	AY012455	AY012512	AY012398

City, CA), 2.0 pM primer, and water to a final volume of 10 μL. Reactions were centrifuged on Sephadex columns (Centri-Sep; Princeton Separations, Adelphia, NJ) and dried under a vacuum.

Sequence alignment and phylogenetic analysis.—Contigs were assembled with Sequencher ver. 3.1 (GeneCodes, Ann Arbor, MI). Multiple sequence alignments of *rbc*L, *atp*B, and 18S rDNA were mostly unambiguous and were performed manually. 18S alignments were guided by those used by Soltis et al. (2000). The new data were analyzed independently and with the previously published cpDNA *trn*L-*trn*F and *rps*16 spacer/intron sequences of Asmussen and Chase (2001) and the morphological and cpDNA restriction fragment length polymorphism (RFLP) data of Uhl et al. (1995). The cpDNA spacer/intron data were kindly provided by B. Baker and C. Asmussen (Royal Botanic Gardens, Kew, London). The alignment analyzed the excluded gap positions as indicated in Asmussen and Chase (2001). The appended binary gap characters were included in some but not all analyses.

For the combined analyses, different species of the same genus were occasionally represented among the different datasets. An assumption was made that genera represented by different species are monophyletic. In only a few cases does evidence contradict this (e.g., *Calamus* and *Prestoea/Euterpe*).

For comparisons with the cpDNA noncoding sequence data of Asmussen and Chase (2001) and the morphology and cpDNA RFLP data of Uhl et al. (1995), the matrix was trimmed to include only genera with complete information on both sides of the partitions (45 genera for DNA sequence data and 33 genera for morphology and RFLP data). A copy of the data matrix is posted at http://cerc.columbia.edu/hahn/datasets.palm3gene.

Phylogenetic analyses used the maximum parsimony (MP) and maximum likelihood (ML) criteria implemented in PAUP* ver. 4.0b8 (Swofford, 2001) on a Power PC G3/350 with MacOS 8.6 and a Sun UltraSPARC 10/350 running Solaris 8.

Incongruence among data partitions was evaluated with the partition-homogeneity (PH) test (the incongruence length difference test of Farris et al., 1994) as implemented in PAUP* (Swofford, 2001). The PH test used 100 resamplings under the MP criterion with only variable characters included, all characters equally weighted, tree bisection-reconnection (TBR) branch swapping, and a maximum of 200 trees held in memory for each character resampled. Specific tests of data partition incongruence were conducted between all plastid and nuclear sequence data, between coding and noncoding cpDNA data, and between morphological and molecular data.

MP analyses were conducted on the 65-taxon data set for (1) 18S alone, (2) cpDNA coding data (*atp*B + *rbc*L), and (3) the combined three-gene data (*atp*B + *rbc*L + 18S). MP analyses were conducted on a reduced 45-taxon set by using (1) 18S data alone, (2) cpDNA coding sequence data, (3) all plastid sequence data (*atp*B + *rbc*L + *rps*16 intron + *trn*L-*trn*F spacer and intron), or (4) all sequence data (18S + cpDNA sequences). MP analyses on a further reduced 33-taxon dataset were conducted with (1) all molecular data (DNA sequence data plus the cpDNA RFLP data of Uhl et al., 1995) and (2) all molecular data plus the morphological data of Uhl et al. (1995). Because cpDNA RFLP and morphological data were not available for the outgroup taxa, the 33-taxon analyses were not rooted with these taxa but rather with a functional outgroup as determined from the 45- and 65-taxon analyses.

MP analyses used a heuristic search strategy with 10 random-order of taxon entry replicates, TBR branch swapping, saving all shortest trees at each step (MULPARS), and branch swapping on all trees saved at each step (STEEPEST descent). The MP analyses weighted all characters and character state transformations equally, scoring gaps as missing data. Tree searches for the partitioned 65-taxon 18S and *atp*B + *rbc*L matrices held a maximum of 5,000 trees. Full heuristic searches swapping on all shortest trees were performed on the 33- and 45-taxon matrices and the 65-taxon three-gene matrix.

Consensus trees and other results from the original publications were referenced as outlined above and used in comparisons with results from the current study. Relative support for each clade was assessed by MP bootstrap analysis (Felsenstein, 1985; Sanderson, 1995) with 1,000 pseudoreplicates of the data and TBR branch swapping in which a maximum of 200 trees were saved during branch swapping. Character statistics (consistency index,

CI; retention index, RI) were calculated with outgroups removed.

ML analyses were conducted on the MP trees to determine which tree(s) scored highest for an external optimality criterion and to estimate model parameters for ML tree searches. For initial evaluation of MP trees, a general time-reversible model was assumed (GTR; Lanave et al., 1984; equivalent to the REV of Yang, 1994a) with a fixed proportion of invariable sites and gamma-distributed rate variation across sites free to vary (I + Γ; Gu et al., 1995). All parameter values were estimated from the data.

A randomly sampled subset of 25 trees from each of the 65-taxon MP searches was evaluated for likelihood model fitting. All 45-taxon 18S and cpDNA sequence data types (coding, noncoding, and combined) were evaluated against the respective 45-taxon trees. Several taxa with long branches in the 18S ML trees (relative to the cpDNA ML trees) were removed to examine whether their presence affected estimates of base composition and the proportion of invariable sites (Steele et al., 2000). Because of the size of the dataset and computational limits of existing software (e.g., PAML; Yang, 1997), mixed-model likelihood analyses were not conducted on the combined 18S + *atp*B + *rbc*L data or the MP trees.

The Shimodaira–Hasegawa (SH) test as implemented in PAUP* (Shimodaira and Hasegawa, 1999; Swofford, 2001) was used to identify trees for which likelihood scores were not significantly worse (at $P < 0.05$) than scores for the optimal ML trees. The RELL method of Kishino et al. (1990) was used for bootstrap replications (Shimodaira and Hasegawa, 1999; Goldman et al., 2000).

Trees with the greatest log-likelihood scores for each of the character/taxon sets were analyzed to choose the simplest acceptable model of substitution (Swofford et al., 1996; Frati et al., 1997; Sullivan and Swofford, 1997; Sullivan et al., 1997; Naylor and Brown, 1998). Five models of base substitution were compared: (1) Jukes–Cantor (JC; Jukes and Cantor, 1969), (2) F81 (Felsenstein, 1981), (3) K2P (Kimura, 1980), (4) HKY-85 (Hasegawa et al., 1985), and (5) GTR. Among-site rate variability was modeled under the following assumptions: (1) all sites were equal in rate (E); (2) invariable sites were a fixed proportion (estimated from the data), with equal rates across sites being free to vary (I; Hasegawa et al., 1985); (3) rate variation was fitted to a discrete gamma distribution (with eight rate categories) across all sites (Γ; Yang, 1994b); and (4) a fixed proportion of invariable sites had gamma-distributed rate variation across sites free to vary (I + Γ; Gu et al., 1995).

Significance of differences in likelihood for the different models (when the simpler model was nested within the more complex model) was assessed with a likelihood-ratio test (e.g., Goldman, 1993; Yang et al., 1994; Whelan and Goldman, 1999). Using the most complex model as a starting point (GTR + I + Γ), each simpler model was tested for a significantly lower likelihood with the goal of using the simplest acceptable model for subsequent tree searches.

Once the appropriate substitution model was identified, all optimal trees and models of change for each of the character/taxon sets were used as starting points for ML tree searches in an iterative procedure (Swofford et al., 1996; Sullivan et al., 1997; Mallatt and Sullivan, 1998). Heuristic searches were conducted, starting with the highest likelihood MP trees followed by TBR branch swapping to completion. If the resulting tree from the first search iteration was different from the starting trees, all model parameter values were reestimated on the new tree and a new search was initiated holding the new parameter values fixed. This procedure was repeated until no new topologies were recovered. The significance of the difference in likelihood between all trees saved was tested with the SH test as described above. Bootstrap support for the ML trees was estimated using the FASTSTEP option in PAUP*.

RESULTS

Sequence Analysis

The three genes sequenced in this study showed relatively little variation in length, base composition, or distribution of indels among the palms sampled (Table 2). Comparisons of the 65- and 45-taxon datasets produced almost identical results for these variables. To facilitate comparison with previously published data on noncoding cpDNA, only the values for the 45-taxon dataset are presented.

Sequences of *atp*B had one 6-base deletion in *Trachycarpus*, whereas *rbc*L sequences had no indels within the coding stretch. For each

TABLE 2. Characteristics of the five DNA sequences used in this study. Values were calculated on the 45-taxon dataset with outgroups excluded. The long-branch taxa removed were *Arenga*, *Caryota*, *Corypha*, *Hyphaene*, *Roystonea,* and *Sabal*.

Sequence	Length analyzed (and total length)	Gap sites analyzed	Variable sites	Parsimony-informative sites	Range of *p*-distances	% GC for variable sites
18S	1,710	8	278 (16.3%)	158 (9.2%)	0.1–6.0%	50–66%
18S w/o long-branch taxa	1,710	7	212 (12.4%)	113 (6.0%)	0.1–4.1%	51–66%
*atp*B	1,515	6	100 (6.6%)	31 (2.0%)	0.1–1.1%	42–50%
*rbc*L	1,428	0	142 (9.9%)	57 (4.0%)	0.3–2.5%	45–52%
*rps*16	785 (1,556)	130	152 (19.4%)	47 (6.0%)	0.4–5.4%	43–49%
*trn*L-*trn*F	1,003 (1,337)	308	123 (12.3%)	42 (4.2%)	0.0–3.1%	39–49%

gene, the position of the first stop codon varied among species, particularly with *atp*B, thus resulting in some length variation. Only five gaps (two of 1 bp and three of 2 bp) were required to align the 18S sequences for the 65 palm genera; two additional gaps (one each of 1 bp and 2 bp) were required to align outgroups. The few indels found in the 18S data were easily aligned with alignments from previous monocot 18S studies (e.g., Hershkovitz et al., 1999; Chase et al., 2000).

Raw *p*-distances among taxa ranged from 0.1% to 6.0%, with 18S demonstrating the greatest and *atp*B the least maximum *p*-distances for the 45-taxon dataset (Table 2). Removal of only three long-branch taxa (*Arenga*, *Caryota*, and *Roystonea*) from the 18S comparisons reduced variable and parsimony-informative sites by ~25% and maximum *p*-distances by ~30%.

Base composition for variable sites in each of the three gene sequences was similar among taxa (Table 2); differences were not significant as determined by the χ^2 test (nonindependence for multiple comparisons with this test is ignored). None of the long-branch taxa in the 18S rDNA analyses showed a significantly heterogeneous base composition. cpDNA sequences showed relatively uniform AT-richness, whereas nuclear rDNA 18S sequences showed relatively uniform GC-richness. There was no significant difference in base composition among variable sites between coding and noncoding cpDNA sequences.

PH tests of the data identified incongruence ($P < 0.01$) between *atp*B + *rbc*L and 18S sequence data in the full 65-taxon set and between all cpDNA sequence data and 18S on the 45-taxon set ($P < 0.01$). Selective removal of numerous taxa from the 45-taxon set identified *Nypa* as responsible for most of the incongruence. PH tests on the 45-taxon data showed no significant heterogeneity among the different cpDNA data (coding and noncoding sequences, RFLP). For the 33-taxon set, morphological data were incongruent with all other datasets, whether combined or partitioned (all $P < 0.01$). Selective removal of taxa identified several that contributed to incongruence, including Caryoteae, Ceroxyloideae, and Iriarteae.

For all character/taxon combinations analyzed, model fitting on the relevant MP trees identified the GTR + I + Γ model as the simplest acceptable model. Likelihood-ratio tests rejected all simpler models ($P \ll 0.001$), whether substitution matrix or among-site rate parameters were involved. Exclusion of 18S long-branch taxa (*Arenga*, *Bentinckia*, *Borassus*, *Caryota*, *Corypha*, *Hyphaene*, *Roystonea*, and *Salacca*) did not change this result.

Removal of these long-branch taxa did influence estimates on the number of invariable sites and the among-site rate heterogeneity gamma shape parameter. For the 65-taxon analysis (outgroups excluded), PInvar was 54% but increased to 63% when the eight long-branch taxa were removed. The gamma shape parameter also changed from 0.39 to 0.43 when long-branch taxa were removed. Even greater differences were seen in the 45-taxon analysis (Table 3). Only minor differences were seen in the cpDNA values when these same taxa were removed.

For 18S data, ML model parameter estimates indicated more CT transitions than expected under an equal rates model (Table 3). In contrast to the effects on among-site rate estimates, removal of long-branch taxa had a relatively minor effect on substitution parameter estimates. Parameter estimates for cpDNA data indicated less bias between transition types but an greater rate

TABLE 3. Maximum parsimony tree statistics. CI, consistency index; RI, retention index. Outgroups have been removed from all calculations. Long-branch taxa removed in the 18S studies were *Arenga*, *Bentinckia*, *Borassus*, *Caryota*, *Corypha*, *Hyphaene*, *Roystonea*, *Sabal*, and *Salacca*. Simple sequence repeat and binary-coded gaps were removed from *trn*L-*trn*F data as described in text.

Dataset	No. Trees	No. Chars.	No. Inform. chars.	Tree length	CI	RI
65 taxa/18S	>5000	1710	190	691	0.535	0.612
65 taxa/18S no long-branch taxa	2601	1710	113	438	0.578	0.638
45 taxa/18S	2248	1710	158	534	0.592	0.599
45 taxa/18S no long-branch taxa	36	1710	96	344	0.625	0.607
65taxa/*atp*B+*rbc*L	>5000	2943	104	541	0.580	0.611
45 taxa/*atp*B+*rbc*L	292	2943	88	410	0.632	0.592
45 taxa/*atp*B+*rbc*L+*rps*16+*trn*L-*trn*F	606	4709	166	736	0.732	0.661
65 taxa/*atp*B+*rbc*L+18S	4209	4653	286	1280	0.534	0.577
45 taxa/*atp*B+*rbc*L+18S	22	4653	299	1197	0.631	0.575
45 taxa/*atp*B+*rbc*L+*rps* 16+ *trn*L-*trn*F+18S	32	6419	406	1667	0.684	0.596
33 taxa/sequence+cpDNA RFLP	29	6562	358	1245	0.682	0.651
33 taxa/all data	2	6603	393	1375	0.655	0.647

of AC transversions (presumably because of silent third-position AC transversions for isoleucine).

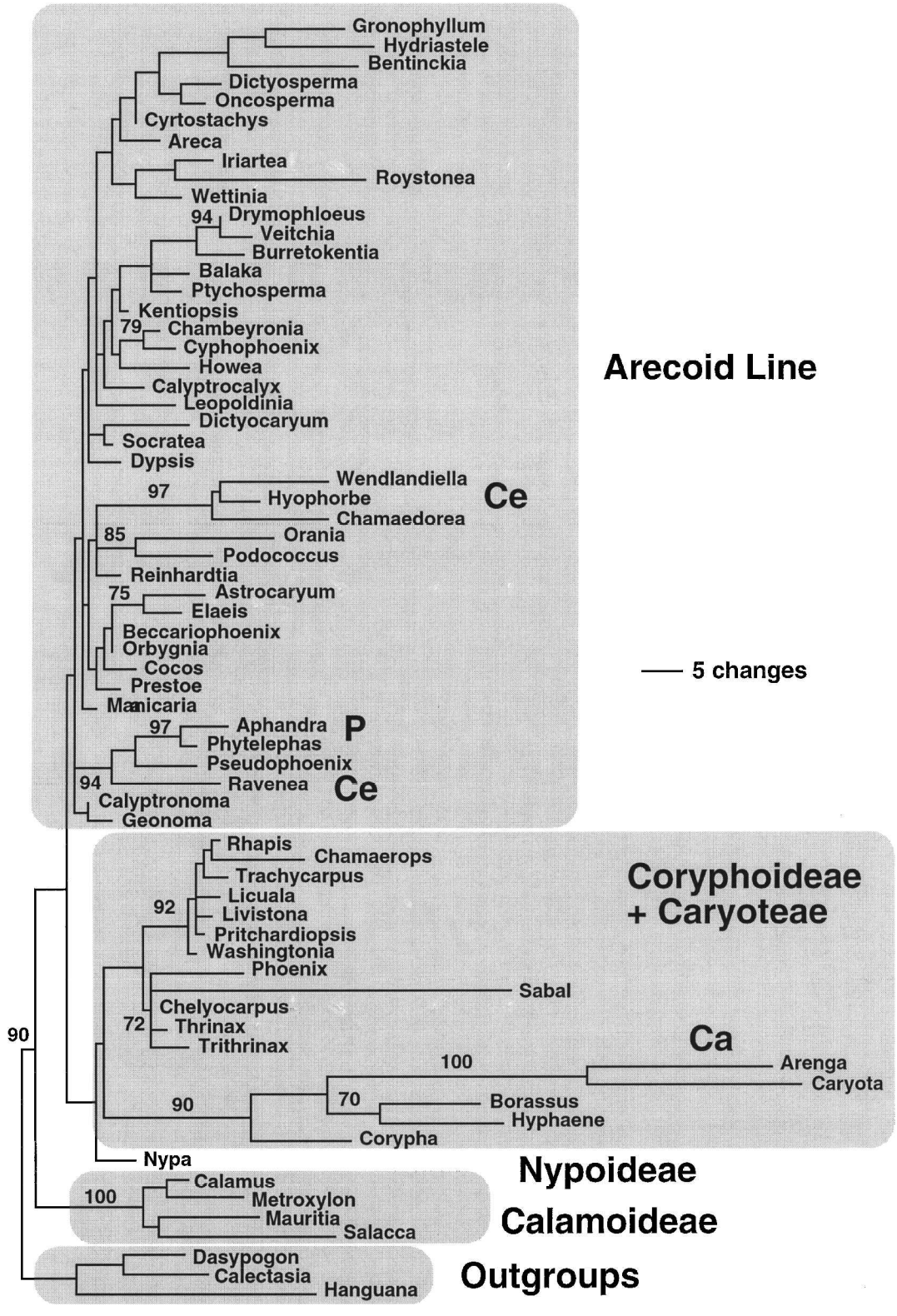
Phylogenetic Analysis

18S data.—MP tree searches of the 18S data for 65 palm genera were terminated at 5,000 shortest trees (L = 691, CI = 0.535, RI = 0.612). A strict consensus of these preserved significant structure with bootstrap support for many clades at >70%. Well-supported clades include Calamoideae, Phytelephantoideae, the three genera of Hyophorbeae (*Chamaedorea*, *Hyophorbe*, and *Wendlandiella*), the clade of Borasseae + Coryphinae + Caryoteae, and a clade of Livistoninae + Old World Thrinacinae. The clade of Coryphoideae + Caryoteae was monophyletic but not strongly supported. MP analysis of 18S data for the reduced 45-taxon set identified 2,248 shortest trees (L = 534, CI = 0.592, RI = 0.599). A strict consensus of these identified the same overall topology with similar patterns of support.

ML analysis of the 65-taxon/18S data recovered a topology (Fig. 1) showing many similarities to previously published cpDNA trees (e.g., Asmussen and Chase, 2001) but differing in several regards. In the 18S tree, *Nypa* is sister to Coryphoideae, tribe Iriarteae is paraphyletic and embedded among various members of tribe Areceae, Geonomeae is unresolved relative to the remainder of the Arecoid Line, and *Phoenix* is part of a clade containing Livistoninae and Thrinacinae. However, very few of the 18S placements are well supported by bootstrap analysis. The 18S ML tree for the 45-taxon dataset maintained the essential features of the 65-taxon ML tree.

Branch lengths were noticeably longer for several taxa in the 18S ML trees. The most visible long-branch taxa are the two Caryotoid palms (*Arenga* and *Caryota*), the two members of Borasseae (*Borassus* and *Hyphaene*), and *Sabal*. Because these taxa sometimes group with each other in the MP trees, we examined the possibility of long-branch attraction by sequentially removing each long-branch taxon in various combinations. Although this strategy greatly reduced the number of MP trees, in no case did removal of any taxon influence the relative resolution of any other taxon or group of taxa in the analysis.

cpDNA data.—MP searches of the 65-taxon/*atp*B + *rbc*L dataset were terminated at 5,000 trees (L = 541, CI = 0.580, RI = 0.611). The strict consensus retained some resolution, mostly within the Coryphoid clade, where relationships were similar but not identical to those uncovered with 18S data. Several other groups were supported as monophyletic by bootstrap analysis including Calamoideae and Phytelephantoideae, and tribes Cocoeae, Geonomeae, Hyophorbeae, and Iriarteae. However, relationships at the base of the family were almost completely unresolved. Analysis of the 45-taxon data recovered 292 MP trees (L = 410, CI = 0.632, RI = 0.592). A strict consensus displayed the same general topology as the 65-taxon *atp*B + *rbc*L consensus tree.



The *atp*B + *rbc*L ML tree was not well resolved and demonstrated many short branches with little or no ML bootstrap support (Fig. 2). None of the basal nodes are supported, and many taxa supported as monophyletic in MP analyses are not recoved in the ML tree (e.g., Cocoeae, Iriarteae).

MP analysis of combined cpDNA sequence data (*atp*B + *rbc*L + *rps*16 intron + *trn*L-*trn*F intron and spacer) for the 45-taxon dataset recovered 606 trees (L = 736, CI = 0.732, RI = 0.661). A strict consensus retained considerable structure, and support for resolution is seen throughout most of the tree. The parsimony score for the ML tree obtained with these data (Fig. 3) was actually one step shorter than the corresponding MP trees and was highly congruent with the MP consensus tree. Calamoideae and Nypoideae are unresolved at the base of the tree but the Coryphoid and Arecoid groups are together supported as monophyletic. The Coryphoid group itself is not monophyletic but the Arecoid Line is.

Within the Coryphoid clade, the position of the Neotropical Thrinacinae is the biggest difference from the 18S trees. Relationships within the Arecoid Line clade are much better resolved than in the 18S ML and MP trees or in the *atp*B + *rbc*L ML trees. Phytelephantoideae is not supported as monophyletic but Cocoeae, Geonomeae, Hyophorbeae, and Iriarteae are. Additionally, a clade of the Indo-Pacific pseudomonomerous Areceae genera (*Areca*, *Balaka*, *Cyphophoenix*, *Cyrtostachys*, *Gronophyllum*, *Hydriastele*, *Kentiopsis*, and *Veitchia*) plus the Malagasy *Dypsis* is identified.

Combined data.—Despite the incongruence between the 18S and cpDNA data, MP analyses of combined data were performed to compare properties of the different datasets. MP analysis of the combined *atp*B + *rbc*L + 18S data for the 65-taxon set identified 4,209 shortest trees (L = 1208, CI = 0.534, RI = 0.577), the strict consensus being resolved mostly among Coryphoids. Analysis of these data for the 45-taxon set recovered only 22 trees (L = 1197, CI = 0.631, RI = 0.575) with the strict consensus (Fig. 4) showing considerable resolution. Subfamily Calamoideae is the first branching lineage followed by an unresolved group with Nypoideae, two groups of Coryphoids, and the Arecoid Line. Each of these is well supported as monophyletic but the relationships among them are uncertain. The most notable difference between these trees and the cpDNA sequence trees is the position of the Neotropical Thrinacinae.

MP analysis of all available molecular sequence data (*atp*B + *rbc*L + *rps*16 intron + *trn*L-*trn*F intron and spacer + 18S) increased the number of trees only slightly to 32 (L = 1667, CI = 0.684, RI = 0.596), the consensus being very similar to that derived from *atp*B + *rbc*L + 18S only.

MP analysis of all available molecular data (cp and nuclear DNA sequence + cpDNA RFLP) on the 33-taxon dataset recovered 29 trees (L = 1,245, CI = 0.682, RI = 0.651), the consensus (Fig. 5a) being similar to that for the all-sequence data trees. MP analysis of all available molecular and morphological data combined identified only two trees (Fig. 5b; L = 375, CI = 0.655, RI = 0.647). These were very similar to the combined molecular data trees.

Discussion

The primary results of this study demonstrate that relationships among the major lineages of palms can be better resolved through a combination of increased character sampling and characterization of the different data forms. Although incongruence is detectable among some partitions of the data analyzed and many of the patterns of relationship identified are only weakly supported, the general trend is toward a more fully resolved and well-supported estimate of phylogenetic relationships for the Palmae.

Character Sample Size

Several authors have discussed the relative merits of increasing character data

FIGURE 1. Maximum likelihood reconstruction for the 18S sequence data for 65 genera of palms plus three outgroups (GTR + I + Γ model, -log likelihood = 6,992.98; AC= 0.665, AG = 3.129, AT = 0.741, CG = 0.998, CT = 9.801, GT = 1, I = 0.520, Γ = 0.384). Parameter values were estimated with outgroups. Bootstrap proportions >60% are listed on the branches. The four major lineages of palms are identified (Calamoideae, Nypoideae, Coryphoideae + Caryoteae, and the Arecoid Line). Subfamilies Ceroxyloideae (*Chamaedorea*, *Hyophorbe*, *Pseudophoenix*, *Ravenea*, and *Wendlandiella*), and Phytelephantoideae (*Aphandra* and *Phytelephas*) are identified as Ce and P, respectively.

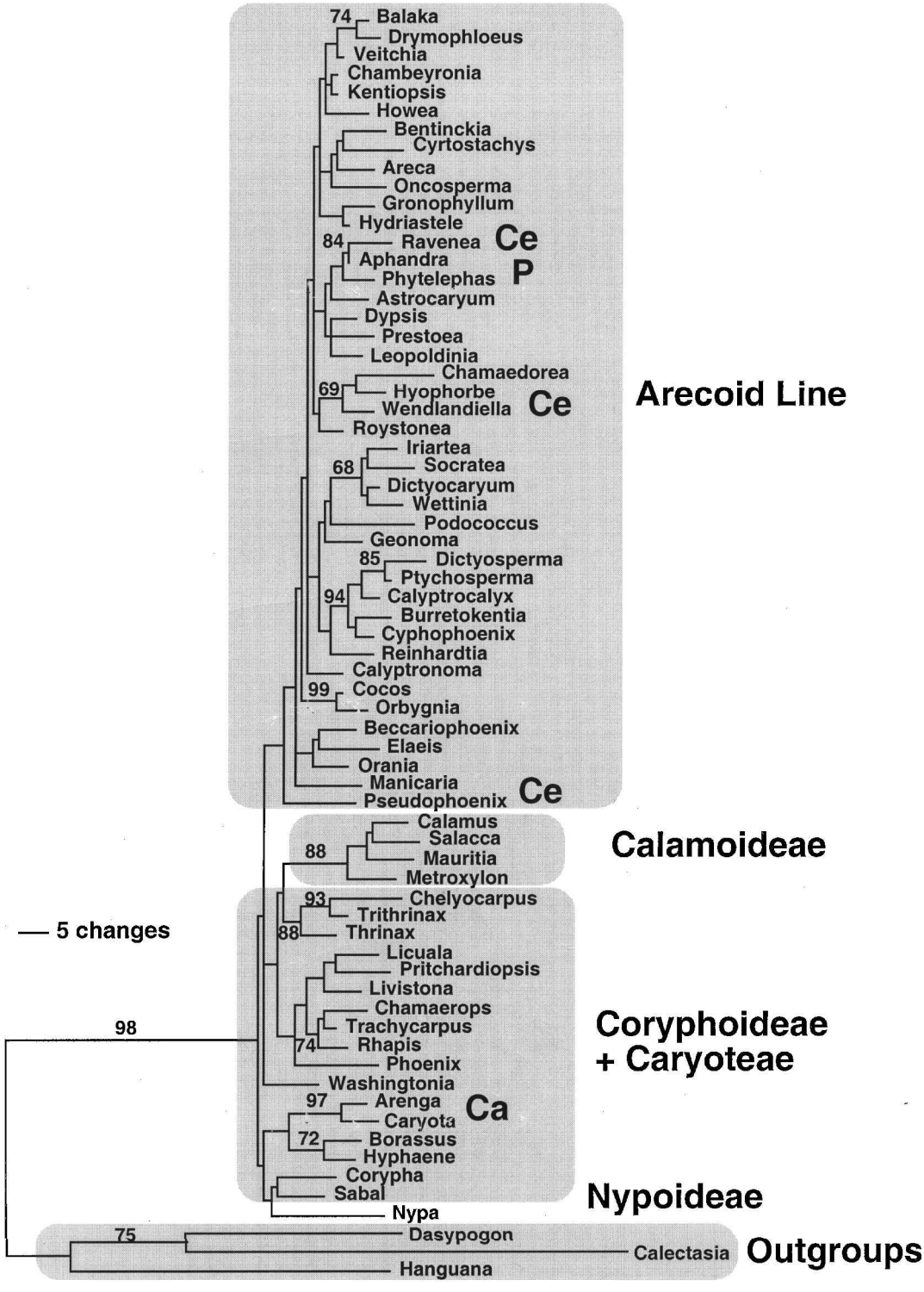


FIGURE 2. Maximum likelihood reconstruction for *atp*B + *rbc*L data for 65 genera of palms plus three outgroups (GTR + I + Γ model, –log likelihood = 9,439.44; AC = 2.034, AG = 4.618, AT = 0.425, CG = 0.981, CT = 5.309, GT = 1, I = 0.637, Γ = 0.518). Parameter values were estimated with outgroups. Bootstrap proportions >60% are listed on the branches. Higher taxa are labeled as in Figure 1.

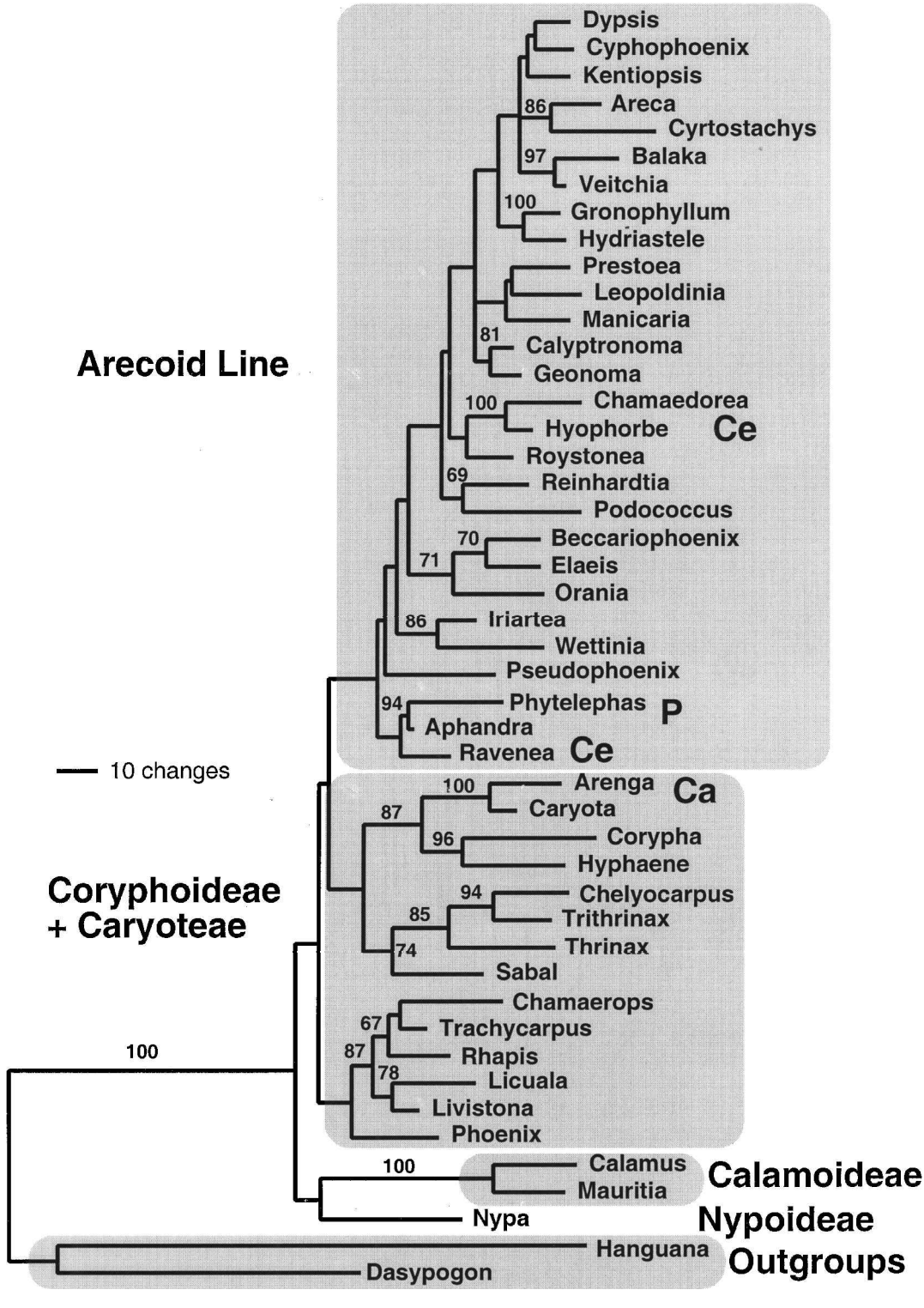


FIGURE 3. Maximum likelihood reconstruction for the combined cpDNA sequence data (*atp*B, *rbc*L, *rps*16, and *trn*L-*trn*F) dataset for 45 genera of palms (GTR + I + Γ model, -log likelihood = 13,321.03; AC = 1.575, AG = 3.297, AT = 0.556, CG = 0.975, CT = 3.506, GT = 1, I = 0.528, Γ = 0.678). Parameter values were estimated with outgroups. Bootstrap proportions >60% are listed on the branches. Higher taxa are labeled as in Figure 1.

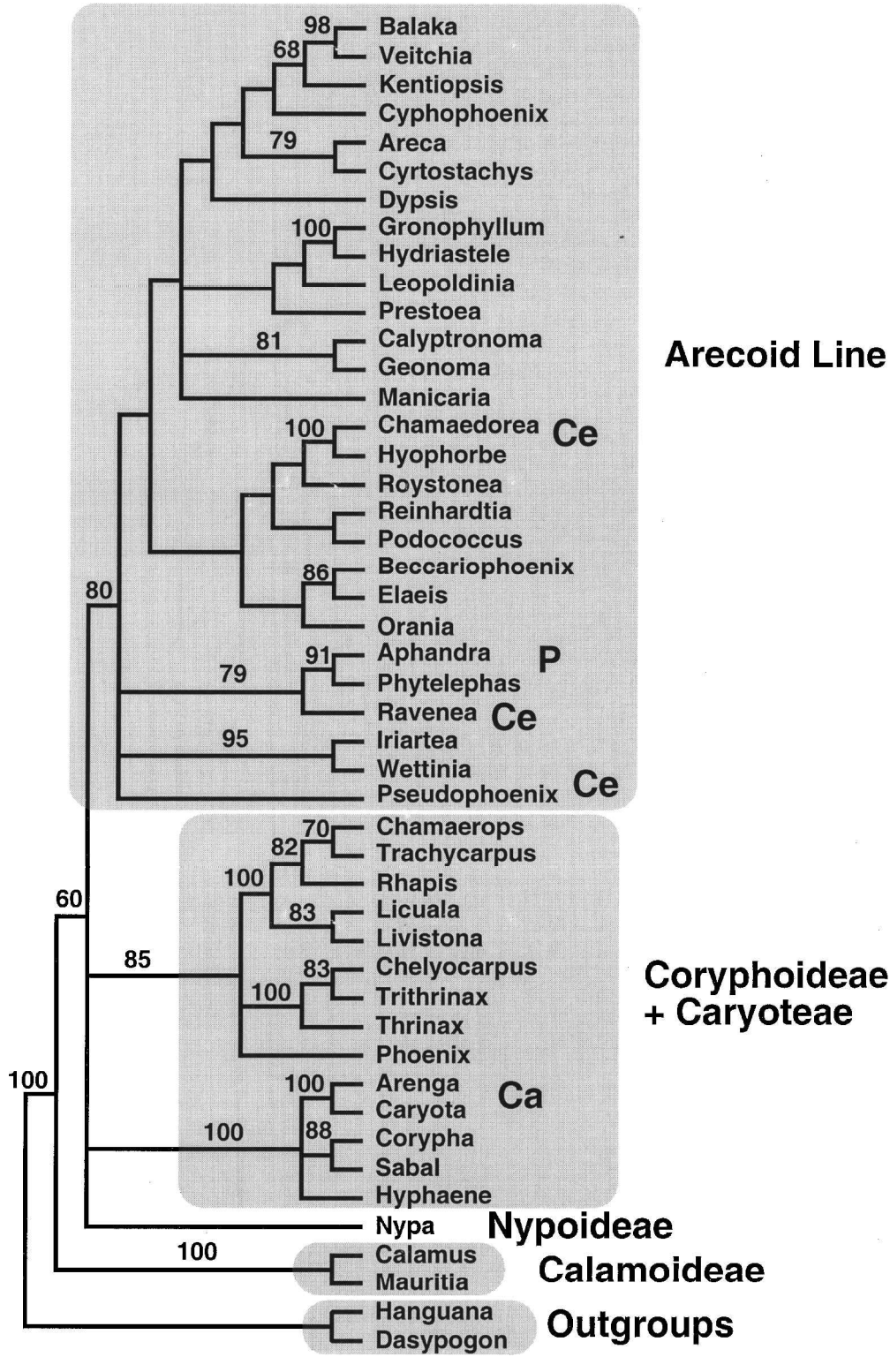


FIGURE 4. Strict consensus of 32 MP trees for the combined molecular sequence data (*at*pB, *rbc*L, *rps*16, *trn*L-*trn*F, and 18S) for 64 taxa of palms. Bootstrap proportions >60% are labeled on the branches. Higher taxa are labeled as in Figure 1.

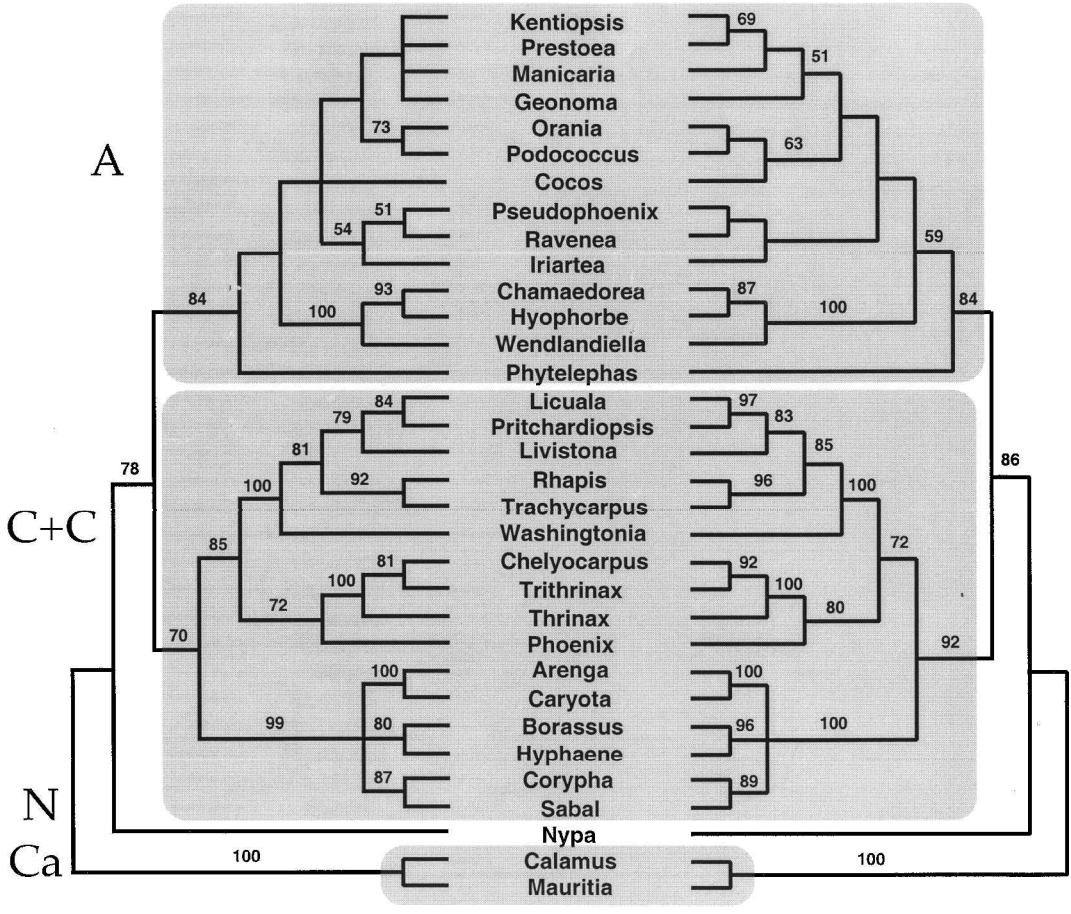


FIGURE 5. Strict consensus of MP trees for the reduced 33-taxon analyses. Bootstrap proportions >50% are labeled on branches. On the left, consensus of 29 trees (L = 1,245, CI = 0.682, RI = 0.651) from the combined molecular data analyses. On the right, consensus of two trees (L = 1,375, CI = 0.655, RI = 0.647) from analysis of the combined morphological and molecular data. The four major lineages of palms are identified as Ca = Calamoideae, N = Nypoideae, C + C = Coryphoideae + Caryoteae, and A = the Arecoid Line.

versus increasing taxon representation (e.g., Graybeal, 1998; Halanych, 1998; Bremer et al., 1999). For the palms, increased character sampling seems to be more important in that a comparison of results for the full (65-taxon) and reduced (45- and 33-taxon) datasets suggests little difference in core topology but a considerable increase in support as more characters are added. Furthermore, the presence of long branches in the family is noted only with 18S data and for only a few taxa. Long-branch attraction (sensu Hendy and Penny, 1989) does not seem to be responsible for grouping of the Caryoteae and Borasseae because that grouping is seen with both 18S (with long branches) and cpDNA data (with comparatively average branch lengths). Relationships among the basal branches of the family, however, may be obscured by long-branch attraction, and additional study is needed to resolve the branching pattern among the Calamoid, Nypoid, and Coryphoid lineages.

The effects of character sample sizes on phylogenetic analysis are widely recognized. Character data must be sufficient in number as well as appropriate in quality. A large number of variable characters may lead to poor phylogenetic resolution because of homoplasy, whereas inadequate numbers of character data, no matter what their quality, will never provide enough evidence for estimates of phylogenetic relationships.

Conflicting or homoplastic character data are seen in almost every phylogenetic dataset, but the lack of adequate signal is probably a more important reason for the poorly resolved estimates of relationship in the Palmae—particularly at the base of the family and at the base of the larger Coryphoid and Arecoid Line clades, where relationships remain uncertain.

Morphological data have been analyzed in the palm family (Uhl et al., 1995) but overall phylogenetic resolution was poor. Much of the lack of resolution was attributable to a lack of unambiguous character information because most of the characters exhibited homoplasy. Additionally, polymorphisms for many characters may have influenced resolving power. Nonetheless, the reported homoplasy indices for the morphological analyses (CI = 0.34, RI = 0.75) are about average for the number of taxa and characters analyzed (Sanderson and Donoghue, 1989). With the total number of character states (41 with 10 multistate for a minimum of 52 steps) significantly fewer than the number of taxa analyzed (67), a lack of resolution is not surprising.

Notoriously slow rates of molecular evolution in palms have also limited the number of characters available for analysis (e.g., Wilson et al., 1990; Gaut et al., 1992). The initial studies of Wilson et al. (1990) clearly demonstrated this, and all subsequent molecular sequences have delivered the same result: a lack of adequate character variation to unambiguously support phylogenetic resolution for the number of taxa sampled. For example, the cpDNA intergenic spacer/intron studies of Asmussen et al. (2000) produced only 110 parsimony-informative sites for the 64 taxa surveyed. Average intergeneric *p*-distances ranged from 0.1% to 5.6% for the cpDNA regions studied—values usually seen for *interspecific* comparisons of the same regions in other taxa.

As first seen in the cpDNA RFLP studies of Wilson et al. (1990), an additional problem exists with palm molecular data: Of the variation observed, most is confined to only a few taxa. For example, in the cpDNA studies of Uhl et al. (1995), a total of 287 steps was recorded in the most-parsimonious trees for the 143 characters analyzed. Of the total tree length reported in that study, ~37% is confined to four clades accounting for only 18 of the 67 terminal taxa analyzed: *Nypa*, Calamoideae (2 spp.), Hyophorbeae (14 spp.), and Caryoteae (1 sp.). If the genera of Hyophorbeae that were sampled more than once were to be represented by only a single species each, this fraction changes to ~36% of the variation being confined to only 14 of the 67 taxa sampled. The cpDNA sequence studies of Asmussen et al. (2000) showed an even stronger pattern with these taxa. Of a total tree length of 255 steps in the trees recovered by these authors 180 steps (71%) were confined to only 14 of the 65 taxa sampled.

The number of characters analyzed in the current analysis (4,653 new characters with 286 parsimony-informative characters among palms) is much greater than the number analyzed in any previous analysis of palms, which has contributed to the increases in phylogenetic resolution obtained among the 65 genera studied. Nonetheless, many points of weak or conflicting resolution remain. Datasets of this size have been adequate to resolve relationships for equivalent number of taxa in other plant families (e.g., Rubiaceae; Bremer et al., 1999), but the specific distributions of variation and branch lengths were more limited in the palm study. This result suggests that at least some aspects of character evolution may be limiting potential phylogenetic resolution.

Congruence Among Character Types

Arguments for and against combined and partitioned analyses are numerous (e.g., Bull et al., 1993; Farris et al., 1994; de Queiroz et al., 1995; Huelsenbeck et al., 1996; Swofford et al., 1996; Ballard et al., 1998) and form the basis for some of the exploratory analyses in the current study. Partitioned analyses of the data were conducted because of (1) the possibility of erroneous homology assessment in sequence alignments (e.g., 18S and cpDNA noncoding regions), (2) heterogeneity in patterns of evolution for nuclear rDNA 18S sequences (e.g., Hershkovitz et al., 1999), and (3) known or suspected patterns of homoplasy in morphological data (Dransfield et al., 1990; Uhl et al., 1995).

In the current study, incongruence between data partitions was centered on only a few taxa. Morphological data were incongruent with all molecular data as a result of apparent morphological homoplasy for Caryoteae, Ceroxyloideae, Iriarteae, and Thrinacinae. Among molecular data,

incongruence was found between 18S and cpDNA data mostly because of the position of *Nypa*. Several other points of incongruence were present between the recovered 18S and cpDNA trees, but most of the differences were poorly supported and suggest limited rather than conflicting signal.

Differences between morphology and molecules are not too surprising, given that the morphological homoplasy within the family is well documented (e.g., Dransfield et al., 1990; Uhl et al., 1995). Unfortunately, many aspects of palm taxonomy are founded on seemingly homoplastic patterns of similarity (Uhl and Dransfield, 1987; Dransfield and Uhl, 1998). Characters such as carpel fusion, floral arrangement, leaf division, and branching pattern were formerly considered strong indicators of relationship but subsequently have been shown to be subject to convergent evolution (e.g., Baker et al., 2000). In fact, some of the most dramatic differences seen between the taxonomies of Moore (1973) and Dransfield and Uhl (1988) center on difficulties in homology determination for these same structures.

The most visibile difference between molecular and morphological phylogenies is with the Caryotoid palms (*Arenga*, *Caryota*, and *Wallichia*). This group is placed either close to Coryphoideae when leaf anatomy is emphasized (as subfamily Caryotoideae sensu Moore, 1960, 1973) or within Arecoideae when floral arrangement is stressed (as tribe Caryoteae sensu Dransfield and Uhl, 1998). Phylogenetic studies offer mixed results on these alternative hypotheses of relationship.

Wilson et al. (1990) demonstrated a long branch for *Caryota* with cpDNA RFLP data and their analysis grouped the genus close to a paraphyletic Coryphoideae. The morphological study of Uhl et al. (1995) suggested an Arecoideae affinity for Caryoteae (represented by *Wallichia*), but their cpDNA RFLP study placed the genus squarely among Coryphoideae. More recent cpDNA studies (e.g., Asmussen and Chase, 2001) have placed Caryoteae within Coryphoideae. While nuclear malate synthase intron data (Lewis and Doyle, 2001) are equivocal on the placement of Caryoteae. The current study firmly resolved Caryoteae with Borasseae of Coryphoideae with both cpDNA and nuclear 18S data. A synthesis of these results supports the grouping of Caryotoid palms with Coryphoideae and suggests that at least some morphological characters are homoplastic, given the consistent pattern displayed by a range of molecular data types.

The pattern of incongruence between morphology and most molecular data sets is stable regarding the position of Caryoteae, but several points of incongruence are present among the different molecular datasets. Specifically, the positions of *Nypa*, Geonomeae, Iriarteae, and Neotropical Thrinacinae differ between cpDNA and 18S trees. Several factors may be responsible but most important may be some properties of 18S. Despite its widespread use in molecular phylogenetics (e.g., Hillis and Dixon, 1991; Hershkovitz et al., 1999), 18S has demonstrated incongruence with many other datasets (e.g., Huelsenbeck, 1997; Stiller and Hall, 1999) and the current study may represent yet another example of this.

For palms, 18S demonstrates CT transitionsabout three times more frequent than AG transitions and 10–15 times as frequent as transversions (Table 4). This observation is common in ribosomal RNA genes where either C or U can form bonds with G, thus leaving fewer constraints on the CT class of transitions than on the AG class. Removing long-branch taxa reduced the compositional heterogeneity between species but the overall pattern remained for both the 65- and 45-taxon sets.

Base composition heterogeneity for 18S that contributed to erroneous phylogenetic resolution in other taxa (e.g., Steel et al., 2000) does not seem to be present in Palmae. For the palms, base composition is relatively even across taxa (50–66%), and long-branch taxa are well within this range (Table 2).

Among-site rate variation is more extreme with 18S than with cpDNA data and does change with removal of long-branch taxa (Table 4). In particular, the percentage of estimated invariable sites (PInvar) was greater when long-branch taxa were removed (0.633 in the 65-taxon set vs. 0.542 when long-branch taxa were included). This is about as severe as the difference seen in the Streptsiptera example discussed by Steele et al. (2000) and may be responsible for some of the variation in resolution between analyses seen in the current study. Further investigation of the evolutionary properties of these taxa is necessary to

TABLE 4. Maximum likelihood model parameter estimates. PInvar = proportion of invariable sites. Alpha = gamma distribution shape parameter. Calculations are based on the GTR + I + Γ model with eight rate categories for the shape parameter. Outgroup taxa are removed for all parameter calculations. Long-branch taxa removed in the 18S studies were *Arenga*, *Bentinckia*, *Borassus*, *Caryota*, *Corypha*, *Hyphaene*, *Roystonea*, and *Salacca*.

Dataset	Log likelihood	CT	AG	AT	AC	CG	GT	PInvar	Alpha
65 taxa/18S	6,611.33	10.457	3.477	0.822	0.605	1.007	1	0.542	0.388
65 taxa/18S w/o long-branch taxa	5,181.10	10.349	3.841	1.044	0.723	0.977	1	0.633	0.431
45 taxa/18S	5,580.42	11.251	3.665	0.994	0.619	0.981	1	0.550	0.440
45 taxa/18S w/o long-branch taxa	4,561.41	10.747	3.695	1.224	0.693	0.988	1	0.660	0.491
65 taxa/*atp*B+*rbc*L	7,929.00	3.332	3.370	0.319	1.746	0.832	1	0.753	0.456
65 taxa/*atp*B+*rbc*L w/o long-branch taxa	7,373.57	3.423	3.096	0.267	1.744	0.773	1	0.763	0.475
45 taxa/*atp*B+*rbc*L	7,021.71	3.477	3.783	0.373	1.903	0.959	1	0.769	0.484
45 taxa/*atp*B+*rbc*L w/o long-branch taxa	6,571.28	3.546	3.771	0.293	1.893	0.926	1	0.788	0.542
45 taxa/*atp*B+*rbc*L + *rps*16 + *trn*L-*trn*F	11,709.60	2.829	2.744	0.464	1.469	0.986	1	0.634	0.654
45 taxa/*atp*B+*rbc*L + *rps*16 + *trn*L-*trn*F w/o long-branch taxa	10,891.91	2.807	2.632	0.357	1.425	0.863	1	0.656	0.665

fully understand the nature of incongruence among datasets.

Phylogenetic Results

The results of the current study indicate a general trend toward a stable estimate of phylogenetic relationships for the Palmae. In the larger-scale 65-taxon analyses, the data available (*atp*B, *rbc*L, and 18S) were insufficient to resolve relationships with any degree of support. Nonetheless, the recovered phylogenies are compatible with those found in the various 45-taxon analyses, which are much better resolved and supported. The 33-taxon topologies are even better resolved but lack several critical taxa and are more subject to the effects of incongruence between molecular and morphological data.

As such, a comparison of results from the 45- and 33-taxon trees offers the best reference for phylogenetic inference on palms. Of the different 45-taxon analyses, the two that provide the best-supported resolution are the cpDNA sequence ML tree (Fig. 3) and the complete DNA sequence MP consensus tree (Fig. 4). The two 33-taxon trees are presented in Figure 5.

Synthesizing the results of the various phylogenetic studies of palms identified four main groups of palms: (1) a monophyletic Calamoideae sister to the remainder of the family, (2) Nypoideae as the next branching element, (3) a monophyletic Coryphoideae plus the Caryotoid palms, and (4) a monophyletic Arecoid Line sensu Moore (i.e., the Arecoideae minus Caryoteae, Ceroxyloideae, and Phytelephantoideae of Dransfield and Uhl, 1998).

The basal branching pattern in palms is still not certain but the weight of evidence suggests that Calamoideae branched first, followed by Nypoideae (e.g., Fig. 4). Both of these taxa have deep fossil records and are associated with comparatively long branches in most available phylogenetic reconstructions. Although cpDNA data are relatively consistent in supporting Calamoideae as the first branching lineage, nuclear data and morphological information are equivocal and introduce some uncertainty (e.g., Fig. 4). A particular concern is the possibility of long-branch attraction among these early diverging lineages. Some evidence for this is found with 18S data in the present study but further investigation is required to verify long-branch attraction and to properly ascertain the basal branching order within the family.

Monophyly of Coryphoideae has been questioned by Dransfield et al. (1990) but that study did not consider the Caryotoid palms directly. Given that all molecular studies to date group the Caryotoid palms with Corypoideae, a morphological synapomorphy of induplicate leaves could be used to define a clade of Coryphoideae + Caryoteae. Molecular data are equivocal, however, on the overall monophyly of this

group. In the current study, monophyly for the group was found with 18S data (Fig. 1) and with combined data in the 33-taxon analyses (Fig. 5) but not in any of the cpDNA-only analyses. Asmussen and Chase (2001) recovered a similar result in their studies of cpDNA sequence data. Monophyly was supported in the combined cpDNA plus 18S analyses but the clade also included *Nypa*. As with the question of basal branching order, monophyly of Coryphoideae + Caryoteae is still incompletely answered.

Although monophyly of the Coryphoid clade is not strongly supported in all analyses, relationships within the Coryphoideae + Caryoteae are relatively stable. The Old World Thrinacinae groups with Livistoninae in most analyses and *Corypha* is usually associated with Borasseae and Caryoteae. Only the position of Neotropical Thrinacinae was unstable among the different analyses. The positions of *Sabal* and *Phoenix* were stable in the current analysis but differed from placements observed in other studies of palm relationships. In the current study, *Sabal* usually grouped with *Corypha*, and *Phoenix* was resolved with Livistoninae. In contrast, previous studies of cpDNA data (e.g., Uhl et al., 1995; Asmussen and Chase, 2001) resolved *Sabal* with Neotropical Thrinacinae and placed *Phoenix* at the base of the Coryphoid assemblage. Although different species of these genera were used in the different studies, other factors seem to be involved.

The grouping of Caryoteae with Coryphoideae has been observed in all cpDNA molecular studies to date (e.g., Uhl et al., 1995; Asmussen et al., 2000) and represents the most noticeable difference between molecular and morphological trees. The resolution of Caryoteae + Coryphoideae with nuclear 18S data in the current serves as additional corroboration of this result. Although Caryoteae show very long branches in the 18S trees and group with other long-branch taxa such as *Borassus* and *Hyphaene*, there is no evidence that long-branch attraction is responsible for the resolution achieved in the current study.

The fourth main group of palms, the Arecoid Line, is well supported as monophyletic in most of the analyses. Within the clade, tribes Cocoeae, Geonomeae, Hyophorbeae, and Iriarteae and subfamily Phytelephantoideae are usually identified as monophyletic. Additionally, the IndoPacific + Malagasy clade identified in the current analysis is also recovered in most other molecular studies. However, resolution among the major lineages of the Arecoid Line is poor and in need of much additional study. These results have been observed in other phylogenetic analyses (e.g., Asmussen and Chase, 2001) but the current study provides additional support and resolution.

In summary, estimates of palm phylogenetic relationships based on combined morphological and molecular data have shown increased resolution and support relative to previously published palm phylogenies. Although incongruence between molecules and morphology and between cpDNA and nuclear DNA is evident, the abundance of cpDNA data and their relatively simple substitution properties seem to make cpDNA estimates of palm phylogeny the most reliable at the present time.

ACKNOWLEDGMENTS

I thank Liz Zimmer, John Kress, and the Laboratory of Molecular Systematics of the Smithsonian Institution for support and laboratory access; Chuck Hubbuch and Scott Zona of the Fairchild Tropical Garden and Larry Noblick of the Montgomery Foundation for access to living collections; John Dransfield, Bill Baker, and Connie Asmussen for unpublished data and many useful comments; Dave Swofford for use of prerelease versions of PAUP*; and Dick Olmstead for helpful comments in the early stages of this study. Chris Simon, Peter Lockhart, and two anonymous reviewers provided many useful comments that greatly improved this manuscript. This work was supported by National Science Foundation grant NEB 9303266 and a grant from the Smithsonian Institution Scholarly Studies program.

REFERENCES

ASMUSSEN, C. B., W. J. BAKER, AND J. DRANSFIELD. 2000. Phylogeny of the palm family (Arecaceae) based on *rps*16 intron and *trn*L-*trn*F plastid DNA sequences. Pages 525–535 *in* Systematics and evolution of monocots (K. L. Wilson and D. A. Morrison, eds.). CSIRO, Collingwood, Australia.

ASMUSSEN, C. B., AND M. L. CHASE. 2001. Coding and noncoding plastid DNA in palms. Am. J. Bot. 88:1103–1117.

BAKER, W. J., C. B. ASMUSSEN, S. C. BARROW, J. DRANSFIELD, AND T. A. HEDDERSON. 1999. A phylogenetic study of the palm family (Palmae) based on chloroplast DNA sequences from the *trn*L-*trn*F region. Plant Syst. Evol. 219:111–126.

BAKER, W. J., J. DRANSFIELD, AND T. A. HEDDERSON. 2000. Phylogeny, character evolution, and a new classification of the Calamoid palms. Syst. Bot. 25:297–322.

BALLARD, J. W. O., M. K. THAYER, A. F. NEWTON, JR., AND E. R. GRISMER. 1998. Data sets, partitions, and

characters: Philosophies and procedures for analyzing multiple data sets. Syst. Biol. 47:367–396.

BREMER, B., R. K. JANSEN, B. OXELMAN, M. BACKLUND, H. LANTZ, AND K.-J. KIM. 1999. More characters or more taxa for a robust phylogeny—Case study from the coffee family (Rubiaceae). Syst. Biol. 48:413–435.

BULL, J. J., J. P. HUELSENBECK, C. W. CUNNINGHAM, D. L. SWOFFORD, AND P. J. WADDELL. 1993. Partitioning and combining data in phylogenetic analysis. Syst. Biol. 42:384–397.

BULT, C., M. KÄLLERSJÖ, AND Y. SUH. 1992. Amplification and sequencing of 16/18S rDNA from gel-purified total plant DNA. Plant Mol. Biol. Rep. 10:273–284.

CHASE, M. W., D. E. SOLTIS, P. S. SOLTIS, P. J. RUDALL, M. F. FAY, W. J. HAHN, S. SULLIVAN, J. JOSEPH, T. J. GIVNISH, K. J. SYTSMA, AND J. C. PIRES. 2000. Higher-level systematics of the monocotyledons: An assessment of current knowledge and a new classification. Pages 3–26 *in* Systematics and evolution of monocots (K. L. Wilson and D. A. Morrison, eds.). CSIRO, Collingwood, Australia.

COOPER, A., AND R. A. FORTEY. 1998. Evolutionary explosions and the phylogenetic fuse. Trends Ecol. Evol. 13:151–156.

DE QUIEROZ, A., M. J. DONOGHUE, AND J. KIM. 1995. Separate versus combined analysis of phylogenetic evidence. Annu. Rev. Ecol. Syst. 26:657–681.

DONOGHUE, M. J., AND M. J. SANDERSON. 1992. The suitability of molecular and morphological evidence in reconstructing plant phylogeny. Pages 340–368 *in* Molecular systematics of plants (P. S. Soltis, D. E. Soltis, and J. J. Doyle, eds.). Chapman and Hall, New York.

DRANSFIELD, J., I. K. FERGUSON, AND N. W. UHL. 1990. The Coryphoid palms: Patterns of variation and evolution. Ann. Mo. Bot. Gard. 77:802–815.

DRANSFIELD, J., AND N. W. UHL. 1986. An outline of a classification of the palms. Principes 30:3–11.

DRANSFIELD, J., AND N. W. UHL. 1998. Palmae. Pages 306–389 *in* Families and genera of vascular plants: Vol. 4. Flowering plants. Monocotyledons (K. Kubitzki, ed.). Springer-Verlag, Berlin.

EYRE-WALKER, A., AND B. S. GAUT. 1997. Correlated rates of synonymous site evolution across plant genomes. Mol. Biol. Evol. 14:455–460.

FARRIS, J. S., M. KÄLLERSJÖ, A. G. KLUGE, AND C. BULT. 1994. Testing significance of incongruence. Cladistics 10:315–319.

FELSENSTEIN, J. 1978. Cases in which parsimony and compatibility methods will be positively misleading. Syst. Zool. 27:401–410

FELSENSTEIN, J. 1981. Evolutionary trees from DNA sequences: A maximum likelihood approach. J. Mol. Evol. 17:368–376.

FELSENSTEIN, J. 1985. Confidence limits on phylogeny: An approach using the bootstrap. Evolution 39:783–791.

FRATI, F., C. SIMON, J. SULLIVAN, AND D. L. SWOFFORD. 1997. Evolution of the mitochondrial cytochrome oxidase II gene in Collembola. J. Mol. Evol. 44: 145–158.

GAUT, B. S., B. R. MORTON, B. C. MCCAIG, AND M. T. CLEGG. 1996. Substitution rate comparisons between grasses and palms: Synonymous rate differences at the nuclear gene *Adh* parallel rate differences at the plastid gene *rbc*L. Proc. Natl. Acad. Sci. USA 93:10274–10279.

GAUT, B. S., S. V. MUSE, W. D. CLARK, AND M. T. CLEGG. 1992. Relative rates of nucleotide substitution at the *rbc*L locus in monocotyledonous plants. J. Mol. Evol. 35:292–303.

GOLDMAN, N. J. 1993. Statistical tests of models of DNA substitution. J. Mol. Evol. 36:182–198.

GOLDMAN, N. J., J. P. ANDERSON, AND A. G. RODRIGO. 2000. Likelihood-based tests of topologies in phylogenetics. Syst. Biol. 49:652–670.

GRAYBEAL, A. 1998. Is it better to add taxa or characters to a difficult phylogenetic problem? Syst. Biol. 47: 9–17.

GU, X., Y.-X. FU, AND W.-H. LI. 1995. Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. Mol. Biol. Evol. 12:546–557.

HAHN, W. J. 1999. Molecular systematic studies of the Palmae. Mem. N.Y. Bot. Gard. 83:47–60.

HAHN, W. J., AND K. J. SYTSMA. 2000. Molecular systematics and biogeography of the Southeast Asian genus *Caryota* (Palmae) Syst. Bot. 24:558–580.

HALANYCH, K. M. 1998. Lagomorphs misplaced by more characters and fewer taxa. Syst. Biol. 47:138–146.

HARLEY, M. M., AND W. J. BAKER. 2001. Pollen aperture morphology in Arecaceae: Application within phylogenetic analyses and a summary of the fossil record for palm-like pollen. Grana 40:45–77.

HASEGAWA, M., H. KISHINO, AND T. YANO. 1985. Dating of the human–ape split by a molecular clock of mitochondrial DNA. J. Mol. Evol. 21:160–174.

HENDY, M. D., AND D. PENNY. 1989. A framework for the quantitative study of evolutionary trees. Syst. Zool. 38:297–309.

HERSHKOVITZ, M., W. J. HAHN, AND E. A. ZIMMER. 1999. Ribosomal DNA evolution and plant systematics. Pages 268–326 *in* Advances in plant molecular systematics (P. Hollingworth, R. Bateman, and R. Gornall, eds.). Taylor and Francis, London.

HILLIS, D. M., AND M. T. DIXON. 1991. Ribosomal DNA: Molecular evolution and phylogenetic inference. Q. Rev. Biol. 66:411–453.

HOOT, S. B., A. CULHAM, AND P. R. CRANE. 1995. The utility of *atp*B gene sequences in resolving phylogenetic relationships: Comparison with *rbcL* and 18S ribosomal DNA sequences in the Lardizabalaceae. Ann. Mo. Bot. Gard. 82:194–207.

HUELSENBECK, J. P. 1995. Performance of phylogenetic methods in simulation. Syst. Biol. 44:17–48.

HUELSENBECK, J. P. 1997. Is the Felsenstein zone a fly trap? Syst. Biol. 46: 69–74.

HUELSENBECK, J. P., J. J. BULL, AND C. W. CUNNINGHAM. 1996. Combining data in phylogenetic analysis. Trends Ecol. Evol. 11:152–158.

HUELSENBECK, J. P., AND D. M. HILLIS. 1993. Success of phylogenetic methods in the four-taxon case. Syst. Biol. 42:247–264.

JUKES, T. H., AND C. H. CANTOR. 1969. Evolution of protein molecules. Pages 21–123 *in* Mammalian protein metabolism (H. M. Munro, ed.). Academic Press, New York.

KIM, J. 1996. General inconsistency conditions for maximum parsimony: Effects of branch lengths and increasing numbers of taxa. Syst. Biol. 45:363–374.

KIMURA, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. 16:111–120.

KISHINO, H., T. MIYATA, AND M. HASEGAWA. 1990. Maximum likelihood inference of protein phylogeny and the origin of chloroplasts. J. Mol. Evol. 30:151–160.

KLUGE, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38:7–25.

KUSUKAWA, N., R. UEMORI, K. ASACA, AND I. KATO. 1990. Rapid and reliable protocol for direct sequencing of material amplified by the polymerase chain reaction. BioTechniques 9:66–72.

LANAVE, C., G. PREPARATA, C. SACCONE, AND G. SERIO. 1984. A new method for calculating evolutionary substitution rates. J. Mol. Evol. 20:86–93.

LEWIS, C., AND J. J. DOYLE. 2001. Phylogenetic utility of the nuclear gene malate synthase in the Palm family (Arecaceae). Mol. Phylogenet. Evol. 19:409–420.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83–103.

MALLATT, J., AND J. SULLIVAN. 1998. 28S and 18S rDNA sequences support the monophyly of lampreys and hagfishes. Mol. Biol. Evol. 15:1706–1718.

MOORE, H. E., JR. 1960. A new subfamily of palms—The Caryotoideae. Principes 4:102–117.

MOORE, H. E., JR. 1973. The major groups of palms and their distribution. Gentes Herb. 11:27–141.

NAYLOR, G. J. P., AND W. M. BROWN. 1998. Amphioxus mitochondrial DNA, chordate phylogeny, and the limits of inference based on comparisons of sequences. Syst. Biol. 47:61–76.

OLMSTEAD, R. G., H. J. MICHAELS, K. M. SCOTT, AND J. D. PALMER. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. Ann. Mo. Bot. Gard. 79:249–265.

POE, S. 1998. Sensitivity of phylogeny estimation to taxonomic sampling. Syst. Biol. 47:18–31.

POE, S., AND D. L. SWOFFORD. 1999. Taxon sampling revisited. Nature 398:299–300.

SANDERSON, M. J. 1995. Objections to bootstrapping phylogenies: A critique. Syst. Biol. 44:299–320.

SANDERSON, M. J., AND M. J. DONOGHUE. 1989. Patterns of variation in levels of homoplasy. Evolution 43:1781–1795.

SHIMODAIRA, H., AND H. HASEGAWA. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Mol. Biol. Evol. 16:1114–1116.

SOLTIS, D. E., P. S. SOLTIS, M. W. CHASE, M. E. MORT, D. C. ALBACH, M. ZANIS, V. SAVOLAINEN, W. J. HAHN, S. B. HOOT, M. F. FAY, M. AXTELL, S. M. SWENSEN, K. C. NIXON, AND J. S. FARRIS. 2000. Angiosperm phylogeny inferred from a combined data set of 18S rDNA, *rbcL*, and *atp*B sequences. Bot. J. Linn. Soc. 133:381–461.

STEELE, M. A., D. HUSON, AND P. J. LOCKHART. 2000. Invariable sites models and their use in phylogeny reconstruction. Syst. Biol. 49:225–232.

STEVENSON, D. W., AND LOCONTE, H. 1995. Cladistic analysis of monocot families. Pages 543–578 *in* Monocotyledons: Systematics and evolution (P. J. Rudall, P. Cribb, D. F. Cutler, and C. J. Humphries, eds.). Royal Botanic Gardens, Kew, London.

STILLER, J. W., AND B. D. HALL. 1999. Long-branch attraction and the rDNA model of early eukaryotic evolution. Mol. Biol. Evol. 16:1270–1279.

SULLIVAN, J., J. A. MARKERT, AND C. W. KIRKPATRICK. 1997. Phylogeography and molecular systematics of the *Peromyscus aztecus* species group (Rodentia: Muridae) inferred using parsimony and likelihood. Syst. Biol. 46:426–440.

SULLIVAN, J., AND D. L. SWOFFORD. 1997. Are guinea pigs rodents? The importance of adequate models in molecular phylogenetics. J. Mammal. Evol. 4:77–86.

SWOFFORD, D. L. 2001. PAUP*. Phylogenetic analysis using parsimony (*and other methods), version 4. Sinauer, Sunderland, Massachusetts.

SWOFFORD, D. L., G. J. OLSEN, P. J. WADDELL, AND D. M. HILLIS. 1996. Phylogenetic inference. Pages 407–514 *in* Molecular systematics, 2nd edition (D. M. Hillis, C. Moritz, and B. K. Mable, eds.). Sinauer, Sunderland, Massachusetts.

TAYLOR, B., AND A. POWELL. 1982. Isolation of plant DNA and RNA. Focus 4:4–6.

UHL, N. W., AND J. DRANSFIELD. 1987. Genera Palmarum: A classification of palms based on the work of Harold E. Moore, Jr. Allen Press, Lawrence, Kansas.

UHL, N. W., AND J. DRANSFIELD. 1999. Genera Palmarum after ten years. Mem. N.Y. Bot. Gard. 83:245–253.

UHL, N. W., J. DRANSFIELD, J. I. DAVIS, M. A. LUCKOW, K. S. HANSEN, AND J. J. DOYLE. 1995. Phylogenetic relationships among palms: Cladistic analyses of morphological and chloroplast DNA restriction site variation. Pages 623–661 *in* Monocotyledons: Systematics and evolution (P. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries, eds). Royal Botanic Gardens, Kew, London.

WHELAN, S., AND N. GOLDMAN. 1999. Distributions of statistics used for the comparison of models of sequence evolution in phylogenetics. Mol. Biol. Evol. 16:1292–1299.

WILSON, M. A., B. GAUT, AND M. T. CLEGG. 1990. Chloroplast DNA evolves slowly in the palm family (Arecaceae). Mol. Bol. Evol. 7:303–314.

YANG, Z. 1994a. Estimating the pattern of nucleotide substitution. J. Mol. Evol. 39:105–111.

YANG, Z. 1994b. Phylogenetic analysis using parsimony and likelihood methods. J. Mol. Evol. 39:294–307.

YANG, Z. 1997. PAML: A program package for phylogenetic analysis by maximum likelihood. CABIOS 13:555–556.

YANG, Z., N. GOLDMAN, AND A. FRIDAY. 1994. Comparison of models for nucleotide substitution used in maximimum likelihood phylogenetic estimation. Mol. Biol. Evol. 11:316–324.

YODER, A. D., J. A. IRWIN, AND B. A. PAYSEUR. 2001. Failure of the ILD to determine data combinability for slow loris phylogeny. Syst. Biol. 50:408–424.

ZURAWSKI, G., B. PERROT, W. BOTTONLEY, AND P. R. WHITFELD. 1981. The structure of the gene for the large subunit of ribulose-1,5-bisphosphate carboxylase from spinach chloroplast DNA. Nucleic Acids Res. 14:3251–3270.

Received 3 February 2001; accepted 13 September 2001
Associate Editor: Peter Lockhart