

Explosive Radiation of Malpighiales Supports a Mid-Cretaceous Origin of Modern Tropical Rain Forests

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ABSTRACT: Fossil data have been interpreted as indicating that Late Cretaceous tropical forests were open and dry adapted and that modern closed-canopy rain forest did not originate until after the Cretaceous-Tertiary (K/T) boundary. However, some mid-Cretaceous leaf floras have been interpreted as rain forest. Molecular divergence-time estimates within the clade Malpighiales, which constitute a large percentage of species in the shaded, shrub, and small tree layer in tropical rain forests worldwide, provide new tests of these hypotheses. We estimate that all 28 major lineages (i.e., traditionally recognized families) within this clade originated in tropical rain forest well before the Tertiary, mostly during the Albian and Cenomanian (112–94 Ma). Their rapid rise in the mid-Cretaceous may have resulted from the origin of adaptations to survive and reproduce under a closed forest canopy. This pattern may also be paralleled by other similarly diverse lineages and supports fossil indications that closed-canopy tropical rain forests existed well before the K/T boundary. This case illustrates that dated phylogenies can provide an important new source of evidence bearing on the timing of major environmental changes, which may be especially useful when fossil evidence is limited or controversial.

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Modern tropical rain forests are one of the most important and species rich biomes on the planet. They can be defined as having a stratified closed canopy, as receiving abundant precipitation, as experiencing equable temperatures, and as containing woody angiosperm species, at least in the understory (Richards 1996; Whitmore 1998; Morley 2000). During the past 20 years the view has become widespread that the expansion and diversification of this vegetation type occurred principally during the past 65 million years, following the mass extinction event at the Cretaceous-Tertiary (K/T) boundary (~65 Ma [Tiffney 1984; Wing and Boucher 1998; Morley 2000; Johnson and Ellis 2002; Ziegler et al. 2003]; Cretaceous and Cenozoic timescales following Gradstein et al. [1995] and Berggren et al. [1995]). This hypothesis was initially supported by the rarity of large stems (Wheeler and Baas 1991; Wing and Boucher 1998) and large diaspores (Tiffney 1984; Wing and Boucher 1998) of angiosperms in the Cretaceous and by the marked increase in diaspore size in the Early Tertiary. Large seeds facilitate the establishment of seedlings under a rain forest canopy (Grime 1979).

Studies of fossil leaves and wood (Upchurch and Wolfe 1987, 1993; Wolfe and Upchurch 1987) partially corroborated this pattern by indicating that most Late Cretaceous floras of southern North America, which was tropical or nearly so, represented open and subhumid (though not deciduous) forests. This contrasts with fossil floras in the same areas after the recovery from the K/T extinction event, which resemble modern tropical rain forests (Wolfe and Upchurch 1987; Johnson and Ellis 2002). However, floras from the early Late Cretaceous (Cenomanian; ~100 Ma) of Kansas, Nebraska, and New Jersey have leaf sizes and morphologies characteristic of wetter climates (Wolfe and Upchurch 1987). Upchurch and Wolfe (1993) interpreted one flora (Fort Harker, KS) as typical megathermal (>20° mean annual temperature [Upchurch and Wolfe

1987]) rain forest and as evidence against the view that such forests did not originate until the Tertiary.

The advent of strongly supported phylogenies of living plants based primarily on molecular sequence data provides a new source of evidence on questions of this sort. Here we argue that insights into the origin of modern tropical rain forests (as defined above) can be obtained by estimating the timing of the diversification of major angiosperm clades that inhabit these forests and by demonstrating that the habitat of the ancestral species of these diversifications most likely occurred in warm, wet, closed-canopy forests. This novel approach to examining biome evolution may help to break the impasse on the question of the age of the modern tropical rain forest when direct fossil evidence is limited.

One large clade of tropical flowering plants that is especially suited for such an analysis is Malpighiales (APG 2003). Members of Malpighiales were previously assigned to 13 different angiosperm orders (Cronquist 1981) and are highly diverse in both morphology and species (Chase et al. 2002). They include ~16,000 species (~6% of all angiosperms; numbers of species from Stevens [2003]; total angiosperm species diversity from Thorne [2002]) belonging to many well-known tropical groups and are an important component of the understory of tropical rain forests worldwide (table 1). We used Bayesian, likelihood, and parsimony methods to estimate the phylogeny and divergence times of Malpighiales from approximately 6,300 base pairs (bp) of DNA sequence data representing all three plant genomes: plastid *atpB* and *rbcl*, nuclear ribosomal 18S, and mitochondrial *nad1B-C*. Given the resulting trees and data on the ecology of all major lineages of Malpighiales, we used both parsimony and maximum likelihood to reconstruct the probable habitat occupied by the first members of this highly diverse clade.

Material and Methods

Gene Sequencing

Our data sets include 124 species representing all traditionally recognized families of Malpighiales (APG 2003); outgroup species from the closely related clades Celastrales, Oxalidales, and Huaceae (APG 2003; Soltis et al. 2003); and members of the core eudicot clades Saxifragales (Davis and Chase 2004) and Caryophyllales (Soltis et al. 2003). Seventy-seven, 32, 20, and 11 sequences were newly obtained for this study for *atpB*, *rbcl*, 18S, and *nad1B-C*, respectively; the remaining were obtained from GenBank. Amplification and sequencing protocols for *atpB*, *rbcl*, 18S, and *nad1B-C* followed Chase et al. (2002), Hoot et al. (1995), Soltis and Soltis (1997), and Davis and Wurdack (2004), respectively. Nucleotide sequences were aligned by eye; the ends of sequences, as well as ambiguous internal regions, were trimmed from each data set to maintain complementary data between taxa. The aligned plastid, nuclear, and mitochondrial data sets included 2,825, 1,653, and 1,887 bp, respectively. Supplementary information, including data matrices and trees analyzed in this study, is available from TreeBASE (<http://www.treebase.org>) or the appendixes to this article.

Phylogenetic Analysis

Parsimony bootstrap percentages (Felsenstein 1985) for each clade were estimated in PAUP* version 4.0b10 (Swofford 2003) from 10,000 heuristic search replicates, tree bisection-reconnection branch swapping, MulTrees on, and simple taxon addition (saving 10 trees per replicate). Parsimony bootstrap consensus trees generated from the three data sets revealed no strongly supported ($\geq 90\%$ bootstrap) incongruent clades between the independent

Table 1: Contemporary importance of tree species of Malpighiales and Ericales (APG 2003) in three tropical rain forests

Location	All species		Malpighiales		Ericales	
	No. spp.	No. ind.	No. spp.	No. ind.	No. spp.	No. ind.
All trees ≥ 10 cm diameter at breast height:						
Gunung Palung	325	2,807	69 (21.2)	671 (23.9)	32 (9.8)	320 (11.4)
Dzanga-Sangha	258	2,254	59 (22.8)	537 (23.8)	23 (8.9)	413 (18.3)
Yasuní	1,092	9,184	107 (9.7)	871 (9.4)	100 (9.1)	832 (9.0)
Trees ≥ 10 cm diameter at breast height: ^a						
Gunung Palung	164	655	46 (28.0)	250 (38.1)	17 (10.3)	114 (17.4)
Dzanga-Sangha	105	407	28 (26.6)	135 (33.1)	7 (6.6)	90 (22.1)
Yasuní	583	2,139	62 (10.6)	270 (12.6)	44 (7.5)	100 (4.6)

Note: Gunung Palung = Gunung Palung National Park, West Kalimantan (Webb 1997; Webb and Peart 2000); Dzanga-Sangha = Dzanga-Sangha National Park, Central African Republic (D. Harris and J. Hall, unpublished data; Hall 2003); Yasuní = Yasuní, Ecuador (Pitman et al. 2001). Figures are the sum of trees and species at a number of sample plots at each site. Percentages of species diversity and of the total number of individuals are shown in parentheses. (Some plant groups at Dzanga-Sangha have not yet been fully separated into morphotype, and the numbers here represent an underestimate of the number of species.)

^a Species that were not observed to have a maximum diameter >25 cm (i.e., understory trees).

analyses of the plastid, nuclear, and mitochondrial data sets and were subsequently analyzed simultaneously with parsimony and Bayesian methods (Whitten et al. 2000; Reeves et al. 2001). Parsimony searches were performed as above, but with 100 random taxon addition replicates saving all optimal trees at each step.

To choose the optimal model of sequence evolution, we performed a series of hierarchical likelihood ratio tests (Felsenstein 1981; Huelsenbeck and Rannala 1997) using Modeltest version 3.06 (Posada and Crandall 1998). Bayesian analyses were implemented in MrBayes version 3.0b4 (Huelsenbeck and Ronquist 2001) under the GTR + I + Γ model with default priors for the rate matrix, branch lengths, gamma shape parameter, and the proportion of invariant sites. A Dirichlet distribution was used for the base frequency parameters, and an uninformative prior was used for the tree topology. Ten chains were initiated with a random starting tree and run for one million generations sampled every 1,000 generations. Following a burn-in period of 200,000 generations, trees were sampled from the posterior distribution to calculate clade posterior probabilities.

Habitat Reconstruction

To infer the ancestral habitat of Malpighiales, we optimized the habitat of major lineages of extant Malpighiales onto the Bayesian tree with the highest likelihood score and onto the 162 most parsimonious trees using parsimony and maximum likelihood as implemented in Mesquite version 1.0 (Maddison and Maddison 2003). The habitat of major lineages of extant Malpighiales was scored as a two-state character: either inhabiting warm, wet, closed-canopy forest (i.e., rain forest) or not. Habitat was either ascertained directly from floristic and monographic treatments or inferred with the aid of distributional information on rain forests in the Americas (Prance 1989a; Richards 1996), Africa (White 1983; Richards 1996), Asia (Richards 1996; Morley 2000), and Australia (Richards 1996). Malpighiales not found in tropical rain forests typically occur in savannahs or open woodland habitats in tropical latitudes. A relatively small number of clades (e.g., some Euphorbiaceae, Salicaceae, and Violaceae), however, occur in temperate zones. We scored tropical open forest and temperate-zone inhabitants as a single state, “nonwarm/wet/closed,” because our primary concern was whether Malpighiales occupied warm, wet, closed-canopy forest ancestrally. Habitat occupancy is a valid character for ancestral state reconstruction because it is directly related to intrinsic (genetically based) physiological characteristics of taxa that inhabit this biome (Webb et al. 2002). For habitat scoring see appendix B.

We performed two reconstructions to ascertain the ancestral habitat of Malpighiales: one in which habitat was

scored for each family (sensu APG [2003]) and the other in which it was scored for all genera sampled in the phylogenetic analysis. The family-level scoring helped to avoid sampling bias by ensuring that habitats occupied by unsampled genera were also included. Taxa inhabiting both rain forest and open tropical/temperate habitats were coded as polymorphic. Assumptions about character weighting were evaluated under parsimony using step matrices (Maddison 1994) to explore how great a cost must be imposed on the transition from rain forest for the ancestral condition to be unambiguously open tropical/temperate (Ree and Donoghue 1998). For the likelihood reconstructions, the single fixed tree topology with the highest likelihood score from Bayesian searches was input with branch lengths and analyzed under the general Mk1 model (Lewis 2001) with the rate parameter estimated from the data. Polymorphic taxa were analyzed as either 1 or 0, and each of these reconstructions was performed twice under the alternative state (i.e., four analyses in total).

Divergence Time Estimates

We chose the Bayesian tree from above to test for rate constancy among lineages. Branch lengths and an associated likelihood score were calculated on this tree in PAUP* under the optimal sequence model and associated parameters with, and without, a molecular clock enforced. The test statistic $2(-\ln L1 - \ln L0)$ was compared to a χ^2 distribution (with $n - 2$ degrees of freedom; $n =$ number of taxa) to assess significance. A global molecular clock was rejected ($P < .05$) for the combined data set.

The nonclock tree was rooted with *Dillenia* and *Peridiscus*, which are members of the core eudicot clades Caryophyllales (Soltis et al. 2003) and Saxifragales (Davis and Chase 2004), respectively (see app. C for full tree). Divergence times were estimated on this tree using penalized likelihood (PL; Sanderson 2002) as implemented in r8s version 1.7 (Sanderson 2003). Penalized likelihood has been shown to outperform both clock and nonclock nonparametric rate smoothing methods when data depart from a molecular clock (Sanderson 2002). This method relies on a data-driven, cross-validation procedure that sequentially removes taxa from the tree, estimates parameters without the removed branch, and calculates the χ^2 error associated with the difference between the predicted and actual values. The optimal smoothing value for the global data set was 31.62.

To estimate standard errors associated with divergence times, we used the parametric bootstrapping strategy outlined by Davis et al. (2002): 100 data sets were simulated on the r8 smoothed topology using the computer software Seq-Gen version 1.2.7 (Rambaut and Grassly 1997); re-

sulting simulated data sets were imported into PAUP*, and branch lengths were estimated on the smoothed topology for each of these data sets with the sequence model and parameters estimated from the original data; and resulting branch length estimates from the simulated data sets were used to calculate the variance in divergence time estimates (i.e., 95% confidence interval).

We used four macrofossils and 11 palynofossils from the Cretaceous and Tertiary as reliable minimum age constraints for several internal clades (table 2). Two maximum age constraints were independently enforced for the basal node of the tree. We first constrained the basal node to be no older than 125 m.yr. This corresponds to the earliest known occurrence of tricolpate pollen, a synapomorphy that marks the eudicot clade, of which Malpighiales are a member (Magallón et al. 1999; Sanderson and Doyle 2001; APG 2003). The pollen fossil record has been intensively studied throughout the initial rise of angiosperms, and tricolpate pollen increases steadily in abundance and diversity from its first isolated reports in the late Barremian, becoming ubiquitous in the Albian. Hence, it has been considered unlikely that the eudicot clade originated much earlier than the late Barremian (Magallón et al. 1999; San-

derson and Doyle 2001). This may be an overestimate for the age of our basal node, which does not correspond to the entire eudicot clade but rather to core eudicots exclusive of Gunnerales (Soltis et al. 2003). We also chose this date because it corresponds to the oldest molecular age estimate by Wikström et al. (2001) for our basal node (their node 12).

We also constrained the basal node to be no older than 109 m.yr., which was the youngest (and therefore the most conservative) age estimate by Wikström et al. (2001) for the same node. Our choice of this constraint was influenced in part by the fact that their youngest estimates dated the entire eudicot clade (their node 6) as 125 m.yr., which we have taken as a maximum age for eudicots based on the fossil record of tricolpate pollen (Magallón et al. 1999; Sanderson and Doyle 2001).

Results

Our phylogenetic analyses and clock-independent dating estimates indicate that all of the 28 major lineages within Malpighiales, plus the previously unplaced taxon *Centroplicus* (APG 2003), originated well before the K/T bound-

Table 2: Fossil age constraints

Extant taxon	Fossil taxon	Fossil type	Oldest reliable age (Ma)	Location
<i>Acalypha</i> ¹	<i>Acalypha</i> type	Pollen	Early Paleocene (61.0)	China (Kiangsu)
<i>Austrobuxus-Dissilaria</i> clade ²	<i>Malvacipollis diversus</i>	Pollen	Late Paleocene (55.5)	Australia
<i>Balanops</i> ³	<i>Balanops caledonica</i>	Pollen	Late Oligocene (23.8)	Scotland (Hebrides)
<i>Caryocar</i> ⁴	<i>Retisyncolporites angularis</i>	Pollen	Early Eocene (55.5)	Venezuela
<i>Casearia</i> ⁵	<i>Casearia</i> type	Pollen	(Late) Middle Eocene (37.0)	Panama
<i>Chrysobalanus</i> ⁶	<i>Chrysobalanus</i> type	Pollen	(Early) Middle Eocene (49.0)	Colorado
Clusiaceae ⁷	<i>Palaeoclusia chevalieri</i>	Flower	Late Turonian (89.0)	New Jersey
<i>Ctenolophon</i> ^{8, 9}	<i>Ctenolophonidites costatus</i>	Pollen	Maastrichtian (66.0)	Nigeria
Cunoniaceae ¹⁰	<i>Platydiscus peltatus</i>	Flower	Early Campanian (83.5)	Sweden (Kristianstad Basin)
<i>Drypetes</i> ¹¹	<i>Drypetes</i> type	Pollen	Late Eocene (33.7)	France (Aisne)
Hippomaneae (<i>Homalanthus</i>) ^{12, 13}	<i>Crepetocarpon perkinsii</i>	Fruit	Middle Eocene (40.0)	Tennessee
<i>Phyllanthus</i> ¹⁴	<i>Phyllanthus</i> type	Pollen	Late Eocene (33.7)	Atlantic Ocean
Rhizophoraceae sensu lato (incl. Erythroxylaceae) ^{15, 16}	<i>Zonocostites ramonae</i>	Pollen	(Early) Late Eocene (36.9)	Colombia
<i>Salix-Populus</i> clade ¹⁷	<i>Pseudosalix handleyi</i>	Twigs, leaves, flowers	Middle Eocene (48.0)	Utah
Stigmaphyllonids (Malpighiaceae crown group) ¹⁸⁻²⁰	<i>Perisyncolporites pokornyii</i>	Pollen	Middle Eocene (49.0)	Colombia

Note: Each fossil taxon provides a reliable minimum age estimate for taxa sampled in this study. In the case of palynofossils, we selected only pollen types that were easily assignable to taxa included in our phylogenetic analyses. Palynofossils assigned to extant taxa are based on taxonomic assessments by Muller (1981) and updated accordingly for taxonomy and stratigraphy following the numerical references in appendix A (which includes a tree showing fossil constraints). For Cretaceous and Cenozoic timescales see Gradstein et al. (1995) and Berggren et al. (1995).

ary. Given our maximum age constraint of 125 m.yr. (fig. 1), Malpighiales originated in the late Aptian (114 Ma), and most major clades began to diversify shortly thereafter. The optimal age estimates for 24 of these 29 clades imply that they originated within a 20-m.yr. time window (114–94 Ma), between the Aptian and through the Cenomanian: five during the late Aptian (114–112 Ma), 16 during the Albian (111–100 Ma), and three during the Cenomanian (98–94 Ma). Three more clades appeared during the Coniacian (89–85 Ma), and the two most recently derived originated during the Campanian (76 Ma).

Optimal age estimates in which the maximum age constraint for our basal node was 109 m.yr. yielded similar results: Malpighiales originated in the mid-Albian (102 Ma), 24 of the 29 clades originated within a 13-m.yr. window (102–89 Ma) from the Albian to the Turonian, one during the Santonian (84 Ma), and four during the Campanian (78–72 Ma). These ages are more consistent with the fossil pollen record because most core eudicots have tricolpate pollen, which does not appear until within the Albian (e.g., Doyle and Robbins 1977).

All of our age estimates for crown group Malpighiales are much older than those inferred by Wikström et al. (2001; their node 22, 81–74 Ma vs. our estimates of 119–101 Ma). The conclusion that their estimates are too young holds even without the use of molecular dating methods because fossil flowers of Clusiaceae, representing a fairly derived clade within Malpighiales (perhaps related to the modern genera *Clusia* and *Garcinia*), are known from the Turonian, about 89 Ma (Crepet and Nixon 1998).

Tropical rain forest was inferred to be the ancestral habitat for Malpighiales, and for most of the clades shown in figure 1. Under parsimony, a cost of between 2.67 and 3.01 for the Bayesian tree, and between 2.64 and 3.01 for the parsimony trees, had to be imposed on the transition from rain forest to open tropical/temperate habitats before the ancestral condition was inferred to be open tropical/temperate. Maximum likelihood reconstructions yielded similarly robust results (table 3).

Discussion

As we have noted, fossil evidence indicates that tropical rain forest appeared after the K/T event in many areas where Late Cretaceous forests were apparently more open and dry adapted (Tiffney 1984; Upchurch and Wolfe 1987, 1993; Wolfe and Upchurch 1987; Wing and Boucher 1998; Morley 2000; Johnson and Ellis 2002; Ziegler et al. 2003). Further expansion and taxonomic diversification of this biome took place during the Cenozoic. The Paleocene-Eocene transition (~50 Ma) was characterized by high global temperatures (Wolfe 1978; Upchurch and Wolfe 1987; Zachos et al. 2001) and coincided with a significant

increase in low-latitude palynofloral diversity (Jaramillo 2002). A similar, although less pronounced, climatic optimum during the mid-Miocene (~15 Ma; Zachos et al. 2001) resulted in the reexpansion and diversification of rain forests worldwide (Morley 2000). Finally, Quaternary (1.6–0 Ma) glacial cycles are thought to account for the diversification of many species-rich rain forest clades (Prance 1982; Whitmore and Prance 1987; Behrensmeyer et al. 1992; Richardson et al. 2001). Major geological events during the Cenozoic also facilitated the intercontinental migration of tropical plants, for example, the closing of the Tethys Seaway (Hall 1998), Paleogene land connections across the North Atlantic (Tiffney 1985a, 1985b; Davis et al. 2002a), and Neogene uplift of the Andes and the closure of the Isthmus of Panama (Gentry 1982; Burnham and Graham 1999).

Although these Cenozoic events surely contributed to the diversification of many rain forest clades, age estimates for Malpighiales suggest that its major lineages originated well before the K/T boundary. The simplest interpretation of our results is that Malpighiales occupied closed-canopy, moist, megathermal forests (i.e., rain forests) during their early evolution in the mid-Cretaceous. The alternative, that preexisting lineages in Malpighiales entered the rain forest habitat independently, would require that all the various morphological and physiological adaptations associated with living in this environment (Richards 1996; Whitmore 1998) evolved independently in most of the 29 major lineages and that all their non-rain forest ancestors went extinct. It could be that Late Cretaceous Malpighiales lived in the wettest, most shaded local habitats in open subhumid forests, as suggested by the fact that Turonian Clusiaceae, used as our oldest minimum age constraint (Crepet and Nixon 1998), are from a flora (South Amboy) thought to represent the subhumid interval (Wolfe and Upchurch 1987) and were “preadapted” to the appearance of rain forest climates. However, under this scenario we would expect to find more lines of Malpighiales persisting today in drier areas.

Limited Cretaceous fossil data (Upchurch and Wolfe 1987, 1993; Wolfe and Upchurch 1987; Morley 2000) suggest that angiosperm-dominated moist megathermal forests had arisen by the Cenomanian in the interval of the inferred origin of most rain forest clades in Malpighiales. Cenomanian leaves from the Dakota Formation of Kansas and Nebraska and the lower Raritan Formation of New Jersey (Woodbridge Clay) are physiognomically diverse and show many of the foliar adaptations characteristic of understory plants of modern tropical rain forests (Richards 1996), including large leaves with entire margins and drip tips, as well as plants with probable vining habits (Upchurch and Wolfe 1987, 1993; Wolfe and Upchurch 1987; Morley 2000). A flora from the Dakota Formation near

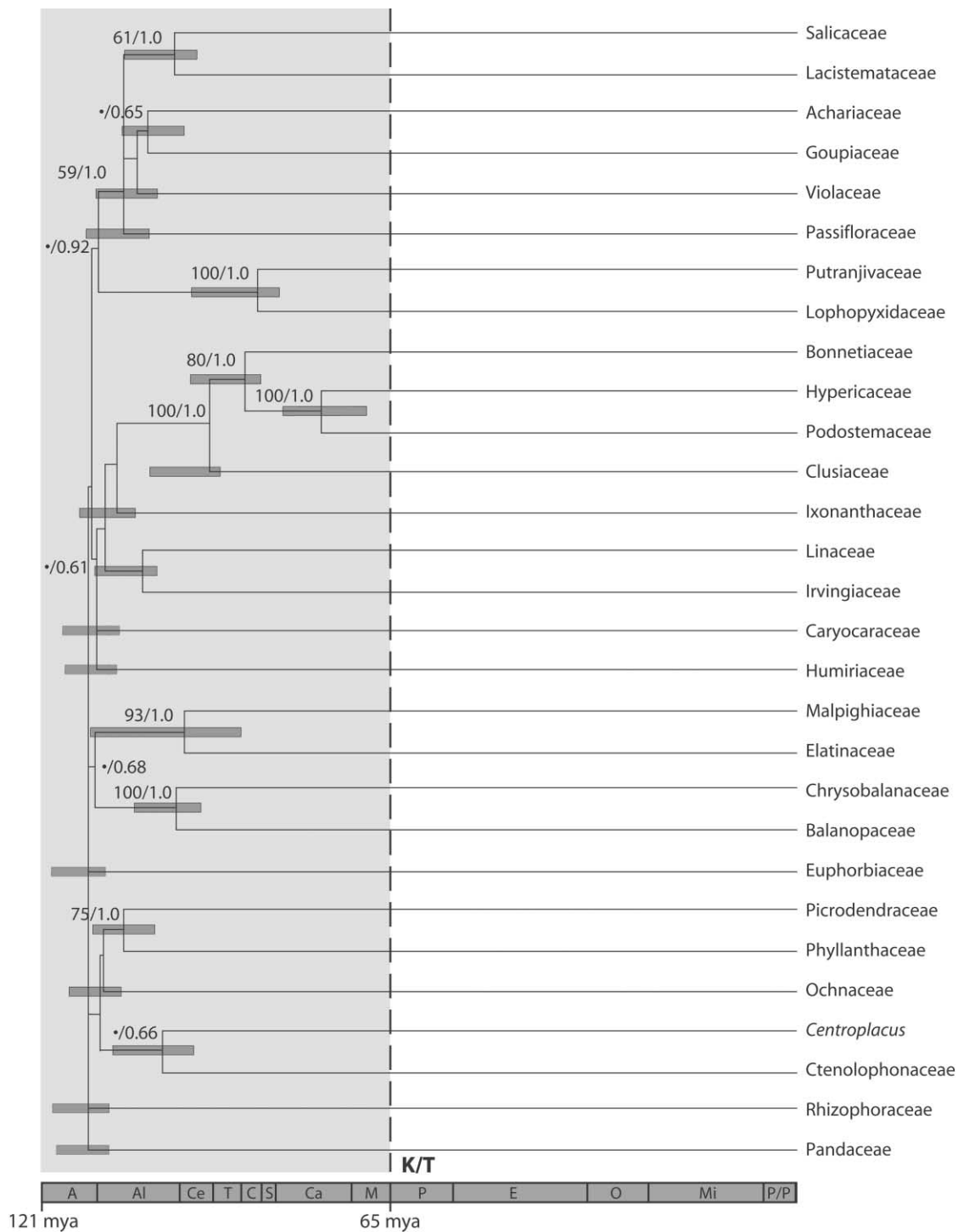


Figure 1: Penalized likelihood chronogram of Malpighiales. Figure reduced from 124-taxon data set to represent only the 28 recommended families of Malpighiales sensu APG (2003) plus the previously unplaced taxon *Centroplacus*. For outgroups and rooting see text. Bootstrap values and Bayesian posterior clade probabilities (>50%/0.50), respectively, indicated near nodes; bullet = support values ≤50%/0.50. The monophyly of Malpighiales was supported by a very high bootstrap value (100%) and posterior probability (1.0). Confidence intervals shown with shaded bars. Divergence times were calculated on this rate-smoothed topology by calibrating nodes with several minimum age constraints from macrofossil and palynological data (table 1). A maximum age constraint of 125 m.yr. was enforced for the root node based on the oldest occurrence of tricolpate pollen grains representing the eudicot clade (see text). The K/T boundary (~65 Ma) is marked with a dashed line. The origin of Malpighiales is estimated at 114 Ma. The scale bar indicates major Cretaceous and Cenozoic intervals: A = Aptian, Al = Albian, Ce = Cenomanian, T = Turonian, C = Coniacian, S = Santonian, Ca = Campanian, M = Maastrichtian, P = Paleocene, E = Eocene, O = Oligocene, Mi = Miocene, P/P = Pliocene/Pleistocene. For complete 124-taxon chronogram, see appendix C.

Table 3: Ancestral habitat for major Malpighiales clades illustrated in figure 1 as inferred from maximum likelihood

Taxa	Family scoring (TRF : OT/T)		Generic scoring (TRF : OT/T)	
	TRF	OT/T	TRF	OT/T
Achariaceae	1.0 : 0 ^a	.11 : .89^a	.96 : .04 ^a	.99 : .01 ^a
Balanopaceae	1.0 : 0 ^a	.99 : .01 ^a	.92 : .08 ^a	.98 : .02 ^a
Bonnetiaceae	.88 : .12	.30 : .70	.61 : .39	.50 : .50
Caryocaraceae	1.0 : 0 ^a	.96 : .04 ^a	.98 : .02 ^a	1.0 : 0 ^a
<i>Centroplocus</i>	1.0 : 0 ^a	.93 : .07 ^a	.97 : .03 ^a	.98 : .02 ^a
Chrysobalanceae	1.0 : 0 ^a	.99 : .01 ^a	.92 : .08 ^a	.99 : .01 ^a
Clusiaceae	.91 : .09 ^a	.78 : .22	.75 : .25	.75 : .25
Ctenolophonaceae	1.0 : 0 ^a	.93 : .07 ^a	.97 : .03 ^a	.99 : .01 ^a
Elatinaceae	1.0 : 0 ^a	.56 : .44	.87 : .13	.78 : .22
Euphorbiaceae	1.0 : 0 ^a	.85 : .15	.99 : .01 ^a	1.0 : 0 ^a
Goupiaceae	1.0 : 0 ^a	.11 : .89^a	.96 : .04 ^a	.99 : .01 ^a
Humiriaceae	1.0 : 0 ^a	.96 : .04 ^a	.98 : .02 ^a	1.0 : 0 ^a
Hypericaceae	.01 : .99^a	.11 : .89^a	.69 : .31	.38 : .62
Irvingiaceae	1.0 : 0 ^a	.95 : .05 ^a	.93 : .07 ^a	.98 : .02 ^a
Ixonanthaceae	1.0 : 0 ^a	.96 : .04 ^a	.95 : .05 ^a	.98 : .02 ^a
Lacistemataceae	1.0 : 0 ^a	.11 : .89^a	.91 : .09 ^a	.82 : .18
Linaceae	1.0 : 0	.95 : .05 ^a	.93 : .07 ^a	.98 : .02 ^a
Lophopyxidaceae	1.0 : 0 ^a	.94 : .06 ^a	.84 : .16	.91 : .09 ^a
Malpighiaceae	1.0 : 0 ^a	.56 : .44	.87 : .13	.78 : .22
Malpighiales (CG)	1.0 : 0 ^a	.86 : .14	.99 : .01 ^a	1.0 : 0 ^a
Ochnaceae	1.0 : 0 ^a	.78 : .22	.97 : .03 ^a	.99 : .01 ^a
Pandaceae	1.0 : 0 ^a	.92 : .08 ^a	.99 : .01 ^a	.99 : .01 ^a
Passifloraceae	1.0 : 0 ^a	.12 : .88^a	.96 : .04 ^a	.98 : .02 ^a
Phyllanthaceae	1.0 : 0 ^a	.22 : .78	.94 : .06 ^a	.96 : .04 ^a
Picrodendraceae	1.0 : 0 ^a	.22 : .78	.94 : .06 ^a	.96 : .04 ^a
Podostemaceae	.01 : .99^a	.11 : .89^a	.69 : .31	.38 : .62
Putranjivaceae	1.0 : 0 ^a	.94 : .06 ^a	.84 : .16	.91 : .09 ^a
Rhizophoraceae	1.0 : 0 ^a	.92 : .08 ^a	.99 : .01 ^a	1.0 : 0 ^a
Salicaceae	1.0 : 0 ^a	.11 : .89^a	.91 : .09 ^a	.82 : .18
Violaceae	1.0 : 0 ^a	.11 : .89^a	.96 : .04 ^a	.98 : .02 ^a

Note: Proportional likelihood values of rain forest habitat (TRF) versus those in open tropical/temperate environments (OT/T) are separated by a colon. Reconstructions for both familial and generic scorings are shown and are further subdivided into analyses in which all taxa that had been scored as polymorphic were coded as either TRF or OT/T. Boldface indicates stem groups for which there is significant statistical support for OT/T environments. Stem clade reconstructions are shown unless otherwise indicated as CG (crown group).

^a Reconstruction judged best as determined by a log-likelihood decline of at least two units between states (i.e., the threshold value).

Fort Harker, Kansas, contains especially large leaves and was cited (Upchurch and Wolfe 1987, 1993; Wolfe and Upchurch 1987) as evidence that typical rain forest originated much earlier than others have argued. This inferred period of wetter climates is also supported by paleoclimatic reconstructions for the Cenomanian (Barron and Washington 1985; Barron et al. 1989; Beerling and Woodward 2001), which indicate that mid latitudes may have been similar in precipitation and temperature to present-day

low latitudes. Moreover, vegetation simulations for the mid-Cretaceous suggest that rain forests could have existed in low-latitude regions of present-day South America, Africa, northern Australia, and India (Beerling and Woodward 2001), and they may have persisted in similar areas until the latest Cretaceous (Otto-Bliesner and Upchurch 1997; Upchurch et al. 1998; Beerling and Woodward 2001).

Extraordinary fossil evidence from the Castle Rock flora of Colorado suggests that highly diverse rain forests were present in North America shortly after the K/T boundary (Johnson and Ellis 2002). Johnson and Ellis (2002) interpreted these forests as a new phenomenon of the Cenozoic, but our phylogenetic evidence from Malpighiales, ancillary evidence from Cenomanian floras such as Fort Harker, and paleoclimate models suggest instead that on a global scale, rain forests may be much older. Any Cretaceous rain forests, however, must have been more geographically restricted than those that developed during the Cenozoic. Although tropical floras are well known at middle latitudes in the Late Cretaceous, most of them indicate subhumid conditions. However, this does not rule out the existence of wet megathermal vegetation at lower latitudes, where there are numerous fossil pollen floras but megafossil floras, which allow more direct inferences on physiognomy of the vegetation, are rare and poorly known (Upchurch and Wolfe 1987).

The rarity of large angiosperm diaspores during the Cretaceous and their increased size after the K/T boundary have also been cited as evidence that closed-canopy environments like those of modern rain forests were not present during the Cretaceous (Tiffney 1984; Wing and Boucher 1998). This assumed that larger diaspores help seedlings become established and survive better in heavily shaded environments such as the understory of tropical rain forests. Recent studies (Grubb 1996, 1998; Grubb and Metcalfe 1996), however, suggest that large diaspores, while an advantage in low-light environments, are not a requirement for successful germination and establishment in the rain forest and may relate more to the ability to germinate on dense leaf litter than to light availability (see also Feild et al. 2004). Seeds of contemporary Malpighiales are on average larger than the mean for samples of all angiosperms (A. Moles, personal communication, Seed Information Database, Kew Gardens). However, the clusiaceous fossil flower from the Turonian of New Jersey was small, with a multiovulate ovary <1 mm in diameter (Crepet and Nixon 1998). It is possible that the paucity of large Cretaceous diaspores is partly a function of poor sampling of low-latitude floras. Large fruits and seeds from the Campanian-Maastrichtian of West Africa were the main exception noted by Wing and Tiffney (1987) to their generalization that Cretaceous angiosperm diaspores were small (cf. Chesters 1955). Another possibility is that the

small size of Cretaceous diaspores reflects not so much open environments as the absence of bird and mammal dispersers, whose radiation after the K/T event has been proposed as an alternative explanation for the Early Tertiary increase in diaspore size (Wing and Tiffney 1987).

Malpighiales account for up to 40% of the understory tree community in tropical rain forests (table 1). We suggest that Malpighiales were among the earliest angiosperm colonizers of the understory in the Cretaceous (Crane 1987), following representatives of the basal ANITA grade, which have been depicted as playing a similar role at the earliest stages of the angiosperm radiation (Feild et al. 2004). ANITA-grade plants, some eumagnoliids, and Malpighiales may have successfully competed with existing nonangiospermous plants in the understory, and Malpighiales may have filled a niche that was less occupied by the other new angiosperm groups: the small, subcanopy tree. Modern Malpighiales are often 2–10 m tall, are able to grow and reproduce without direct sunlight, and are more flexible in growth habit than cycad-like seed plants (Crane 1987; Feild et al. 2004), that is, like ANITA-grade plants but generally taller. The recently documented (Schneider et al. 2004) Late Cretaceous radiation of derived ferns (Polypodiaceae sensu lato) may represent a parallel occupation of forest floor and epiphytic niches.

Most angiosperm wood fossils from the mid-Cretaceous are relatively small (Crane 1987; Wing and Boucher 1998), suggesting that the forest canopy at the beginning of the radiation of Malpighiales was dominated by large conifers (Crane 1987). The diversity of conifers remained relatively steady during the late Albian–early Cenomanian, whereas cycadophytes, pteridophytes, and pteridosperms exhibited dramatic declines. Crane (1987) suggested that the latter taxa were replaced by angiosperm shrubs or small trees. A similar mixture of dicotyledonous trees and conifers is found today in the heath and montane forests of southeast Asia, which contain emergent *Agathis* or *Dacrydium* species, and the giant *Araucaria*- and *Agathis*-dominated rain forests of Queensland, New Guinea, New Caledonia, and New Zealand (Richards 1996). By the time of the Cenomanian Dakota and Raritan floras, however, the shift in the dominant trees from conifers to angiosperms had probably occurred (Upchurch and Wolfe 1987, 1993; Wolfe and Upchurch 1987; Cantrill and Poole 2005).

The pattern exhibited by Malpighiales may be paralleled

by other similarly diverse tropical clades. Ericales (APG 2003), for example, form a well-supported clade (Bremer et al. 2002) and are morphologically heterogeneous; their members have been placed in 11 different angiosperm orders (Cronquist 1981), and they are similarly species rich (~11,000 species; see Stevens 2003 and Thorne 2002). Ericales also form an important component of the understory diversity in tropical rain forests (up to ~22%; table 1). Together, Ericales and Malpighiales account for more than half of the understory stems in some of these forests (~55% in Asia and Africa). Molecular divergence-time estimates for Ericales suggest that they originated in the Cretaceous during approximately the same time period as Malpighiales (~106 Ma [Wikström et al. 2001]). Like Malpighiales, Ericales have a fossil record dating back to the Turonian (Magallón et al. 1999), and it appears that many of their major lineages may extend back to the Cretaceous (Bremer et al. 2002) and originated rapidly (Anderberg et al. 2002). The coincident pattern of diversification in these two major clades may mark the origin of tropical rain forests as we know them today. In the case of Malpighiales, we have demonstrated that dated phylogenies can provide an important new source of evidence on the timing of major environmental changes, which may be especially useful in such cases where direct fossil evidence is limited or controversial.

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APPENDIX A

Numbered references for fossil minimum age constraints presented in table 2 and figure A1. Exact placement of fossil constraints are shown in figure A1 using the same numbered references. Palynofossils assigned to extant taxa sampled in our data set were based on taxonomic assessments by Muller (1981) and updated accordingly for taxonomy and stratigraphy using the references below. Maximum age constraints of 125 and 109 Ma assigned to the basal node from Magallón et al. (1999) and Wikström et al. (2001), respectively.

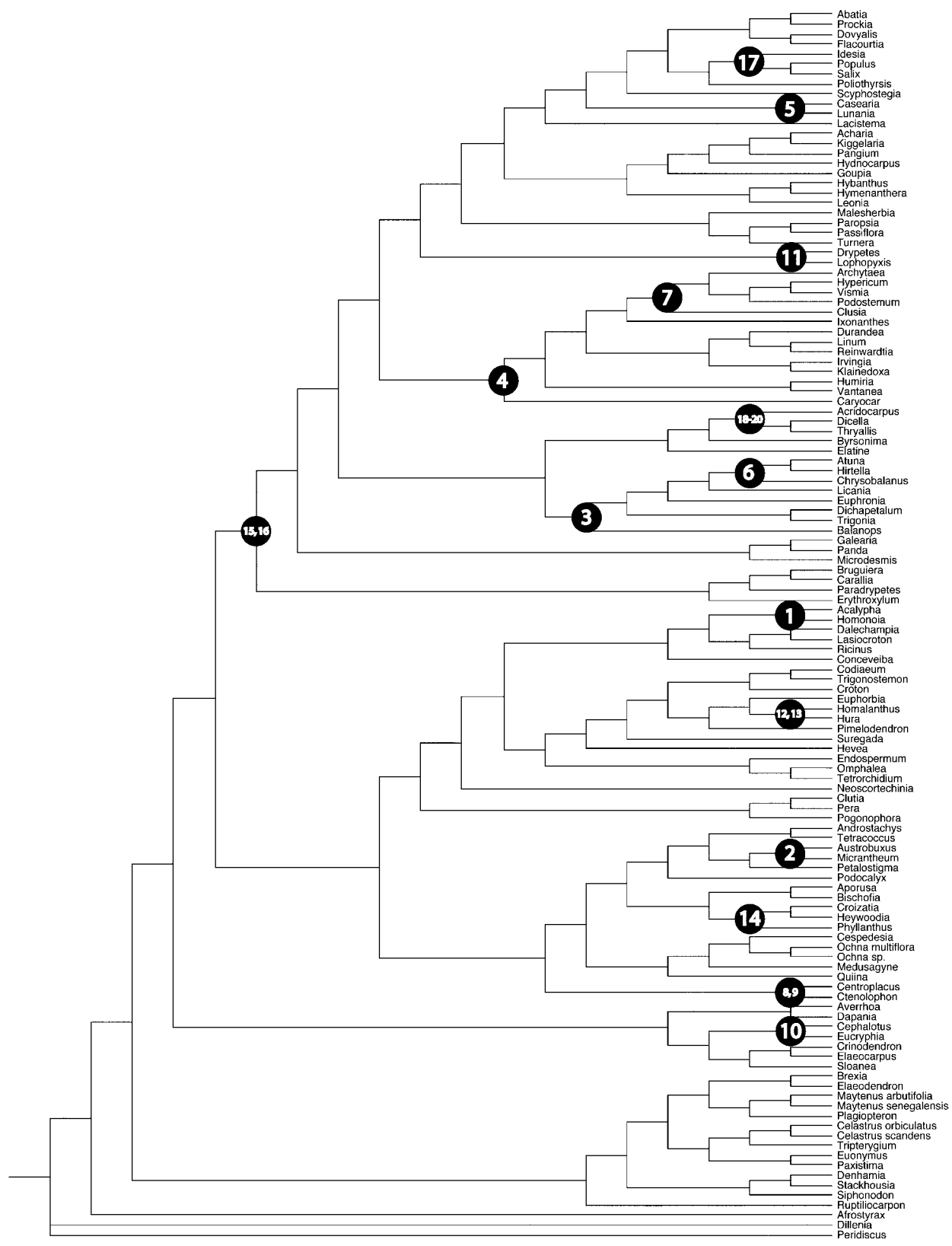


Figure A1: Fossil constraints; minimum age fossil constraints shown on tree using numbered references in appendix A

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APPENDIX B

Table B1: Taxa sequenced, voucher information, and GenBank accession numbers

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbL</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Achariaceae						OT/T and TRF (Cronquist 1981) (SRFG)
<i>Acharia tragodes</i> Thunb.	Cloete s.n. (BOL)	AF209520	AJ418795	AY674643	AF206728	OT/T (Cronquist 1981)
<i>Hydnocarpus</i> sp.	Chase 1301 (K) (origi- nally misdet. as <i>Ixonanthes</i> <i>icosandra</i>)	AF209607	AF206783	AY674714	AF206941	TRF (Sleumer 1938, 1954)
<i>Kiggelaria</i> sp.	Alford 51 (BH)	AY788231	AY788180	AY674719	AY674609	TRF (Sleumer 1975)
<i>Pangium edule</i> Reinw.	Chase 1285 (K)	AF209644	AJ18801	AY674742	AF206979	TRF (Sleumer 1954) TRF (Carlquist 1980; Cronquist 1981)
Balanopaceae						
<i>Balanops vieillardii</i> Baill.	Chase 1816 (K)	AF209534; AF089760	AF089760	AY674479	AF206860	TRF (Carlquist 1980; Cronquist 1981)
Bonnetiaceae						OT/T (Maguire 1972; Robson 1981; Gen- try 1996)
<i>Archytaea multiflora</i> Benth.	Kubitzki & Feuerer 97-26 (HBG)	AY788202	AY380342	AY674648; AY674649	AY674574	OT/T (Maguire 1972; Gentry 1996) TRF (Prance 1973; Prance and Freitas da Silva 1973; Cronquist 1981)
Caryocaraceae						
<i>Caryocar glabrum</i> Pers.	Mori 22997 (NY)	AF206745	Z75671	AY674662	AF206881	TRF (Prance 1973; Prance and Freitas da Silva 1973; Cronquist 1981)
Celastraceae ^a						OT/T and TRF (SRFG)
<i>Brexia madagascariensis</i> Thouars	Schwerdtfeger 25471 (B); Kew 1977- 14901 (K?); Wur- dack s.n. (US)	AJ235419	L11176	AY674655	U42543	OT/T (Fosberg and Renvoize 1980)
<i>Celastrus orbiculatus</i> Thunb.	Simmons 1773 (BH)	AY788263	AY788194	AY674664	AY788162	OT/T and TRF (Hou 1955, 1962)
<i>Celastrus scandens</i> L.	Simmons 1783 (BH)	AY788264	AY788195	AY674665	AY674581	OT/T and TRF (Hou 1955, 1962)
<i>Denhamia celastro- ides</i> (F. Muell.) L. W. Jessup	Chase 2050 (K)	AY788267	AJ402941	AY674680	AY674591	TRF (Jessup 1984)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
<i>Elaeodendron orientale</i> Jacq.	Chase 1213 (K)	AY788269	AY380347	AY674689	AY674593	OT/T (de la Bathie 1946; Fosberg and Renvoize 1980)
<i>Euonymus alatus</i> Siebold	Simmons 1772 (BH)	AY788270	AY788197	AY674694	AY788164	OT/T and TRF (Blacklock 1951; Hou 1962)
<i>Maytenus arbutifolia</i> (Hochst. ex A. Rich.) R. Wilczek	Collenette 2/93 (K)	AY788271	AY380352	AY674732	AY674616	OT/T and TRF (Hou 1962; Demissew 1985)
<i>Maytenus senegalensis</i> (Lam.) Exell	Collenette 4/93 (K)	AY788272	AY380353	AY788286	AY788165	OT/T and TRF (Hou 1962; Demissew 1985)
<i>Paxistima canbyi</i> A. Gray	Simmons 1775 (BH)	AY788273	AY788198	AY674746	AY674623	OT/T (Navaro and Blackwell 1990)
<i>Plagiopteron suaveolens</i> Griff.	Chase 1335 (K)	AJ235562	AJ235787	AY674751	AF206993	TRF (Baas et al. 1979)
<i>Siphonodon celastri- neus</i> Griff.	Chase 2097 (K)	AF209676	AF206821	AY674771	AF207021	OT/T and TRF (Hou 1964; Jessup 1984)
<i>Stackhousia minima</i> Hook. f.	Molloy s.n. (CHR)	AJ235610	AJ235795	AY674773	AF207026	OT/T (Barker 1984; Carlquist 1987)
<i>Tripterygium regelii</i> Sprague & Takeda	Simmons 1776 (BH)	AY788260	AY788193	AY674781	AY788161	OT/T (Ma et al. 1999) OT/T (Lowrie 1998)
Cephalotaceae ^a <i>Cephalotus foli- cularis</i> Labill.	Chase 147 (NCU)	AY788265	L01894	AY674666	U42516	OT/T (Lowrie 1998) TRF (Prance 1970, 1972a, 1973, 1989a; 1989b)
Chrysobalanaceae s.s. ^b <i>Atuna racemosa</i> Rafin.	Chase 2118 (K)	AY788203	AF089758	AY674650	AY674575	TRF (Prance 1989b)
<i>Chrysobalanus icaco</i> L.	FTG 76-311 (voucher loc.); Wurdack	AF209562	L11178	AY674668	U42519	TRF (Prance 1970, 1972a)
<i>Hirtella bicornis</i> Mart. & Zucc.	Ducke Res. 2-303Z.489 (K?)	AY788225	AF089756	AY674706	AY674603	TRF (Prance 1972a, 1973)
<i>Licania</i> sp.	Ducke Res. 2-302 (K?); FTG 64-734 (FTG?)	AF209617	L11193	AY788279	U42520	TRF (Prance 1972a, 1973, 1989b)
Clusiaceae						TRF (Kubitzki 1978; Cronquist 1981; Robson 1981)
<i>Clusia gundlachii</i> Stahl	Chase 341 (NCU)	AY788209	Z75673	AY788278	AY674584	TRF (Cronquist 1981)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbL</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Ctenolophonaceae						TRF (Van Hooren and Nooteboom 1988a)
<i>Ctenolophon engleri-anus</i> Mildbr.	Dourse 1572 (K); Mc-Pherson 16911 (MO)	AY788215	AJ402940	AY674676	AY674589	TRF (Van Hooren and Nooteboom 1988a)
Cunoniaceae ^a						OT/T and TRF (Hoogland 1979, 1981; Bradford 1998, 2002)
<i>Eucryphia</i> sp.	Strybing Arb 86-0250; Chase 2528 (K)	AF209584	L01918	AY674693	U42533	OT/T (Bentham and Mueller 1864)
Dichapetalaceae						TRF (Prance 1972b, 1973; Breteler 1991)
<i>Dichapetalum</i> spp.	Fisson s.n. (K); Chase 624 (K)	AJ235455	AF089764	AY674683	AF206902	TRF (Prance 1972b, 1973; Breteler 1991)
Dilleniaceae ^a						TRF (Hoogland 1951, 1952)
<i>Dillenia philippinensis</i> Rolfe	Chase 2102 (K)	AY788268	L01903	AY674684	AY788163	TRF (Hoogland 1952)
Elaeocarpaceae ^a						OT/T and TRF (Bri-zicky 1965; Baker et al. 1998)
<i>Crinodendron hookerianum</i> Gay	Chase 909 (K?)	AF209570	AF206754	AY674673	AF206893	OT/T and TRF (Bricker 1991)
<i>Elaeocarpus</i> spp.	D. M. Hicks 8455 (K?); Alverson s.n. (WIS)	AF209581	AF20675	AY788285	AF206906	TRF (Baker et al. 1998; Coode 2001)
<i>Sloanea</i> spp.	Alverson 2211 (WIS); Chase 343 (NCU)	AJ235603	AF022131	AY674772	U42826	TRF (Smith 1944, 1954)
Elatinaceae						OT/T (Tucker 1986; Leach 1989)
<i>Elatine triandra</i> Schkuhr	Brunton et al. 13384 (MICH); Crins & Stabb 9600 (MICH)	AY788219	AY380349	AY674690	AY674594	OT/T (Tucker 1986)
Erythroxylaceae						OT/T and TRF (Cronquist 1981) (SRFG)
<i>Erythroxylum</i> spp.	FTG63-251E; Chase 134 (NCU?); Wurdack D713 (US)	AJ235466	L13183	AY674692	AF206909	OT/T and TRF (de la Bathie 1952; Payens 1958; Cronquist 1981; Verdcourt 1984; Plowman 1989; Webster 1994b; Plowman and Berry 1999)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Euphorbiaceae						OT/T and TRF (Cronquist 1981; Webster 1994a; 1994b) (SRFG)
<i>Acalypha californica</i> Benth.	Levin 2192 (SD)	AY788199	AY380341	AY674642	AY674571	OT/T and TRF (Webster 1994b)
<i>Clusia tomentosa</i> L.	Geumshuizan 6505 (MO)	AY788210	AY788168	AY674669	AY674585	OT/T (Webster 1994a, 1994b)
<i>Codiaeum variegatum</i> (L.) Blume	Wurdack D33 (US)	AY788211	AY788169	AY674670	AY674586	TRF (Airy Shaw 1980a; Radcliffe-Smith 1987; Webster 1994b)
<i>Conceveiba martiniana</i> Baill.	Bell 93-176 (US)	AY788212	AY788170	AY674671	AY674587	TRF (Webster 1994b; Murillo 2000)
<i>Croton alabamensis</i> var. <i>alabamensis</i> E. A. Smith ex Chapman	Wurdack D8 (US)	AY788214	AY788171	AY674675	AY674588	OT/T (Webster 1993, 1994b)
<i>Dalechampia spathulata</i> (Scheidw.) Baill.	Wurdack D10 (US)	AY788216	AY788172	AY674677	AY788149	OT/T and TRF (Webster and Armbruster 1991; Webster 1994b)
<i>Endospermum moluccanum</i> (Teijsm. & Binn.) Kurz	Chase 1258 (K)	AY788220	AJ402950	AY674691	AY674595	TRF (Airy Shaw 1972; Webster 1994b)
<i>Euphorbia</i> spp.	Chase 102 (NCU); voucher unknown for U42535	AJ235472	AY788174	AY674695	U42535	OT/T and TRF (Webster 1994b)
<i>Hevea</i> sp.	Gillespie 4272 (US)	AY788223	AY788175	AY674703	AY674601	TRF (Schultes 1990; Webster 1994b)
<i>Homalanthus populneus</i> (Geiseler) Pax	Chase 1266 (K)	AY788226	AY380350	AY674707	AY674604	TRF (Airy Shaw 1968; Webster 1994b)
<i>Hura crepitans</i> L.	Wurdack D89 (US)	AY788228	AY788177	AY674711	AY674606	OT/T and TRF (Stanley and Steyermark 1949; Webster 1994b)
<i>Lasiocroton bahamensis</i> Pax & K. Hoffm.	Wurdack D58 (US)	AY788233	AY788181	AY674723	AY788152	OT/T (Adams 1972; Webster 1994b)
<i>Neoscortechinia kingii</i> (Hook. f.) Pax & K. Hoffm.	Chase 1265 (K)	AY788239	AJ402977	AY674738	AY674619	TRF (Webster 1994b)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
<i>Omphalea diandra</i> L.	Chase 570 (K)	AY788241	AY788183	AY674740	AY674622	OT/T and TRF (Airy Shaw 1980a; Webster 1994b)
<i>Pera bicolor</i> Muell. Arg.	Gillespie 4300 (US)	AY788244	AY380355	AY674747	AY674624	TRF (Webster 1994b)
<i>Pimelodendron</i> <i>zoanthogyne</i> J. J. Sm.	Chase 1268 (K)	AY788247	AJ418812	AY674750	AY674628	TRF (Airy Shaw 1980a, 1980b; Webster 1994b)
<i>Pogonophora schomburgkiana</i> Miers ex Benth.	Larpin 1022 (US)	AY788250	AY788185	AY674755	AY788156	TRF (Webster 1994b)
<i>Ricinus communis</i> L.	Wurdack D9 (US); Hills, unvouchered	AY788253	AY788188	AY674763	AY674633	OT/T (Webster 1994b)
<i>Spathiostemon javanensis</i> Blume	Chase 1261 (K)	AY788227	AY788176	AY674708	AY788151	TRF (Airy Shaw 1972; Webster 1994b)
<i>Suregada boiviniana</i> Baill.	Rakotomalaza et al. 1292 (MO)	AY788255	AY788189	AY788284	AY788157	TRF (Airy Shaw 1975, 1980a; Webster 1994b)
<i>Tetrorchidium</i> sp.	Bell 93-204 (US)	AY788257	AY788191	AY674777	AY788159	TRF (Radcliffe-Smith 1987; Webster and Huft 1988; Webster 1994b)
<i>Trigonostemon verrucosus</i> J. J. Sm.	Chase 1274 (K)	AY788259	AY788192	AY674780	AY788160	TRF (Airy Shaw 1975, 1980a; Webster 1994b)
Euphroniaceae						OT/T (Steyermark 1987)
<i>Euphronia guianensis</i> (R. H. Schomb.) H. Hallier	Mori 23699 (NY)	AY788221	AF089762	AY674696	AY674597	OT/T (Steyermark 1987)
Goupiaceae						TRF (Lundell 1985; Takhtajan 1997)
<i>Goupia glabra</i> Aubl.	Prevost 3031 (CAY)	AJ235484	AJ235780	AY674699	AF206920	TRF (Lundell 1985; Takhtajan 1997)
Huaceae ^a						TRF (Perkins 1909; Baas 1972; Takhtajan 1997)
<i>Afrostryrax</i> sp.	Cheek 5007 (K)	AJ235385	AJ235771	AY674645	AF206840	TRF (Perkins 1909; Baas 1972; Takhtajan 1997)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbL</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Humiriaceae						TRF (Cuatrecasas 1961; Cronquist 1981)
<i>Humiria</i> spp.	Anderson 13654 (MICH), Wurdack s.n. (US)	AJ235495	L01926	AY674710	AF206930	TRF (Cuatrecasas 1961; Cronquist 1981)
<i>Vantanea guianensis</i> Aubl.	Pennington 13855 (K)	AY788261	Z75679	AY674783	AY674639	TRF (Cuatrecasas 1961; Cronquist 1981)
Hypericaceae						OT/T (Hutchinson 1973; Robson 1974, 1977, 1981, 1987, 1990)
<i>Hypericum</i> spp.	Chase 837 (K); Wurdack D492 (US)	AF209602	AF206779	AY674715	AF206934	OT/T (Hutchinson 1973; Robson 1974, 1977, 1981, 1987, 1990)
<i>Vismia</i> spp.	Miller et al. 9313 (MO); Gustafsson 302 (NY)	AY788262	AF518382	AY674784	AF674640	OT/T (Hutchinson 1973; Robson 1974)
Irvingiaceae						TRF (Harris 1996)
<i>Irvingia malayana</i> Oliv.	Simpson 2638 (K?)	AF209605	AF123278	AY674717	AF206939	TRF (Harris 1996)
<i>Klainedoxa gabonensis</i> Pierre	Bradley et al. 1092 (MO)	AY788232	AY663630	AY674720	AY674610	TRF (Harris 1996)
Ixonanthaceae ^c						TRF (Kool 1988)
<i>Ixonanthes chinensis</i> Champ.	Chen 9812087 (K?)	AY788230	AY788179	AY674718		TRF (Kool 1988)
<i>Ochthocosmus longipedicellatus</i> Steyer. & Luteyn	Berry 6561 (MO)				AY674621	TRF (Kool 1988)
Lacistemataceae						TRF (Adams 1972; Sleumer 1980; Cronquist 1981; Takhtajan 1997)
<i>Lacistema aggregatum</i> Rusby	Pennington et al. 583 (K)	AF206949	AF206787	AY674722	AF206949	TRF (Adams 1972; Sleumer 1980; Cronquist 1981; Takhtajan 1997)
Lepidobotryaceae ^a						TRF (Hammel and Zamora 1993; Takhtajan 1997)
<i>Ruptiliocarpon caracolito</i> Hammel & Zamora	Pennington & Zamora 631 (K); Hammel 19102 (MO)	AY788275	AJ402997	AY674765	AY788166	TRF (Hammel and Zamora 1993; Takhtajan 1997)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbL</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Linaceae						OT/T and TRF (Rogers and Mildner 1976; Cronquist 1981; Van Hooren and Nooteboom 1988b)
<i>Durandea pentagyna</i> K. Schum.	Takeuchi 7103 (MO)	AY788218	AY788173	AY674688	AY788150	TRF (Van Hooren and Nooteboom 1988b)
<i>Linum</i> spp.	Chase 111 (NCU); Chase 478 (K); Nickrent 2900 (SIU)	L24401	AY380351	AY674726	L24401	OT/T (Rogers 1969; Rogers and Mildner 1976; Cronquist 1981)
<i>Reinwardtia indica</i> Dumort.	Chase 230 (NCU)	AJ235577	L13188	AY674762	AF207005	OT/T (Robertson 1971; Cronquist 1981)
Lophopyxidaceae						TRF (Hutchinson 1973; Takhtajan 1997)
<i>Lophopyxis maingayi</i> Hook. f.	Adelbai P-10203 (US)	AY788235	AY663643	AY674728	AY674614	TRF (Hutchinson 1973; Takhtajan 1997)
Malesherbiaceae						OT/T (Cronquist 1981; Gentry 1996; Gengler-Novak 2002)
<i>Malesherbia linearifolia</i> Poir.	Chase 609 (K)	AF209622	AF206792	AY674731	AF206957	OT/T (Cronquist 1981; Gentry 1996; Gengler-Novak 2002)
Malpighiaceae						OT/T and TRF (Cronquist 1981) (SRFG)
<i>Acridocarpus natalitius</i> Adr. Juss.	Goldblatt s.n. (PRE)	AY788200	AF344455	AY674644	AY674573	OT/T and TRF (Davis et al. 2002b)
<i>Byrsonima crassifolia</i> (L.) H.B.K.	FTG 81-680A (MICH)	AY788206	L01892	AY674658	AY674579	OT/T (Anderson 2001)
<i>Dicella nucifera</i> Chodat	Anderson 13607 (MICH)	AJ235453	AJ235802	AY674681	AF206901	OT/T and TRF (Chase 1981; Gentry 1996)
<i>Thryallis longifolia</i> Mart.	Anderson 13657 (MICH)	AY788258	AF344516	AY674778	AY674638	OT/T (Anderson 1995)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Medusagynaceae						TRF (Robinson et al. 1989; Fay et al. 1997)
<i>Medusagyne oppositifolia</i> Baker	Fay s.n. (K) [Kew 1981–2059]	AJ235530	Z75670	AY674733	AF206959	TRF (Robinson et al. 1989; Fay et al. 1997)
Ochnaceae s.s. ^b						OT/T and TRF (Kanis 1968, 1971; Cronquist 1981; Amaral 1991)
<i>Cespedesia bonplandii</i> Goudot	Chase 1325 (K)	AY788208	AJ420168	AY674667	AY674583	TRF (Kanis 1971; Amaral 1991)
<i>Ochna multiflora</i> DC.	Chase 229 (NCU)	AJ235546	Z75273	AY788280	AF206974	OT/T and TRF (Kanis 1968, 1971; Amaral 1991)
<i>Ochna</i> sp.	Davis 31-01 (A)	AY788240	AY380354	AY674739	AY674620	OT/T and TRF (Kanis 1968, 1971; Amaral 1991)
Oxalidaceae ^a						OT/T and TRF (Robertson 1975)
<i>Averrhoa carambola</i> L.	Chase 214 (NCU)	AJ235404	L14692	AY674651	AF206859	TRF (Veldkamp 1971; Robertson 1975)
<i>Dapania racemosa</i> Korth.	Ambri & Arifin 1014 (K)	AY788266	AY788196	AY674678	AY674590	TRF (Veldkamp 1967, 1971; Robertson 1975)
Pandaceae						TRF (Forman 1966, 1971; Airy Shaw 1975; Cronquist 1981; Webster 1994b)
<i>Galearia filiformis</i> (Blume) Boerl.	Chase 1334 (K)	AY788222	AJ418818	AY674698	AY674598	TRF (Forman 1966, 1971; Airy Shaw 1975; Webster 1994b)
<i>Microdesmis</i> spp.	Gereau et al. 5654 (MO); Cheek 5986 (K)	AY788238	AJ402975; AJ403029	AY674737	AY674618	TRF (Léonard 1961; Forman 1966; Airy Shaw 1975; Webster 1994b)
<i>Panda oleosa</i> Pierre.	Schmidt et al. 2048 (MO)	AY788242	AY663644	AY788281	AY788153	TRF (Forman 1966, 1971; Webster 1994b)
Passifloraceae s.s. ^b						OT/T and TRF (Killip 1938; Brizicky 1961a; de Wilde 1971, 1972; Holm-Nielsen et al. 1988; MacDougal 1994)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
<i>Paropsia madagascariensis</i> (Baill.) H. Perrier	Zyhra 949 (WIS)	AF209645	AF206802	AY674744	AF206980	OT/T and TRF (Sleumer 1954; de Wilde 1975)
<i>Passiflora</i> spp.	Chase 2475 (K); MO 876630	AJ235553	L01940	AY674745	AF206981	OT/T and TRF (Killip 1938; Brizicky 1961a; de Wilde 1972; Holm-Nielsen et al. 1988; MacDougal 1994) TRF (Sandwith 1962)
Peridiscaceae ^a <i>Peridiscus lucidus</i> Benth.	Soares 205 (CEPEC)	AY372816	AY380356	AY674748	AY372815	TRF (Sandwith 1962)
Phyllanthaceae						OT/T and TRF (Airy Shaw 1975; Radcliffe-Smith 1987; Webster 1994b; Dorr 1999)
<i>Aporosa frutescens</i> Blume	Chase 1251 (K)	AY788201	Z75674	AY674647	AY788147	TRF (Airy Shaw 1975; Webster 1994b)
<i>Bischofia javanica</i> Blume	Levin 2200 (SD)	AY788205	AY663571	AY674654	AY674578	TRF (Webster 1994b)
<i>Croizatia</i> spp.	Berry et al. 4121 (US); Dorr & Yustiz 8555 (US)	AY788213	AY663579	AY674674	AY788148	TRF (Webster 1994b; Dorr 1999)
<i>Heywoodia lucens</i> Sim	Saufferer et al. 1544 (US)	AY788224	AY663587	AY674704	AY674602	OT/T and TRF (Radcliffe-Smith 1987)
<i>Phyllanthus epiphyllanthus</i> L.	Wurdack D56 (US)	AY788246	AY380358	AY674749	AY674627	OT/T and TRF (Webster 1994b) OT/T and TRF (Webster 1994b)
Picrodendraceae						
<i>Androstachys johnsonii</i> Prain	Chase 1904 (K)	AF209527	AJ402922	AY674646	AF206848	OT/T (Webster 1994b)
<i>Austrobuxus megacarpus</i> P. I. Forster	Forster 21239 (BRI)	AY788204	AY380343	AY788276	AY674576	TRF (Webster 1994b)
<i>Micrantheum hexandrum</i> Hook. f.	Chase 1940 (K)	AY788237	AJ418816	AY674736	AY674617	TRF (Bentham 1873; Webster 1994b)
<i>Petalostigma pubescens</i> Domin	Clifford s.n. (BRI)	AY788245	AY380357	AY788283	AY674626	OT/T (Airy Shaw 1980b)
<i>Podocalyx loranthoides</i> Klotzsch	Berry & Aymard 7226 (MO)	AY788248	AY663647	AY674752	AY674629	TRF (Webster 1994b)
<i>Tetracoccus dioicus</i> Parry	Levin 2202 (DUKE)	AY788256	AY788190	AY674774	AY788158	OT/T (Webster 1994b)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Podostemaceae						OT/T (van Royen 1953, 1954; Graham and Wood 1975; Cronquist 1981)
<i>Podostemum ceratophyllum</i> Michx.	Cusick 30042 (NY); Horn & Wurdack s.n. (DUKE)	AY788249	AJ418819	AY674754	AY788155	OT/T (van Royen 1953, 1954; Graham and Wood 1975; Cronquist 1981)
Putranjivaceae ^c						TRF (Airy Shaw 1975, 1980a; Webster 1994b)
<i>Drypetes diversifolia</i> Krug & Urb.	Wurdack D57 (US)			AY674687		TRF (Airy Shaw 1975, 1980a; Webster 1994b)
<i>Putranjiva roxburghii</i> Wall.	FTG-83463A	AF209578	M95757		U42534	TRF (Airy Shaw 1975, 1980a; Webster 1994b)
Quiinaceae						TRF (Cronquist 1981; Schneider et al. 2002)
<i>Quiina pteridophylla</i> (Radlk.) Pires	Pires S. A. (CPATU) ^d	AF209664	Z75689	AY674759	AF207003	TRF (Cronquist 1981; Schneider et al. 2002)
Rhizophoraceae s.s. ^b						TRF (Cronquist 1981; Juncosa and Tomlinson 1988a, 1988b; Schwarzbach and Ricklefs 2000)
<i>Bruguiera gymnorhiza</i> Lam.	Chase 12838 (K)	AF209547	AF127693	AY674656	AF206875	TRF (Cronquist 1981; Juncosa and Tomlinson 1988a, 1988b; Schwarzbach and Ricklefs 2000)
<i>Carallia brachiata</i> (Lour.) Merr.	Chase 2151 (K)	AJ235425	AF206744	AY674660	AF530810	TRF (Cronquist 1981; Juncosa and Tomlinson 1988a, 1988b; Schwarzbach and Ricklefs 2000)
<i>Paradrypetes subintegrifolia</i> G. A. Levin ^e	Acevedo-Rdgz. & Cedeño 7560 (US)	AY788243	AY788184	AY788282	AY788154	TRF (Levin 1992; Webster 1994b)
Salicaceae						OT/T and TRF (Cronquist 1981) (SRFG)
<i>Abatia parviflora</i> Ruiz & Pav.	Pennington 676 (K)	AF209519	AF206726	AY674641	AF206836	OT/T (Sleumer 1980)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
<i>Casearia</i> spp.	Chase 337 (K); Litt 17 (NY); Alford 26 (BH)	AF209557	AF206746	AY674663	AF206882	OT/T and TRF (Sleumer 1954, 1980)
<i>Dovyalis rhamnoides</i> Burch. ex Harv. & Sond.	Chase 271 (NCU)	AY788217	Z75677	AY674686	AY674592	TRF (Sleumer 1975)
<i>Flacourtia jangomas</i> Steud.	Chase 2150 (K)	AF209588	AF206768	AY674697	AF206912	OT/T and TRF (Sleumer 1954, 1975)
<i>Idesia polycarpa</i> Maxim.	Chase 561 (K); Wurdack D22 (US)	AF209604	AF206781	AY674716	AF206936	OT/T (Mabberley 1997)
<i>Lunania</i> sp.	Alford 69 (BH)	AY788236	AY788182	AY674729	AY674615	OT/T and TRF (Sleumer 1980)
<i>Poliothyrsis</i> sp.	Alford 44 (BH)	AY788251	AY788186	AY674756	AY674631	OT/T (Mabberley 1997)
<i>Populus</i> spp.	Chase 996 (K); Soltis & Soltis 2552 (WS)	AF209658	AJ418836	AY674757	AF206999	OT/T (Cronquist 1981; Mabberley 1997)
<i>Prockia</i> sp.	Alford 85 (BH)	AY788252	AY788187	AY674758	AY674632	OT/T and TRF (Sleumer 1980)
<i>Salix reticulata</i> L.	Chase 840 (K)	AJ235590	AJ235793	AY674767	AF207011	OT/T (Cronquist 1981)
<i>Scyphostegia borneensis</i> Stapf	Beaman 911 (BH)	AY788254	AJ403000	AY674770	AY674635	TRF (van Steenis 1957)
Trigoniaceae						TRF (Cronquist 1981)
<i>Trigonia nivea</i> Cambess.	Anderson 13656 (MICH)	AF209691	AF089761	AY674779	AF207047	TRF (Cronquist 1981)
Turneraceae						OT/T (Lewis 1954; Brizicky 1961a; Cronquist 1981; Arbo 1987, 1995)
<i>Turnera ulmifolia</i> L.	Chase 220 (NCU); Wurdack s.n. (US)	AJ235634	Z75691	AY674782	U42817	OT/T (Lewis 1954; Brizicky 1961a; Cronquist 1981; Arbo 1987, 1995)
Violaceae						OT/T and TRF (Brizicky 1961b; Cronquist 1981; Hekking 1988)
<i>Hybanthus</i> sp.	Alford 89 (BH)	AY788229	AY788178	AY674712	AY674607	OT/T and TRF (Brizicky 1961b)
<i>Hymenanchera alpina</i> Oliv.	Chase 501 (K)	AJ235499	Z75692	AY674713	AF206933	OT/T (Brizicky 1961b; Cronquist 1981; Hekking 1988)
<i>Leonia glycyarpa</i> Ruiz. & Pav.	Pennington 13852 (K)	AY788234	Z75693	AY674725	AY674613	TRF (Brizicky 1961b; Cronquist 1981; Hekking 1988)

Table B1 (Continued)

Taxon	Voucher	Plastid (<i>atpB</i>)	Plastid (<i>rbcl</i>)	Mitochondrial (<i>nad1B-C</i>)	Nuclear (<i>18S</i>)	Habitat
Incertae sedis (Centroplacaceae) <i>Centroplacus glauci-</i> <i>nus</i> Pierre	White 128, ser. 1 (MO)	AY788207	AY663646	AY788277	AY674582	TRF (Webster 1994a)

Note: Families follow APG (2003; but see footnoted modifications), and herbarium acronyms follow Holmgren et al. (1990). Primary habitat shown with source in parentheses: TRF = tropical rain forest; OT/T = open tropical/temperate forest. SRFG = see references for genera; s.s. = sensu stricto.

^a Indicates outgroups.

^b Several small segregate families sampled were maintained for the family-level scoring of habitat following the strict circumscriptions of APG (2003). For example, representatives of Chrysobalanaceae, Dichapetalaceae, Euphroniaceae, and Trigoniaceae were scored separately rather than as Chrysobalanaceae sensu lato. Other similar strict circumscriptions were followed for Ochnaceae, Passifloraceae, and Rhizophoraceae. Peridiscaceae have been excluded from Malpighiales following Davis and Chase (2004). Recent molecular evidence indicates that holoparasitic Rafflesiaceae s.s. are members of Malpighiales (Barkman et al. 2004; Davis and Wurdack 2004). They were not included in our data sets due to missing data. This is because the genes sampled here are largely unsuited for phylogenetic placement of Rafflesiaceae s.s. due to their reduced chloroplast genome (specifically, the loss of *atpB* and *rbcl*) and hypothesized horizontal gene transfer of mitochondrial *nad1B-C* from their obligate hosts *Tetrastigma* (Davis and Wurdack 2004).

^c Both genera are combined as one family OTU for molecular analysis.

^d Empresa Brasileira de Pesquisa Agropecuária.

^e Newly proposed family affiliation.

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APPENDIX C

Table C1: Clade age estimates

Clade name	Maximum age constraint 125 Ma			Maximum age constraint 109 Ma		
	Minimum	Optimal	Maximum	Minimum	Optimal	Maximum
1. Malpighiales	110.7	113.8	119.4	101.1	101.6	105.9
2. Euphorbiaceae	110.7	113.8	119.4	101.1	101.6	105.9
3. Rhizophoraceae s.l.	110.2	113.8	119.3	102.1	101.6	105.7
4. Pandaceae	110.2	113.8	118.7	101.9	101.6	105.5
5. Caryocaraceae	108.5	112.3	117.6	99.5	100.7	103.8
6. Humiriaceae	108.9	112.2	117.2	100.3	101.6	102.8
7. Ochnaceae s.l.	108.2	111.2	116.6	98.8	99.6	103.8
8. Ixonanthaceae	105.9	109.2	114.9	97.5	98.7	102.0
9. Phyllanthaceae	105.8	108.1	114.0	95.6	97.1	101.9
10. Picodendraceae	105.8	108.1	114.0	95.6	97.1	101.9
11. Passifloraceae s.l.	103.7	108.1	113.9	96.5	96.9	102.1
12. Violaceae	102.4	105.7	112.3	94.4	94.8	99.7
13. Irvingiaceae	102.5	105.0	112.5	93.3	94.5	98.4
14. Linaceae	102.5	105.0	112.5	93.3	94.5	98.4
15. Achariaceae	98.1	104.2	108.1	90.9	93.4	96.1
16. Goupiaceae	98.1	104.2	108.1	90.9	93.4	96.1
17. <i>Centroplacus</i>	96.6	101.8	109.6	88.1	91.0	97.1
18. Ctenolophonaceae	96.6	101.8	109.6	88.1	91.0	97.1
19. Lacistemataceae	96.1	99.8	107.7	89.0	90.1	95.9
20. Salicaceae	96.1	99.8	107.7	89.0	90.1	95.9
21. Balanopaceae	95.5	99.6	106.2	88.5	90.2	94.9
22. Chrysobalanaceae s.l.	95.5	99.6	106.2	88.5	90.2	94.9
23. Elatinaceae	89.0	98.2	113.2	85.0	89.1	99.6
24. Malpighiaceae	89.0	98.2	113.2	85.0	89.1	99.6
25. Clusiaceae	92.4	94.1	103.7	87.1	89.0	94.7
26. Bonnetiaceae	85.9	88.5	97.2	83.0	83.8	88.3
27. Lophopyxidaceae	82.9	86.7	97.0	74.8	77.8	85.2
28. Putranjivaceae	82.9	86.7	97.0	74.8	77.8	85.2
29. Hypericaceae	68.9	76.4	82.4	66.4	72.4	73.9
30. Podostemaceae	68.9	76.4	82.4	66.4	72.4	73.9

Note: Optimal age estimates, with minimum and maximum error estimates, for major Malpighiales clades (i.e., families [stem group], except for *Centroplacus*). Sensu lato (s.l.) designations follow APG (2003). See figure C1 for full penalized likelihood chronogram and figure C2 for Bayesian tree with likelihood branch lengths.

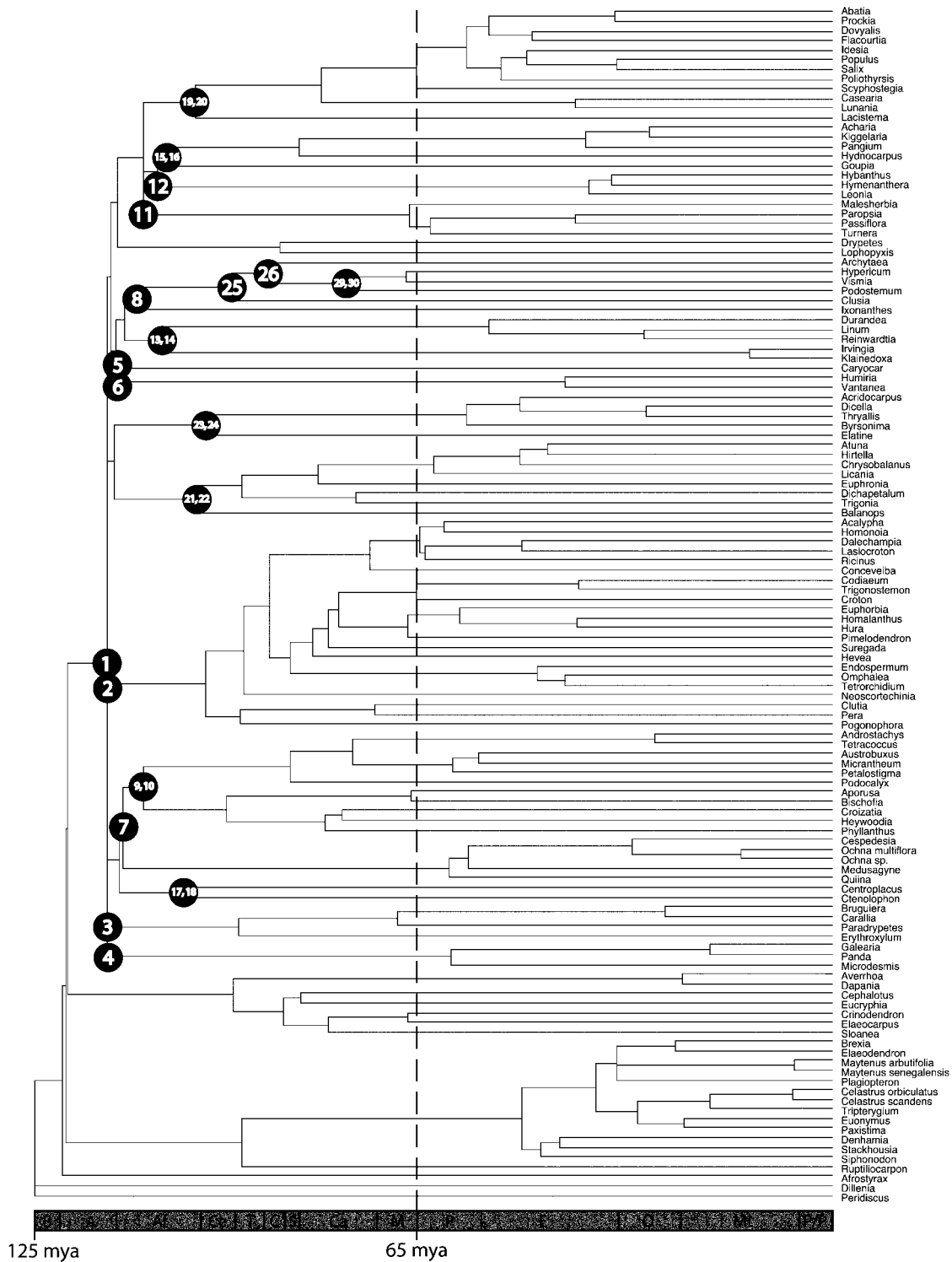


Figure C1: Complete 124-taxon penalized likelihood chronogram (from main text, fig. 1). Numbered nodes on chronogram correspond to numbered clades shown in table C1. The K/T boundary (~65 Ma) is marked with a dashed line. The scale bar indicates major Cretaceous and Cenozoic intervals: *B* = Barremian, *A* = Aptian, *Al* = Albian, *Ce* = Cenomanian, *T* = Turonian, *C* = Coniacian, *S* = Santonian, *Ca* = Campanian, *M* = Maastrichtian, *P* = Paleocene, *E* = Eocene, *O* = Oligocene, *Mi* = Miocene, *P/P* = Pliocene/Pleistocene.

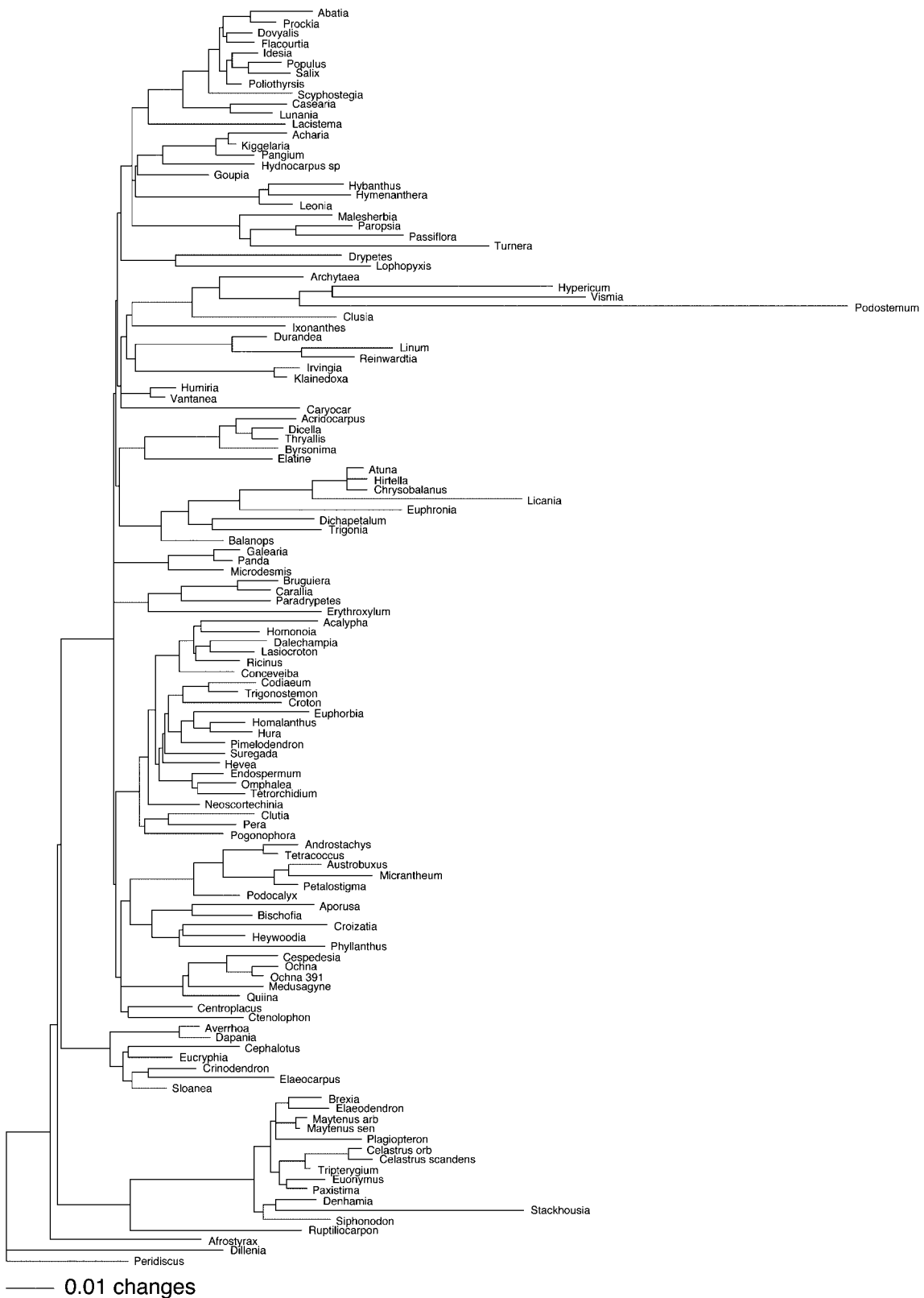


Figure C2: Complete 124-taxon Bayesian tree with likelihood branch lengths used for r8s analysis

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