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Phlogeny and Biogeography of the Prayer Plant Family

Linda M. Prince
Rancho Santa Ana Botanic Garden

W. John Kress
Smithsonian Institution

PHYLOGENY AND BIOGEOGRAPHY OF THE PRAYER PLANT FAMILY: GETTING TO THE ROOT PROBLEM IN MARANTACEAE

LINDA M. PRINCE[1,3] AND W. JOHN KRESS[2]

[1]*Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711-3157, USA;*
[2]*National Museum of Natural History, Department of Botany, MRC-166, Smithsonian Institution,
Washington, D.C. 20013-7012, USA*
[3]*Corresponding author (linda.prince@cgu.edu)*

ABSTRACT

Marantaceae are the second largest family in the order Zingiberales, with approximately 31 genera and 535 species. Earlier studies based on morphological and molecular characters could not confidently determine the relationships among major lineages of the family, nor could they identify the basal branch of the family tree. Phylogenetic analyses of DNA sequence data from all three genomic compartments (chloroplast: *mat*K, *ndh*F, *rbc*L, *rps*16 intron, and *trn*L–*trn*F intergenic spacer; mitochondrion: *cox*1; nucleus: ITS region and the 5′-end of 26S) for a restricted set of taxa were conducted under parsimony criteria to define the root node and to assess geographical distribution patterns. Our results support the recognition of five major lineages, most of which are restricted to a single geographical region (tropical America, tropical Africa, or tropical Asia). The phylogenies and character reconstructions (Fitch parsimony optimization, Bremer ancestral areas, and DIVA) support an African origin for the family, followed by a minimum of two dispersal events to the New World tropics and four or more dispersal events to the Asian tropics. Less likely are two alternative hypotheses: (1) vicariance of a western Gondwanan group (the Americas and Africa) followed by several dispersals to Asia and Africa, or (2) an American origin followed by several dispersals to Africa and Asia. The low specific diversity in Africa may be due to higher extinction rates as a result of shrinking lowland tropical forests during the Tertiary.

Key words: character evolution, Marantaceae, phylogeny, systematics.

INTRODUCTION

The family Marantaceae includes 31 genera and ca. 535 species distributed throughout warm temperate and tropical regions of the world (Andersson 1998), with 14 genera in the New World, 11 in Africa, and 8 in Southeast Asia. *Halopegia* K. Schum. is the only transcontinental genus with three representatives in Africa and one in Southeast Asia. Species distributions are significantly skewed with the vast majority of the species (ca. 450) restricted to the New World. The numbers of species listed below generally follow Andersson (1998), but may not reflect the current estimates of diversity for some genera.

New World taxa (14 genera/ca. 450 spp.) include the most species-rich genus of the family *Calathea* G. F. W. Meyer with as many as 300 species. Also found in the New World are *Ctenanthe* Eichler with ca. 10 spp., *Hylaeanthe* A. M. E. Jonker & Jonker (5–6 spp.), *Ischnosiphon* Körn. (ca. 35 spp.), *Maranta* L. (ca. 25 spp.), *Monophyllanthe* K. Schum. (1–2 spp.), *Monotagma* K. Schum. (37 spp.), *Pleiostachya* K. Schum. (2 spp.), *Saranthe* (Regel & Körn.) Eichler (5–10 spp.), *Stromanthe* Sonder (10–15 spp.), and *Thalia* L. (5–7 spp.). *Thalia* is restricted to the New World tropics except for a single species (*T. geniculata* L.) that is naturalized in both Africa (Andersson 1981) and India (Sijimol et al. 2000). The three monotypic genera from this region are *Koernickanthe* L. Andersson, *Myrosma* L. f., and *Sanblasia* L. Andersson. At least one genus (*Calathea*) has been shown to be polyphyletic and should be divided into two genera (Prince and Kress in press).

The African genera include *Afrocalathea* K. Schum. (monotypic), *Ataenidia* Gagnep. (monotypic), *Halopegia* (2 African spp.), *Haumania* J. Léonard (2 spp.), *Hypselodelphys* (K. Schum.) Milne-Redh. (4 spp.), *Marantochloa* Brogn. ex Gris (ca. 15 spp.), *Megaphrynium* Milne-Redh. (4 spp.), *Sarcophrynium* K. Schum. (ca. 3 spp.), *Thalia* (1 sp., introduced), *Thaumatococcus* Benth. (monotypic), and *Trachyphrynium* Benth. (monotypic), which were all revised in the 1950s by Milne-Redhead (1950, 1952). A few new African species and subspecies of *Marantochloa* have been described (D'Orey 1981; Dhetchuvi 1996) and phylogenetic relationships within some genera are currently being investigated (A. Ley pers. comm.). As stated above, the genus *Halopegia* occurs in both Africa (2 spp.) and Asia (1 sp. from Indonesia).

The Asian taxa (8 genera/ca. 47 spp.) are the least understood, but are currently under investigation using a combination of molecular and morphological methodologies (Suksathan and Borshenius pers. comm.). For tropical Asia, Andersson (1998) lists *Cominsia* Hemsl. (1 sp.), *Donax* Lour. (3–4 spp.), *Halopegia* (1 sp. in Asia), *Monophrynium* K. Schum. (2–3 spp.), *Phacelophrynium* K. Schum. (ca. 6 spp.), *Phrynium* Willd. (ca. 20 spp.), *Schumannianthus* Gagnep. (2 spp.), and *Stachyphrynium* K. Schum. (ca. 10 spp.). The number of species recognized will likely increase and generic circumscriptions of *Phacelophrynium, Phrynium,* and *Schumannianthus* will require modification based on the results of recent investigations using molecular data (Prince and Kress in press; P. Suksathan and F. Borchsenius pers. comm.).

The family has been divided into two tribes based on the number of fertile locules: Maranteae with one fertile locule, and Phrynieae with three fertile locules per ovary (Petersen 1889; Loesener 1930a). The results of Andersson (1998), Andersson and Chase (2001), and Prince and Kress (in press) suggest the classifications based on number of fertile locules do not adequately reflect phylogenetic relationships in the family.

Andersson (1998) published an informal classification based on an investigation of a number of morphological, anatomical, and biochemical characters. He recognized five groups plus five genera of uncertain affinity. His *Phrynium* group was primarily Asian and included *Monophrynium, Phacelophrynium, Phrynium, Stachyphrynium,* and the African genus *Ataenidia.* The *Donax* group was primarily African and included *Hypselodelphys, Megaphrynium, Sarcophrynium, Trachyphrynium,* and the Asian genera *Donax* and *Schumannianthus.* The *Myrosma* group was entirely American and included the genera *Ctenanthe, Hylaeanthe, Myrosma, Saranthe,* and *Stromanthe.* The *Calathea* group was composed entirely of the American taxa *Calathea, Ischnosiphon, Monotagma, Pleiostachya,* and *Sanblasia.* Finally, his *Maranta* group was a mixture of American (*Koernickanthe, Maranta, Monophyllanthe*) and African (*Afrocalathea, Marantochloa*) genera. The taxa of "uncertain affinity" included representatives from all three continents (Asia: *Cominsia* and *Halopegia*; Africa: *Halopegia, Haumania,* and *Thaumatococcus*; the Americas: *Thalia*).

The validity of the earlier formal and informal classifications was tested by Andersson and Chase (2001) using cladistic analyses of plastid *rps*16 intron data. Their data strongly refute the earlier classifications based on the number of fertile locules and provide support for portions of the Andersson (1998) informal classification. More recently, Prince and Kress (in press) also tested the validity of earlier classification systems using a different set of molecular characters from the plastid genome: the *trn*K intron and the *trn*L–*trn*F intergenic spacer region (IGS). Based on those results, a different informal classification of five major clades was proposed (Table 1).

A few genera (*Monophrynium, Monophyllanthe,* and *Sanblasia*) were not included in the analysis and therefore could not be placed in any of the five groups. Additionally, four potentially para- or polyphyletic genera were identified: *Calathea, Marantochloa, Phacelophrynium,* and *Schumannianthus.*

Biogeographic studies of Marantaceae are limited. Raven and Axelrod (1974) may have been the first to formally suggest a western Gondwanan origin for the family based on the distribution of members of the tribe Phrynieae in both South America and Africa. Biogeographical patterns were investigated by Andersson and Chase (2001) using results from Bremer's (1992) ancestral area methods. They found a rescaled gains-to-losses index of 1.0 for Africa, 0.5 for Asia, and 0.4 for the neotropics. From this, they concluded the primary center of diversity for Marantaceae is Africa. They also proposed three possible scenarios for the present distribution: (1) migration out of an ancestral area prior to the split-up of tropical continents, (2) long-distance dispersal after the split, or (3) a combination of scenarios 1 and 2. They were unable to discriminate between the various scenarios

Table 1. Informal classification of Marantaceae (Prince and Kress in press).

Clade name	Genera included	Geographic distribution
CALATHEA CLADE	*Calathea* (in two parts)	Americas
	Haumania	Africa
	Monotagma	Americas
	Pleiostachya	Americas
DONAX CLADE	*Cominsia*	Asia
	Donax	Asia
	Phrynium	Asia
	Phacelophrynium	Asia
	Schumannianthus dichotomus	Asia
	Thalia	Americas
MARANTA CLADE	*Ctenanthe*	Americas
	Halopegia	Africa, Asia
	Hylaeanthe	Americas
	Koernickanthe	Americas
	Maranta	Americas
	Myrosma	Americas
	Saranthe	Americas
	Schumannianthus virgatus	Asia
	Stromanthe	Americas
STACHYPHRYNIUM CLADE	*Afrocalathea*	Africa
	Ataenidia	Africa
	Marantochloa	Africa
	Stachyphrynium	Asia
SARCOPHRYNIUM CLADE	*Hypselodelphys*	Africa
	Megaphrynium	Africa
	Sarcophrynium	Africa
	Thaumatococcus	Africa
	Trachyphrynium	Africa
UNCERTAIN AFFINITY	*Monophrynium*	Asia
	Monophyllanthe	Asia
	Sanblasia	Americas

due to a lack of reliable dating for the different lineages. Biogeographical patterns were not investigated by Prince and Kress (in press) due to the lack of resolution and poor statistical support for the relationships among the five clades.

The goal of the current study is to utilize additional molecular data from all three genome compartments in order to: (1) better resolve relationships of the major clades, (2) provide better statistical support for the basal branches of the family phylogeny, and (3) infer biogeographic patterns. The genomic regions sampled include coding or structural regions (*cox*1, 5.8S, 26S, *mat*K, *ndh*F, and *rbc*L) that would be easy to align across all taxa, but which might provide too few characters to fully resolve relationships within Marantaceae. Noncoding regions (*rps*16 intron, *trn*L–*trn*F intergenic spacer) were included to provide additional resolution within Marantaceae, but proved difficult to align across the order.

MATERIALS AND METHODS

Taxa and DNA Regions Examined

Taxon sampling was predominantly from the living collections, many of which were wild collected, of the Smithsonian Institution Botany Research Greenhouses (Table 2). Sampling includes multiple representatives of each of Andersson's groups (1998) and representatives of all of the taxa

of "uncertain affinity," as well as the five clades of Prince and Kress (in press). A total of 25 Marantaceae taxa and one representative for each of the other seven families in Zingiberales were sampled. Sampling within Marantaceae included 26 species representing 19 genera as currently circumscribed. This represents approximately 61% of the genera and 6% of the species in the family. Taxa included in the analysis were chosen as exemplars of each of the five major clades identified by the earlier analysis of the family (Prince and Kress in press) that sampled 27 genera (87%) and 80 species (18%). Earlier studies provided two of the seven data sets (matK and trnL–trnF IGS) used here.

Genomic regions for analysis were selected to span a range of evolutionary rates. The regions sampled included:

(1) mitochondrion: cox1 (442 basepairs [bp], excluding intron and the co-conversion track; see explanation below)
(2) nucleus: 40 bp of 18S through ca. 240 bp of 26S (442 bp, excluding ITS)
(3) plastid: matK (1388 aligned bp), ndhF (2133 aligned bp), rbcL (1344 aligned bp), rps16 intron (1179 aligned bp), and trnL–trnF IGS (506 aligned bp)

The mitochondrial cox1 gene of many flowering plants includes a group 1 intron (Vaughn et al. 1995; Cho et al. 1998; Cho and Palmer 1999; Palmer et al. 2000). The intron encodes a homing endonuclease (Bonitz et al. 1980; Delahodde et al. 1989; Sargueil et al. 1990; Belfort and Roberts 1997) that cuts the gene in a precise position, leaving a small co-conversion track region within the coding portion of the gene as a result of DNA repair mechanisms. The co-conversion track (21 bp) was also excluded from all analyses. Data was also collected for the nad1 intron, rpl16 intron, and the trnE–trnT IGS, but the alignments were so ambiguous that these data sets were excluded from the analysis.

DNA Extraction, Amplification, and Sequencing

Total genomic DNAs were extracted, amplified, and cycle sequenced following methods described in Kress et al. (2002) using Applied Biosystems (Foster City, California, USA) Big-Dye III (1/8 concentration) chemistry Terminator Cycle Sequencing Ready Reaction Kit. Both new and previously published primers for PCR and sequencing were used (Table 3). Amplification for ndhF was done in two parts following the methods of Pires and Sytsma (2002). All new sequences were generated on an ABI 3100 Genetic Analyzer (Applied Biosystems) at Rancho Santa Ana Botanic Garden. Both strands were sequenced with a minimum of 95% overlap unless otherwise indicated (Table 2). DNA fragments were compiled and edited in Sequencher 3.1.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA), aligned manually in Se-Al vers. 2.0a11 (Rambaut 1996), and imported into PAUP* vers. 4.0b10 (Swofford 2002) for analysis. Alignment was relatively unambiguous for coding and other highly constrained regions (nuclear ribosomal genes, cox1, matK, ndhF, and rbcL), but not so for intergenic spacer regions and introns. Alignment for coding and structural regions required the insertion of a number of in-frame gaps. Gaps were also introduced to the IGS and intron matrices. Additionally, ambiguously aligned regions were present in the rps16 matrix (nine regions totaling 366 characters, or ca. 31% of the ma-

trix) and the trnL–trnF IGS matrix (six regions totaling 73 characters, or ca. 14% of the matrix). Analyses in which gaps were coded, ambiguous areas included, or protein-coding sequences translated to amino acid sequence will be presented elsewhere. Ambiguously aligned regions were excluded from all analyses presented here.

Phylogenetic Analyses

The families of the order can be divided into two groups, the "banana families" (Heliconiaceae, Lowiaceae, Musaceae, and Strelitziaceae) and the "ginger families" (Cannaceae, Costaceae, Marantaceae, and Zingiberaceae). Representatives of all families of Zingiberales were included in the analyses, with Musaceae representative Musella (Franch.) C. Y. Wu as the defined outgroup taxon for all "order" analyses based on earlier work by Kress et al. (2001). Additional analyses using only members of the ginger families were also conducted in which Siphonochilus J. M. Wood and M. Franks (Zingiberaceae) and Costus L. (Costaceae) were defined as outgroup taxa.

Maximum parsimony.—Separate and combined Fitch parsimony analyses (Fitch 1971) of all aligned sequence data (excluding ambiguously aligned regions) were conducted. Parallel analyses were run, one set using Musella as the designated outgroup, another with representatives of the banana families excluded, and Siphonochilus + Costus as the designated outgroup. For each analysis 500 random sequence addition replicates were conducted with tree-bisection-reconnection (TBR) branch swapping, saving all shortest trees.

Estimates of support.—Statistical support for branches was estimated via jackknife (JK: Penny and Hendy 1985) and Bayesian analyses. Jackknife estimates were run on all data sets using the fast JK methods with a large number (10,000) of replicates with 33% replacement (Mort et al. 2000). Bayesian analyses were conducted in MrBayes 3.0 (Huelsenbeck and Ronquist 2001) using three replicates of 5-million generations (sampling every 100 generations) for each of the individual data partitions and one combined data set as indicated in the maximum parsimony description above. The first 40 likelihood values (generations 1–4000) were included as the first data partition. Appropriate burn-in times for each analysis were determined by treating each successive half-million generations (= 5000 trees) as a data pool from which 40 likelihood tree values were randomly drawn, creating a total of 11 "generation" samples per Bayesian analysis. Generation sample likelihood values were subjected to a Bartlett's test for homogeneity of variance (Bartlett 1937a, b) to determine whether the data were heteroscedastic (as expected due to the inclusion of the first 40 data points). A Tukey-like multiple comparison test for differences among variances (Levy 1975a, b) was used to determine where the change from heteroscedasticity to homoscedasticity occurred. Only the homoscedastic data from the latter part of each MrBayes run were used to calculate posterior probabilities. In all cases at least the first 500,000 generations were discarded as burn-in.

Biogeographical Reconstruction

Studies by Kress and Specht (2006) provide an estimate of at least 95 millions of years ago (mya) for the divergence

Table 2. Taxa sampled to examine biogeographical patterns in Marantaceae with associated voucher and GenBank numbers.

Taxon	Voucher	GenBank accession numbers						
		*mat*K	*ndh*F	*rbc*L	*rps*16	*trn*L–F	*cox*1	18S–26S
Marantaceae								
Ataenidia conferta (Benth.) Milne-Redh.	*Kress 99-6572* (US)	AY140263	AY656082	AY656111	AY656134	AY140342	AY673012	AY673044
Calathea crotalifera S. Watson	*Kress 78-0899* (DUKE)	AY140268	AY656083	AY656112	AY656135	AY140347	AY673013	AY673045
Calathea metallica Planch. & Linden	*Kress 99-6586* (US)	AY140275	AY656084	AY656113	AY656136	AY140354	AY673014	AY673046
Calathea micans (L. Mathieu) Körn.	*Madison et al. 5486* (SEL)	AY140276	AY656085	AY656114	AY656137	AY140355	AY673015	AY673047
Calathea rufibarba Fenzl	*Kress 01-6856* (US)	AY140281	AY656086	AY656115	AY656138	AY140360	AY673016	AY673048
Calathea warscewiczii (L. Mathieu ex Planch.) Planch. & Linden	*Conde 8* (DUKE)	AY140285	AY656087	AF278773	AY656139	AY140364	AY673017	AY673049
Cominsia gigantea K. Schum.	ex hort. Lyon Arboretum (no voucher)	AY140286	AY656088	AY656116	AY656140	AY140365	AY673018	AY673050
Ctenanthe setosa Eichl.	*Kress 94-3684* (no voucher)	AY140288	AY656089	AY656117	AY656141	AY140368	AY673019	AY673051
Donax canniformis (G. Forst.) K. Schum.	*Kress 99-6527* (US)	AY140290	AY656090	AY656118	AY656142	AY140371	AY673020	AY673052
Haumania sp. #1	*Harris 6672* (RBGE)	AY140293	AY656091	AY656119	AY656143	AY140374	AY673021	AY673053
Hypselodelphys sp. #1	*Harris 6670* (RBGE)	AY140295	AY656092	AY656120	AY656144	AY140376	AY673022	AY673054
Ischnosiphon helenae L. Andersson	*Kress & Bordelon 01-6830* (US)	AY140298	AY656093	AY656121	AY656145	AY140379	AY673023	AY673055
Maranta bicolor Ker Gawl.	*Kress 94-3724* (US)	AY140302	AY656094	AF278768	AY656146	AY140385	AY673024	AY673056
Marantochloa purpurea (Ridley) Milne-Redh.	*Kress 78-0894* (US)	AY140306	AY125004	AF278769	AY656147	AY140389	AY673025	AY673057
Monotagma laxum (Poepp. & Endl.) K. Schum.	*Kress 99-6381 (US)*	AY140309	AY656095	AY656122	AY656148	AY140392	AY673026	AY673058
Phrynium pubinerve Blume	*Kress et al. 00-6798* (US)	AY140320	AY656096	AF656123	AY656149	AY140402	AY673027	AY673059
Pleiostachya pruinosa (Regel) K. Schum.	*Prince s. n.* 10 Jun 2001 (NCU)	AY140323	AY656098	AF378781	AY656151	AY140406	AY673029	AY673061
Saranthe sp. #1	*Kress 96-5737* (US)	AY140324	AY656099	AY656125	AY656152	AY140407	AY673030	AY673062
Sarcophrynium brachystachys (Benth.) K. Schum.	*Kress & Bordelon 01-7007* (US)	AF478912	AY656100	AY656126	AY656153	AY140408	AY673031	AY673063
Schumannianthus dichotomus (Roxb.) Gagnep.	ex hort. Lyon Arboretum (no voucher)	AY140327	AY656101	AY656127	AY656154	AY140410	AY673032	AY673064
Schumannianthus virgatus Rolfe	*Kress 99-6563* (US)	AY140328	AY656102	AY656128	AY656155	AY140411	AY673033	AY673065
Stachyphrynium jagorianum K. Schum.	*Kress 99-6319* (US)	AY140321	AY656097	AY656124	AY656150	AY140403	AY673028	AY673060
Thalia geniculata L.	*Wurdack 261* (NCU)	AY140337	AY656103	AY626129	AY656156	AY140420	AY673034	AY673066
Thaumatococcus daniellii (Bennet) Benth. & Hook. f.	*Kress 98-6288* (US)	AY140338	AY656104	AY626130	AY656157	AY140421	AY673035	AY673067
Trachyphrynium braunianum (K. Schum.) Baker	*Kress 01-6954* (US)	AY140339	AY656105	AY656131	AY656158	AY140422	AY673036	AY673068
OUTGROUP TAXA								
Cannaceae								
Canna paniculata Ruiz & Pav.	*Prince 95-211* (NCU)	AY140340	AY656106	AY656132	AY656159	AY140423	AY673037	AY673069
Costaceae								
Costus pulverulentus C. B. Presl.	*Turner s. n.* (no voucher)	AF478907	AY656107	AF278776	AY656160	AY140424	AY673038	AY673070

Table 2. Continued.

Taxon	Voucher	GenBank accession numbers						
		matK	ndhF	rbcL	rps16	trnLF	coxI	18S-26S
Heliconiaceae								
Heliconia irrasa R. R. Sm.	*Kress 76-0519* (DUKE)	AF478908	AY656108	AY378778	AY656161	AY140425	AY673039	AY673071
Lowiaceae								
Orchidantha fimbriata Holttum	*Atkins s. n.* Aug 1978 (DUKE)	AF478910	AY656109	AF243841	AY656163	AY140426	AY673041	AY434879
Musaceae								
Musella lasiocarpa (Franch.) C. Y. Wu	*Kress 94-3709* (US)	AF478909	AY124992	AF243844	AY656162	AY140428	AY673040	AY673072
Strelitziaceae								
Phenakospermum guyanense (Rich.) Endl.	*Kress 86-2099D* (US)	AF478911	AY124995	AF243845	AY656164	AY140427	AY673042	AY673073
Zingiberaceae								
Siphonochilus decorus (Druten) Lock	GH 01-135 US (no voucher)[a]	AF478894	AY656110	AY656133	AY656165	AY656166	AY673043	AF478793[b]

[a] Living material at Smithsonian Institution Botany Research Greenhouse, Suitland, Maryland, USA.
[b] Sequence extended for this study.

of Cannaceae and Marantaceae. It is possible that Marantaceae may owe their current pantropical distribution to dispersal or vicariance events. Fitch parsimony optimization (FPO: Fitch 1971) and Bremer ancestral areas analyses (AA: Bremer 1992) only allow for dispersal, while dispersal-vicariance analysis (DIVA: Ronquist 1996) allows for both vicariance and dispersal events. Since dispersal only and vicariance plus dispersal are possible explanations given the estimated divergence time, both methods were employed here.

Trimmed strict consensus trees from this and earlier studies (Andersson and Chase 2001; Prince and Kress in press) were used to generate a master tree matrix of 37 taxa representing 28 ingroup genera and three outgroup taxa (Cannaceae, Zingiberaceae, and Costaceae). Multiple representatives of the paraphyletic genera *Calathea* (6 taxa) and *Schumannianthus* (2 taxa) were included. All other genera of Marantaceae were treated as monophyletic, since prior studies failed to provide strong statistical support ($\geq$70% jackknife or bootstrap) of paraphyly. Source trees were redrawn in MacClade (Maddison and Maddison 2000) then imported into PAUP* for matrix translation. Master matrix construction and analysis were also implemented in PAUP*. This method is an indirect supertree approach (Ponstein 1966; Ragan 1992; Bininda-Emonds et al. 2002). Phylogenetic analysis of the supertree matrix was identical to those described above for maximum parsimony.

The strict consensus tree (of 12 shortest trees) from analysis of the supertree matrix was saved and arbitrarily dichotomized (two nodes affected; fully resolved trees required for mapping in MacClade). An alternative topology, with *Haumania* as part of the *Sarcophyrnium* clade was also evaluated. A data matrix of a single character (geographic distribution: Africa, America, or Asia) was mapped onto the two trees under either ACCTRAN or DELTRAN optimization using MacClade (FPO analysis). Outgroup taxa (Costaceae and Zingiberaceae) were coded as polymorphic (Africa, America, and Asia). The same fully resolved trees were used in the AA analyses, and in DIVA analyses (one with "max areas = 2" and one with "max areas = 3").

RESULTS

Phylogenetic Analyses of Seven DNA Regions

The large number of maximum parsimony and Bayesian posterior probability (PP) analyses conducted prohibits their full discussion here, but a summary of all results is provided (Tables 4, 5), including tree statistics for various maximum parsimony analyses, JK percentages, and PP values. The plastid data sets provided the majority of the clade resolution (Table 5). This was expected given the conservative regions sampled from the nuclear and mitochondrial genome. Similarly, the mitochondrial and nuclear data sets produced phylogenies with low resolution, low statistical support for internal branches, and some anomalous relationships within the ginger families.

The use of *Musella lasiocarpa* (Musaceae) or *Siphonochilus decorus* (Zingiberaceae), plus *Costus pulverulentus* (Costaceae) as the designated outgroup did not alter ingroup topology. The inclusion of the more distantly related taxa (the banana families representatives: *Musella lasiocarpa*,

Table 3. Primers used in the amplification of DNA from all three genomes to address phylogenetic relationships in Marantaceae.

Genomic region	Primer name	Primer sequence 5' to 3'	Description	Reference
*cox*1	445F	GCCATTCTGGAGGAGCAGTTGA	bp 254–275 of *Croton cox*1 (gene)	here (designed by K. J. Wurdack)
*cox*1	1146F	GCGATCAGGTGCTAAAGCTTATC	bp 950–972 of *Croton cox*1 (intron)	here (designed by K. J. Wurdack)
*cox*1	1203R	AAGTAGTCGTGCTGAATGTCGAATATG	bp 1024–1050 of *Croton cox*1 (intron)	here (designed by K. J. Wurdack)
*cox*1	1951R	CGGTGAAGTAGGCACGSGTATC	bp 1715–1736 of *Croton cox*1 (gene)	here (designed by K. J. Wurdack)
18S–26S	241R	CAGTGCCTCGTGGTGCGACA	bp 240–259 of *Zingiber* 26S	here (designed by K. J. Wurdack)
18S–26S	ITS 5a	TTATCATTTAGAGGAAGGAGAAGTCG	alternative to ITS 5 from White et al. 1990	here (designed by K. J. Wurdack)
18S–26S	5.8S–F	TCACGGCAACGGATATCTCGG	bp 9–29 of 5.8S	here (designed by L. M. Prince)
18S–26S	5.8S–R	ACGGGATTCTGCAATTCACAC	bp 70–90 of 5.8S	here (designed by L. M. Prince)
*mat*K	8R	AGCACAAGAAAGTGCAAG	complement of 8F from Steele and Vilgalys 1994	Steele and Vilgalys 1994
*mat*K	8Fa	TACTTCGACTTTCCTGTGCC	modification of 8F from Steele and Vilgalys 1994	here (designed by L. M. Prince)
*mat*K	5F	GGATCCTTTCATGCATT	see Steele and Vilgalys 1994	Steele and Vilgalys 1994
*mat*K	5Fa	CTCTATGGGTCTTCAAGGAT	bp 806–825 of tobacco *mat*K	here (designed by L. M. Prince)
*mat*K	5R	AGGATCCTTGAAAATCCATAGA	bp 807–828 of tobacco *mat*K	here (designed by L. M. Prince)
*mat*K	5Ra	TGATACCGAACATAATGCATG	bp 831–851 of tobacco *mat*K	here (designed by L. M. Prince)
*mat*K	mlF	GTTCAGTACTTGTGAAACGTT	bp 164–184 of tobacco *mat*K	here (designed by L. M. Prince)
*mat*K	trnK2R	AACTAGTCGGATGGAGTAG	see Steele and Vilgalys 1994	Steele and Vilgalys 1994
*mat*K	trnK1F	CTCAACGGTAGAGTACTCG	see Manos and Steele 1997	Manos and Steele 1997
*rbc*L	1370R	TCTCGTTCCATACTTCACAAGCAG	bp 1370–1393 of tobacco *rbc*L	here (designed by L. M. Prince)
*rbc*L	1F	ATGTCACCACAAACAGAGACTAAAG	bp 1–25 of tobacco *rbc*L	here (designed by L. M. Prince)
*rbc*L	481F	AGGTTGAACAAGTATGGTCGTC	bp 481–502 of tobacco *rbc*L	here (designed by L. M. Prince)
*rbc*L	486R	TAGAGGACGACCATACTTGTTC	bp 486–507 of tobacco *rbc*L	here (designed by L. M. Prince)
*rbc*L	894F	GCAGTTATTGATAGACAGAA	bp 894–914 of tobacco *rbc*L	here (designed by L. M. Prince)
*rbc*L	894R	TTCTGTCTATCAATAACTGC	bp 894–914 of tobacco *rbc*L	here (designed by L. M. Prince)
*ndh*F	32	TACCTTTTCTTCCACTTCCAGTT	see Terry et al. 1997	Terry et al. 1997
*ndh*F	451	TGGGAACTTGTGGGAATGTG	see Terry et al. 1997	Terry et al. 1997
*ndh*F	451R	CACATTCCCACAAGTTCCCA	see Terry et al. 1997	Terry et al. 1997
*ndh*F	803	CTATGGTAGCGGCGGGAATTTTTC	see Olmstead and Sweere 1994	see Olmstead and Sweere 1994
*ndh*F	1101	GGAACCTATTGTTGGATATTCACC	see Terry et al. 1997	Terry et al. 1997
*ndh*F	1101R	GGTGAATATCCAACAATAGGTTCC	see Terry et al. 1997	Terry et al. 1997
*ndh*F	1318	GGATTAACCGCATTTTATATGTTTC	minor modification of 1318 from Terry et al. 1997	see Olmstead and Sweere 1994
*ndh*F	1318R	GAAACATATAAAATGCGGTTAATCC	minor modification of 1318R from Terry et al. 1997	see Olmstead and Sweere 1994
*ndh*F	1600R	CATAGTATTGTCCGATTCGTGAGG	minor modification of 1603R from Terry et al. 1997	see Olmstead and Sweere 1994
*ndh*F	2110R	CCCCTATATATTTGATACCTTCTCC	minor modification of 2110R from Terry et al. 1997	see Olmstead and Sweere 1994
*rps*16	F	GTGGTAGAAAGCAACGTGCGACTT	see Oxelman et al. 1997	Oxelman et al. 1997
*rps*16	R2	TCGGGATCGAACATCAATTGCAAC	see Oxelman et al. 1997	Oxelman et al. 1997
*rps*16	IF	TCAATTCTTCGTATTCTATTTC	bp 342–363 of *Maranta bicolor* intron	here (designed by L. M. Prince)
*rps*16	IR	AATAGTGTTTCCTTGTTCCG	bp 477–496 of *Maranta bicolor* intron	here (designed by L. M. Prince)
*trn*L–F	IGStrnLe	GGTTCAAGTCCCTCTATCCC	see Taberlet et al. 1991	Taberlet et al. 1991
*trn*L–F	IGStrnFf	ATTTGAACTGGTGACACGAG	see Taberlet et al. 1991	Taberlet et al. 1991

Table 4. Statistics for maximum parsimony analyses of relationships in Marantaceae using data from all three genomes.

Data partition	Outgroup	Total characters	Included characters	Constant characters	Variable characters	Parsimony informative characters	MPT[a]	Islands	Length	CI[b]	RI[c]	RC[d]
MITOCHONDRIAL												
cox1	Musella	1470	442	363	40	39	156	1	83	0.6747	0.7065	0.4767
cox1	Costus + Siphonochilus	1470	442	369	38	35	130	1	71	0.6901	0.7027	0.4850
NUCLEAR												
18S–26S	Musella	941	442	289	82	71	7035	1	206	0.5146	0.5690	0.2928
18S–26S	Costus + Siphonochilus	941	442	306	77	59	261	1	162	0.5617	0.5943	0.3338
PLASTID												
matK	Musella	1397	1388	930	243	215	8	1	476	0.5714	0.6782	0.3876
matK	Costus + Siphonochilus	1397	1388	980	220	188	4	1	377	0.6260	0.6817	0.4268
ndhF	Musella	2145	2133	1511	319	303	8	1	756	0.5198	0.6063	0.3152
ndhF	Costus + Siphonochilus	2145	2133	1595	290	248	8	1	553	0.5606	0.6185	0.3467
rbcL	Musella	1344	1344	1130	120	94	79	9	239	0.4561	0.6012	0.2742
rbcL	Costus + Siphonochilus	1344	1344	1152	106	86	17	1	200	0.4950	0.6217	0.3078
rps16	Musella	1222	1197	848	218	131	2361	175	266	0.6241	0.7481	0.4669
rps16	Costus + Siphonochilus	1222	1197	888	206	103	45	1	183	0.7049	0.7939	0.5596
trnLF	Musella	527	506	381	66	59	3627	331	126	0.5556	0.7172	0.3984
trnLF	Costus + Siphonochilus	527	506	398	64	44	3570	1	86	0.5930	0.7569	0.4489
COMBINED												
combined	Musella	9046	7452	5452	1008	912	2	1	2225	0.5267	0.6241	0.3287
combined	Costus + Siphonochilus	9046	7452	5688	1001	763	2	1	1688	0.5717	0.6389	0.3652

[a] Maximum parsimony trees
[b] Consistency index
[c] Retention index
[d] Rescaled consistency index

Table 5. Critical relationships and identification of root node for majority rule consensus tree of maximum parsimony and of Bayesian analyses for relationships in Marantaceae using data from all three genomes. Values are jackknife support (≥50%) and posterior probabilities (≥0.95) of clade monophyly. [1.00] indicates support for partial clades.

Data partition	Ginger[a]	CO[b] + ZI[c]	MA[d] + CA[e]	MA	SaC[f]	StC[g]	MC[h]	DC[i]	CC[j]	Root node
MITOCHONDRIAL										
cox1_order					[98, 1.00]				[1.00]	unresolved
cox1_ginger	n/a				[99, 1.00]				[0.99]	unresolved
NUCLEAR										
18S26S_order					[73, 0.91]		[56, 0.98]	[80, 0.87]	[70–97, 1.00]	*Haumania Siphonochilus* [0.67]
18S26S_ginger	n/a				[74, 0.92]		[55, 0.99]	[83, 0.85]	[83–97, 1.00]	*Haumania* [0.64]
PLASTID										
matK_order	57, 1.00	69, 0.97	82, 1.00	100, 1.00	74, 1.00	98, 1.00	100, 1.00	[88], 0.76	[73–96, 0.69–1.00]	deep split
matK_ginger	n/a	n/a	93, 1.00	100, 1.00	68, 1.00	97, 1.00	100, 1.00	[88] 0.74	[74–96, 0.69–1.00]	deep split
ndhF_order	71, 1.00	59, 0.54	91, 1.00	100, 1.00	grade, split between two clades	0.71	98, 1.00	[100, 1.00]	[57–97, 0.99–1.00]	*Sarcophrynium, Sarcophrynium & Thaumatococcus*
ndhF_ginger	n/a	n/a	100, 0.99	100, 1.00	grade, split between two clades	52, 0.79	98, 1.00	[100, 1.00]	[57–96, 0.99–1.00]	*Sarcophrynium, Sarcophrynium & Thaumatococcus*
rbcL_order			62, 0.98	0.79	[83, 0.72–1.00]	[93, 1.00]	62, 0.97	[99, 1.00]	[56–86, 0.56–1.00]	*Hypselodelphys & Trachyphrynium*
rbcL_ginger	n/a	n/a	0.91	0.58	[81, 0.69–1.00]	[98, 1.00]	62, 0.98	[100, 1.00]	[85, 1.00]	*Hypselodelphys & Trachyphrynium*
rps16_order			96, 1.00	100, 1.00	[98, 1.00]	53, 0.83	99, 1.00	[99, 1.00]	[90–92, 0.82]	SaC and *Haumania*
rps16_ginger	n/a	n/a	100, 1.00	100, 1.00	[55, 1.00]	53, 0.85	99, 1.00	[98, 1.00]	[90–92, 0.88]	SaC and *Haumania* 55, 1.00
trnLF_order				95, 1.00	[86, 0.99]	[65, 1.00]	64, 0.61	[73] 0.50	[61–89, 0.76–1.00]	unresolved
trnLF_ginger	n/a	n/a	57	91, 1.00	[85, 0.99]	[61, 1.00]	61, 0.61	[73] 0.58	[58–86, 0.71–1.00]	*Calathea micans*, unresolved
COMBINED										
combined_order	81	100	100	100	73	96	100	58	[84–100]	SaC and *Haumania*
combined_ginger	n/a	n/a	100	100	65	97	100	52	[83–100]	SaC and *Haumania*

[a] Ginger = "Ginger families," [b] CO = Costaceae, [c] ZI = Zingiberaceae, [d] MA = Marantaceae, [e] CA = Cannaceae, [f] SaC = SARCOPHRYNIUM CLADE, [g] StC = STACHYPHRYNIUM CLADE, [h] MC = MARANTA CLADE, [i] DC = DONAX CLADE, [j] CC = CALATHEA CLADE.

Heliconia irrasa, Orchidantha fimbriata, and *Phenakospermum guyanense*) did not alter relationships within the ginger families noticeably, but instead almost uniformly resulted in lower jackknife and posterior probability values, decreased branch resolution, and increased numbers of tree islands.

Overall, parsimony tree topologies within the ingroup were similar to those produced by Bayesian analyses with minor differences in resolution. As expected, combined analyses produced far fewer trees than individual analyses (2 vs. up to 3570; Table 4) and greatly improved clade support (jackknife and posterior probability values), but did not improve general tree indices (consistency index, retention index, and rescaled consistency index). The largest differences in tree topology were related to the method of data analysis. For example, in the nuclear data analyses the position of *Cominsia* changed depending on analysis method (parsimony vs. Bayesian) but with low statistical support (59–70% JK). Parsimony placed *Cominsia* sister to *Monotagma* with 70% JK support (an unexpected location) while Bayesian analysis placed it in a clade with *Donax, Schumannianthus virgatus,* and *Phrynium* (0.87 PP).

The ability of individual data sets to resolve critical clades (with significant statistical support) varied dramatically. The mitochondrial and nuclear data analyses did not resolve any of the expected family relationships (Table 5). This is consistent with the expectation of slow substitution rates in these portions of the plant genome (Wolfe et al. 1987; Palmer and Herbon 1989; Palmer 1990). Similarly, only portions of the five Marantaceae clades were resolved. The various plastid data sets were more successful in resolving within and among family relationships. In all cases the expected family relationships were resolved ((Zingiberaceae, Costaceae)(Marantaceae, Cannaceae)), and ingroup clades were also frequently resolved. Two "wild card" ingroup taxa were identified, *Haumania* and *Thalia.* Earlier studies (Prince and Kress in press) suggested *Haumania* was part of the *Calathea* clade (<50% JK support, <0.95 PP). This study placed *Haumania* in unresolved polytomies of a more basal position than the earlier study, or as a member of the *Sarcophrynium* clade (weakly supported, Table 5). Similarly, *Thalia* was placed within the *Donax* clade by Prince and Kress (in press) (80% JK, <0.95 PP), but was sometimes placed in the basal polytomies in this study.

Both combined analyses (*Musella* as outgroup, or *Siphonochilus* and *Costus* as the outgroup) produced the two shortest trees (one tree shown in Fig. 1; branches that collapse in the strict consensus tree are shown with dashed lines). These two trees differed in the relationship among the three major clades: the *Calathea* clade (CC), the *Donax* clade (DC), and the *Maranta* (MC) + *Stachyphrynium* (StC) clades. Bayesian analysis strongly supported (1.00 PP) the tree shown: ((CC, DC) (MC, StC)), over the alternative: ((CC (MC, StC)) DC). Parsimony favored the alternative topology but with weak (57%) JK support. The first diverging taxon in the Marantaceae tree, based on the combined seven region analyses, was *Haumania* followed by the *Sarcophrynium* clade.

Supertree Construction

Phylogenetic analysis of the supertree matrix resulted in twelve shortest trees. The trees were identical in topology

with the exception of the resolution of *Monotagma* and *Cominsia* as indicated by an upward directed arrow in Fig. 2 and 3, and resolution within *Calathea* I. The figures shown are a summarized (five representatives of *Calathea* reduced to *Calathea* I and *Calathea* II), fully resolved version of the tree used for FPO, AA, and DIVA analyses of biogeography.

Biogeographical Analyses

Biogeographical analysis requires multiple (7–8) migration events within Marantaceae to account for current distribution patterns (Fig. 2, 3; Table 6). Some FPO reconstructions (Fig. 2; ACCTRAN) indicate an African origin for the family, while others suggest an American origin (Fig. 3; both ACCTRAN and DELTRAN), or are equivocal (Fig. 2; DELTRAN). Bremer ancestral area analyses also indicate an African origin for the family (Table 6). DIVA analyses indicate either an African (Fig. 2, max areas = 2; Fig. 3, max areas = 3) or an African-American (Fig. 2, max areas = 2; Fig. 3, max areas = 2 or 3) origin for the family.

DISCUSSION

All prior estimates of relationships based on morphology and anatomy (Kirchoff 1983a, b; Kress 1990; Kress et al. 2001) predict the following relationship among the ginger families: ((Zingiberaceae, Costaceae) (Marantaceae, Cannaceae)). The relationships among these four families have never been contested although Costaceae have been treated as a subfamily or tribe of Zingiberaceae in the past (Schumann 1904; Loesener 1930b; Hutchinson 1934, 1959, 1973), thus it can reasonably be considered a known phylogeny. Independent phylogenetic estimates that deviate from this topology may be due to homoplasy, lack of resolution due to limited sequence divergence (low power) or poor taxon sampling, or analysis limitations such as long-branch attraction (e.g., Soltis et al. 2000; Davis et al. 2004). Similarly, overwhelming morphological and anatomical data support the monophyly of each of the four families in the ginger families, including Marantaceae (Kirchoff 1983a, b; Kress 1990; Kress et al. 2001). Finally, earlier molecular studies by Prince and Kress (in press) identified five major lineages within Marantaceae. Each data set was evaluated on its ability to resolve those family-level relationships and major clades as described above.

The addition of almost 5000 nucleotides from all three genome compartments to the earlier plastid data set (Prince and Kress in press) of 2543 characters provides improved resolution for relationships among the major clades of Marantaceae (Fig. 1). Although the additional plastid data sets are the source of most of the characters for tree building, the combined data set provides the best estimate of relationships in the family at this time. The recovery of the same taxa at the base of the family tree using multiple data sets under both Bayesian and parsimony criteria suggests the *Haumania* + *Sarcophrynium* clade as the root node or grade. Additional studies will be needed to determine if *Haumania* is better included within the *Sarcophrynium* clade or as the earliest diverging taxon in the family. Both *Haumania* and all members of the *Sarcophrynium* clade grow in the African tropics, suggesting an African origin for the family. Results of supertree analyses also identify *Haumania* as the first
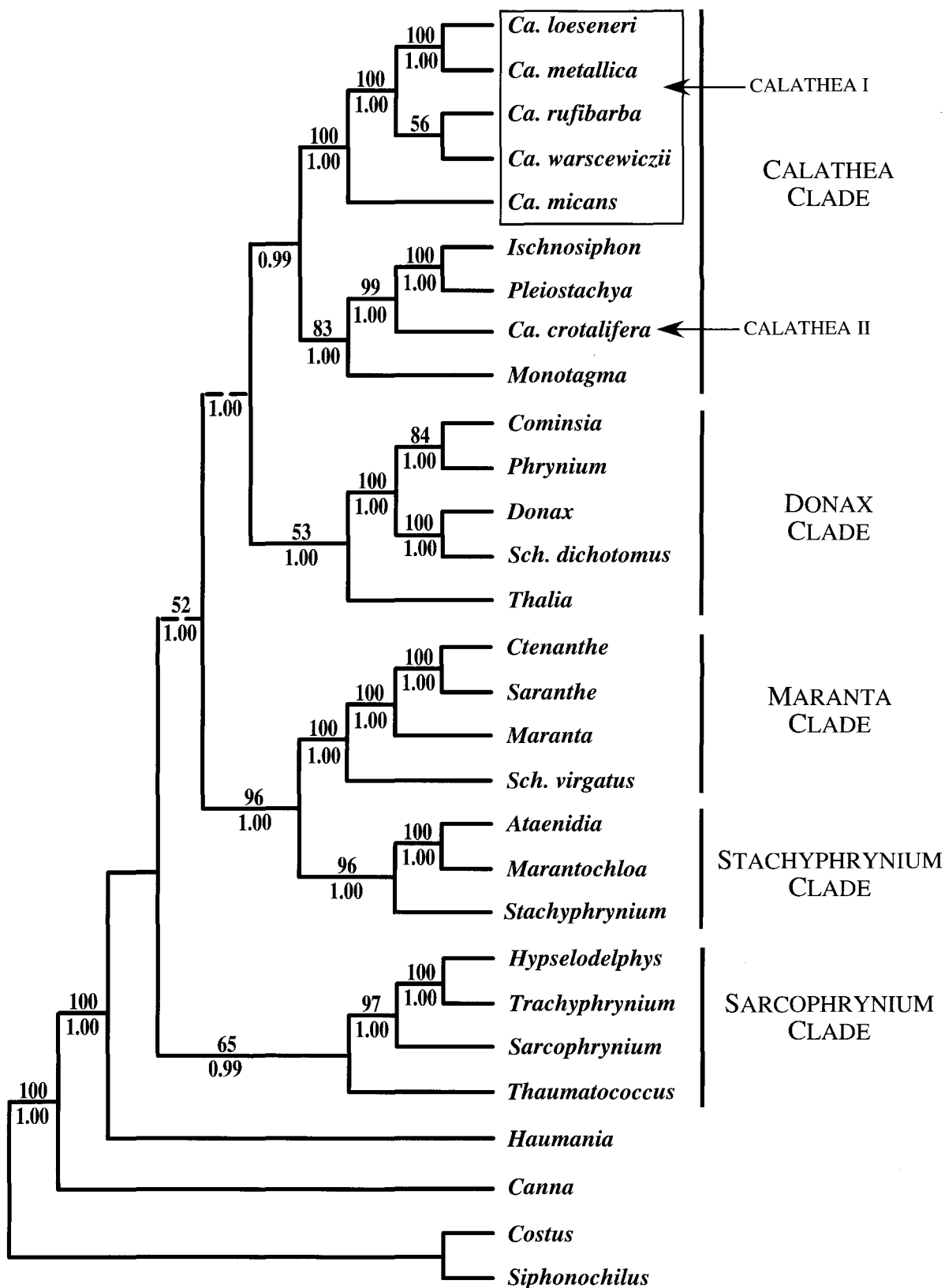
Fig. 1.—Cladogram of the two shortest trees produced in a maximum parsimony analysis of all data for members of Marantaceae. Dashed branches indicate branches that collapse in the strict consensus tree. Numbers above branches are fastswap bootstrap values, numbers below branches are posterior probabilities. *Sch.* = *Schumannianthus, Ca.* = *Calathea.*
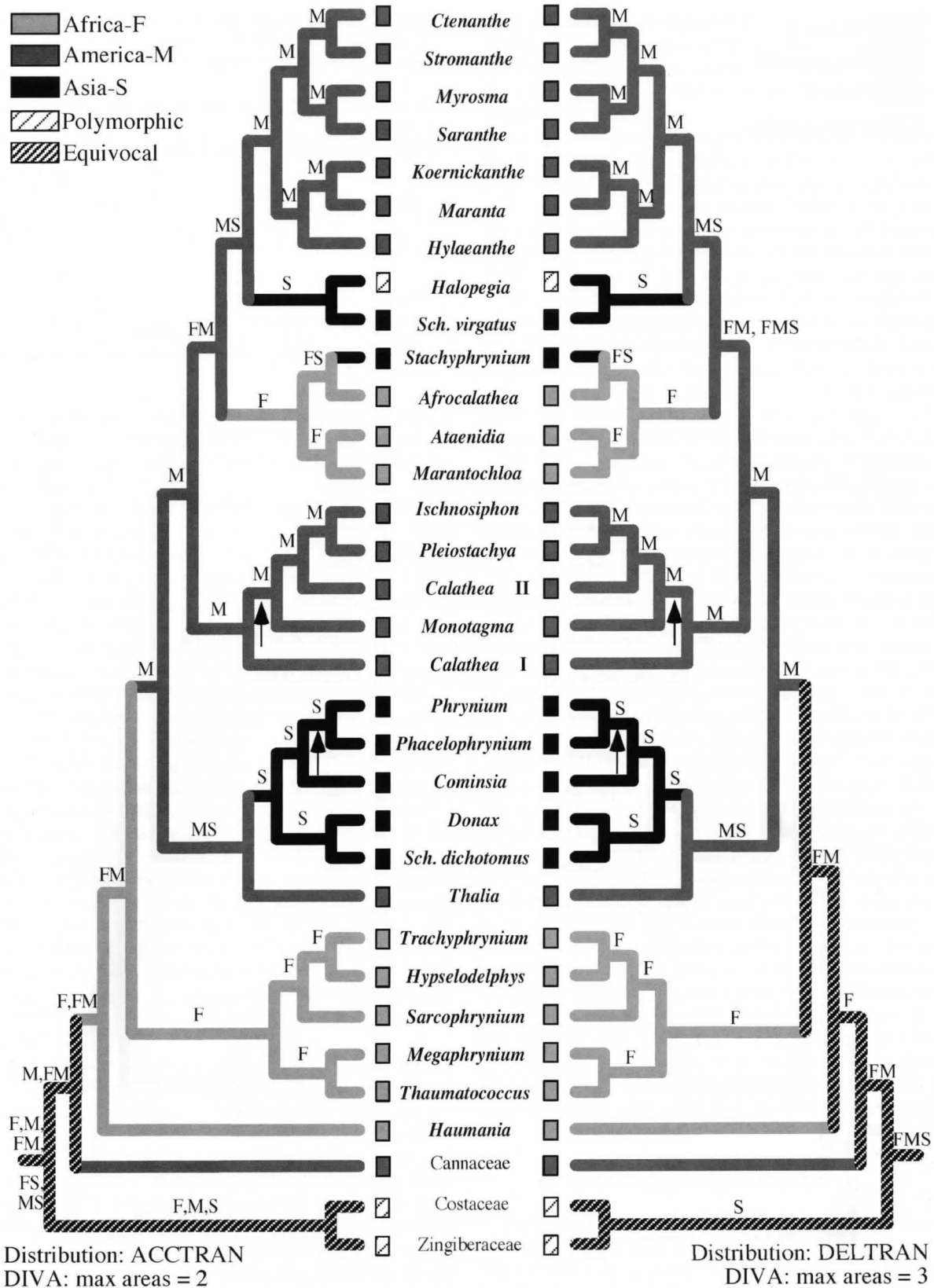
Fig. 2.—Supertree depicting current estimates of phylogenetic relationships in Marantaceae. Arrows indicate two arbitrarily resolved branches not present in the strict consensus tree. Left side = FPO-ACCTRAN optimization, DIVA (max areas = 2). Right side = FPO-DELTRAN optimization, DIVA (max areas = 3). *Sch.* = *Schumannianthus. Calathea* I = *C. loeseneri, C. metallica, C. micans, C. rufibarba,* and *C. warscwiczii; Calathea* II = *C. crotalifera.*
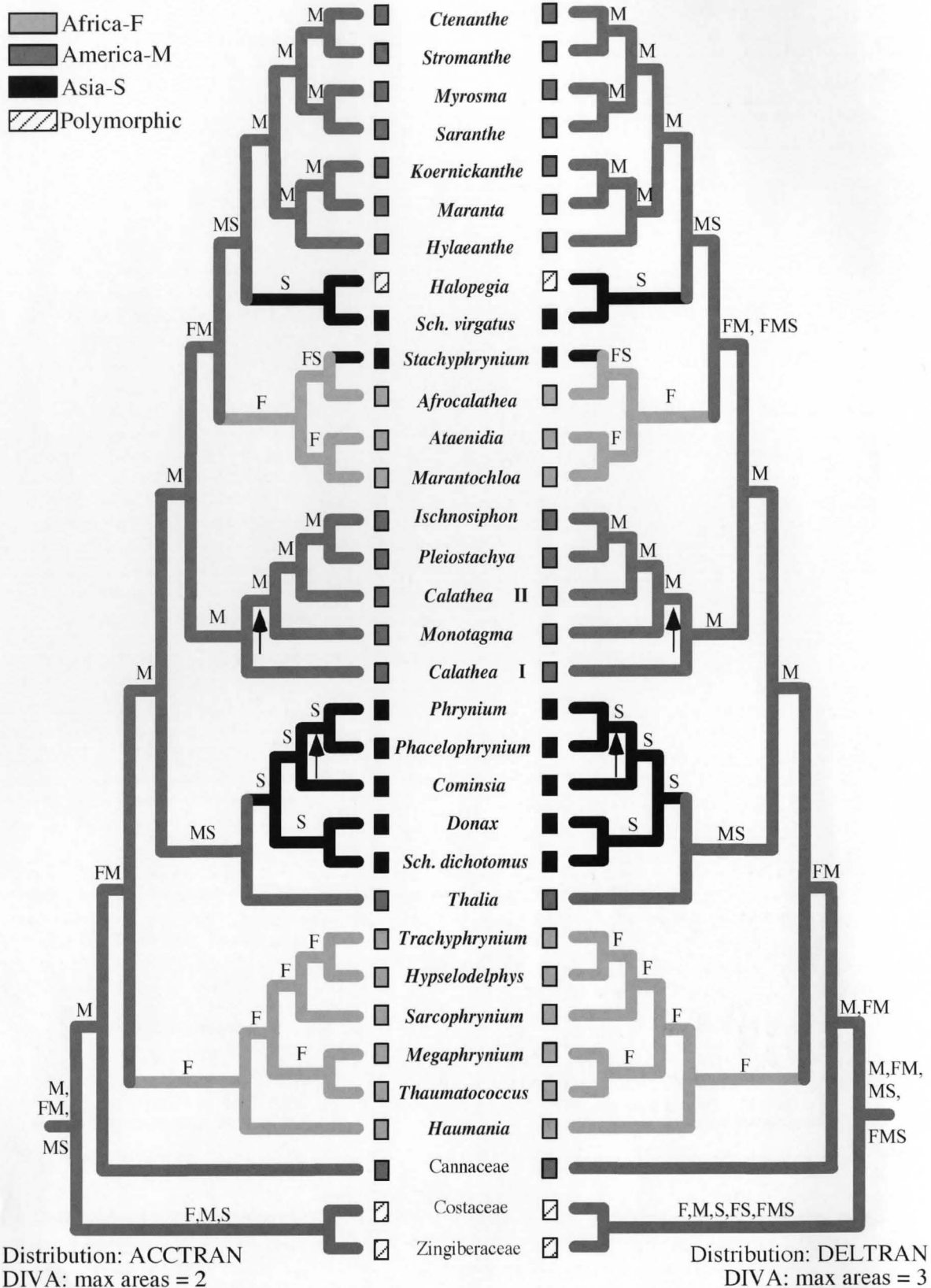
Fig. 3.—Modified supertree of Marantaceae with *Haumania* as part of the *Sarcophrynium* clade. Arrows indicate two arbitrarily resolved branches not present in the strict consensus tree. Left side = FPO-ACCTRAN optimization, DIVA (max areas = 2). Right side = FPO-DELTRAN optimization, DIVA (max areas = 3). *Sch.* = *Schumannianthus*. *Calathea* I = *C. loeseneri*, *C. metallica*, *C. micans*, *C. rufibarba*, and *C. warscwiczii*; *Calathea* II = *C. crotalifera*.

Table 6. Estimated gains and losses for the area cladograms associated with Fig. 2 and 3 under Camin-Sokal (1965) parsimony (= irreversible). Ancestral area value rescaled to a maximum value of 1 (Bremer 1992).

Area	Gains	Losses	Gains/Losses	Ancestral area value
[Tree 1: Fig. 2]				
Africa	5	5	1.00	1.00
America	3	5	0.60	0.60
Asia	3	7	0.43	0.43
[Tree 2: Fig. 3]				
Africa	4	5	0.80	1.00
America	3	4	0.75	0.94
Asia	3	6	0.50	0.63

branch of the Marantaceae family tree (see Fig. 2, 3), followed by the Sarcophrynium clade. These results are not surprising given the overlap in data sets used to generate the supertree matrix.

Biogeographical analyses (FPO, AA, DIVA) differed slightly in their reconstruction of the basal nodes for Marantaceae. DIVA (max areas = 2 or 3), AA, and the FPO-ACCTRAN reconstructions suggest an African origin for the family when Haumania is treated as the first branch of the family phylogeny (Fig. 2; Table 6). An African origin for the family was unexpected since the closest relatives, Canna (Cannaceae), are endemic to the New World (but see Tanaka 2001). This finding is similar to the publication of an African origin for the more distantly related family Zingiberaceae (Kress et al. 2002). Thus, the ginger families may form two pairs of families following parallel biogeographical paths, with the two larger families (Marantaceae and Zingiberaceae) originating in Africa, while their smaller sister families (Cannaceae and Costaceae, respectively) originated in the American tropics.

Inclusion of Haumania in the Sarcophrynium clade results in an American origin for the family only in the FPO analysis (Fig. 3; both ACCTRAN and DELTRAN). There is currently no statistical support for this placement, but the scenario deserves some consideration. Similarly, some DIVA reconstructions (Fig. 2, 3) suggested a more widespread origin for the family, perhaps equivalent to western Gondwana (Africa and America).

Kress and Specht (2006) suggest a divergence of Marantaceae and Cannaceae of at least 95 ± 5 mya, based on a local clock and three fossil calibration points within the order Zingiberales. This date is compatible with a western Gondwanan distribution for the ancestor of Cannaceae and Marantaceae, however, Marantaceae do not begin to diversify until ca. 63 ± 5 mya according to the local clock analysis. Although these numbers may change with the inclusion of additional data sets, we may conclude that Marantaceae are probably not a Gondwanan group, i.e., Marantaceae are not distributed pantropically due to vicariant events ca. 110 mya (Kearey and Vine 1996).

The data presented here suggest that current distribution patterns for Marantaceae may be best explained by long-distance dispersal events. The number and direction of events differs depending on reconstruction method. DIVA analyses require 7–8 dispersal events to account for the current distribution patterns in the family. A large number of possibilities exist from stepping-stone progression around the globe, such as Africa to America to Asia followed by several back migrations.

The lack of resolution regarding migration direction is in sharp contrast to the obvious evidence for localized radiations. Four of the five major clades are strongly associated with a particular geographic region. These strong geographic associations suggest an early dispersal event followed by diversification. For example, one interpretation is that Africa is the source of all historic propagules. Ancient dispersal events brought plants to the Americas in two separate events with subsequent speciation for the Calathea clade and the New World representatives of the Maranta clade. Secondary dispersal into Asia occurred at least three times: (1) Donax clade, (2) Stachyphrynium, and (3) Schumannianthus virgatus and Halopegia pro parte, or as a series of dispersal events to Asia and recolonization events back to Africa.

The above scenario suggests extensive extinction events that are difficult to demonstrate. Specifically, Africa is home to far fewer species than Asia or the Americas. The reduced number of taxa in Africa may be due to extensive extinction as a result of severe climate change (eventual cooling and drying) during the Tertiary. Literature documenting the fossil flora of Africa is limited relative to North America, Europe, and northern Asia, however, plant communities can be reconstructed for several regions and times (Greenway 1970; Axelrod and Raven 1978; Ziegler et al. 1981; Ehleringer et al. 1991; Wing and Sues 1991; Retallack 1992; Cerling et al. 1993; Quade and Cerling 1995). Greenway (1970) specifically describes the shrinking lowland rainforest belts in Africa, the primary community where Marantaceae grow. In contrast, tropical habitats in the Pacific Ocean and between North and South America have been expanding due to the creation of island chains via uplift and volcanic activity.

In summary, the geographic history of Marantaceae is complex and uncertain. Early efforts using molecular phylogenies were hampered by poor resolution along the backbone of the family tree. Current data provides improved resolution and better estimates, although statistical support is still lacking for a few critical nodes. The family has likely undergone several dispersal events from Africa to both the New World and to Asia. The lower specific diversity in Africa may be due to extinction events associated with the constriction of tropical forests during the Tertiary. Extensive diversification, especially in the neotropics, may be due to habit expansion associated with mountain-building processes.

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