High-latitude Tertiary Migrations of an Exclusively Tropical Clade: Evidence from Malpighiaceae

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HIGH-LATITUDE TERTIARY MIGRATIONS OF AN EXCLUSIVELY TROPICAL CLADE: EVIDENCE FROM MALPIGHIACEAE

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Explanations of tropical intercontinental disjunctions involving South America and Africa typically invoke vicariance of western Gondwanan biotas or long-distance dispersal. However, many plant groups originated and diversified well after the last direct connection between Africa and South America (ca. 105 million years before the present [mybp]), and it is unlikely that long-distance dispersal accounts for the distribution of all of these. A less commonly invoked explanation, the boreotropics hypothesis, indicates that some tropical disjunctions arose during the Tertiary via high-latitude land connections when northern forests supported tropical vegetation. Malpighiaceae are widely distributed across Africa and South America and have been explained as ancient "Gondwanian aborigines" (i.e., vicariants of western Gondwanan biotas) or more recent "American colonists" (i.e., long-distance dispersalists from South America into the Old World). Fossil and phylogenetic evidence from clock-independent estimates of molecular divergence times indicate that Malpighiaceae originated in South America during the latest Cretaceous (ca. 68 mybp), in isolation from Africa, and that six amphi-Atlantic disjunctions within the family occurred during three major episodes: late Paleocene (ca. 60 mybp), latest Eocene–earliest Oligocene (ca. 34–31 mybp), and early Miocene (ca. 21–17 mybp). These age estimates reject a Gondwanan origin for Malpighiaceae, and strict dispersal scenarios ignore paleoclimate, paleoland configurations, and fossil evidence that indicates that the family once inhabited northern latitudes. Instead, these data suggest that Paleocene–Oligocene amphi-Atlantic disjunct groups in Malpighiaceae moved into North America from South America via the Caribbean Basin, crossed the North Atlantic into Eurasia, and subsequently reached the Old World Tropics during warm intervals when land configurations would have facilitated this migration. Whether Miocene migrations of evergreen thermophilic Malpighiaceae proceeded via northern latitudes or long-distance dispersal is less clear.

Keywords: Africa, biogeography, long-distance dispersal, nonparametric rate smoothing, penalized likelihood, South America, vicariance, western Gondwana.

Introduction

Numerous tropical flowering plant lineages have disjunct distributions in Africa (including Madagascar) and South America, and many of these also include a minor Asian component (Thorne 1972). Vicariance of western Gondwanan biotas is often invoked to explain these tropical intercontinental disjunctions (Raven and Axelrod 1974; Gentry 1982, 1993). For example, on the basis of fossil and phylogenetic evidence, Doyle and Le Thomas (1997) inferred that many modern genera of Annonaceae originated and diversified in western Gondwana during the Cretaceous, when lineages moved easily between these connected, or nearly connected, land masses (their fig. 3B).

Although vicariance is a plausible scenario for some amphi-Atlantic tropical disjunct lineages, it is apparent that many such plant groups originated and diversified well after the last

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direct connection between Africa and South America, ca. 105 million years before the present (mybp; Magallón et al. 1999; Magallón and Sanderson 2001; continental breakup *sensu* McLoughlin 2001; Wikström et al. 2001). Vicariance cannot account for the distribution of these groups. Instead, long-distance dispersal across the southern Atlantic is often invoked as an alternative scenario (Smith 1973; Thorne 1973; Bremer 1993). For example, *Rhipsalis baccata* (J. S. Muell.) Stearn is a widespread cactus species that occurs throughout the American Tropics, Africa, Madagascar (and adjacent islands), and Ceylon (Thorne 1973; Barthlott 1983; Barthlott and Taylor 1995). The mid-Tertiary origin of Cactaceae (ca. 30 mybp; Hershkovitz and Zimmer 1997; Nyffeler 2002) and the sticky, copious seeds (Barthlott 1983) of this derived species (Nyffeler 2002) suggest that it traveled by long-distance bird dispersal from the New World, where cacti originated, across the Atlantic to the Old World Tropics (Thorne 1973; Barthlott 1983; Gibson and Nobel 1986; Barthlott and Hunt 1993; Nyffeler 2002).

Despite the importance of long-distance dispersal in the distribution of plants, it cannot account for all of the
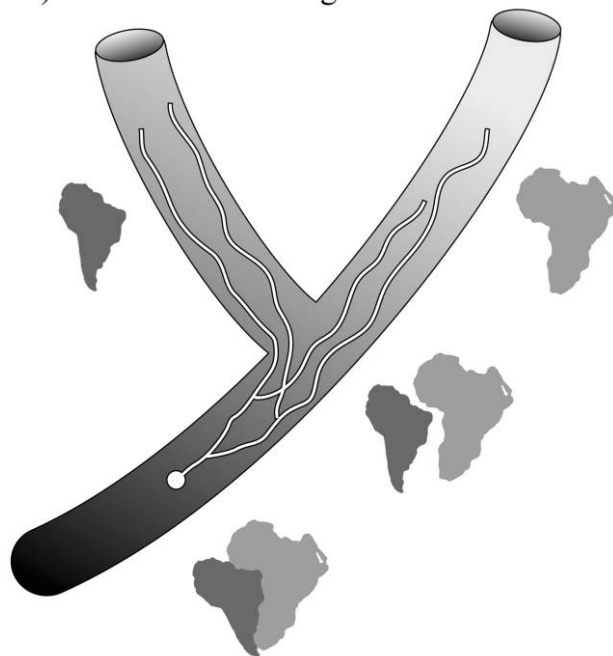
amphi-Atlantic tropical disjunctions that do not result from vicariance. Many taxa with very different dispersal capabilities have nearly identical distributions, suggesting that other mechanisms come into play (Tiffney and Manchester 2001). The existence of a tropical-like, or "boreotropical" (Wolfe 1975), flora extending across the high-latitude regions of the Northern Hemisphere during the Tertiary indicates that conditions were amenable to the northerly intercontinental migration of thermophilic lineages. Moreover, a North Atlantic land bridge connecting North America, Greenland, and Europe is thought to have served as an important conduit for plant migration starting in the Paleocene/Eocene, when local climates were warm enough for frost-intolerant lineages to occur in this region. The low-latitude position of the bridge (perhaps to 45°N) would have provided light levels and climatic conditions sufficient for the presence of evergreen lineages (Tiffney 1985a, 1985b; Donoghue et al. 2001; Sanmartín et al. 2001; Tiffney and Manchester 2001; Zachos et al. 2001). Although the North Atlantic has been recognized as a viable corridor for the migration of thermophilic lineages now restricted to tropical regions, including those with African/South American disjuncts (Raven and Axelrod 1974), mounting evidence from paleontological and phylogenetic studies indicates that this corridor may have been far more important than previously realized for the intercontinental migration of such groups (Krutzsch 1989; Lavin and Luckow 1993; Doyle and Le Thomas 1997, their fig. 3C;

Fritsch 1999, 2001; Lavin et al. 2000; Chanderbali et al. 2001; Renner et al. 2001; Davis et al. 2002a, 2002b).

Most of the hypotheses for the biogeographical history of amphi-Atlantic tropical disjuncts have not been tested within a molecular phylogenetic framework. Recent advances in the methods for estimating divergence times in the absence of a molecular clock, and in methods for incorporating fossils into analyses of divergence times (Sanderson 1997, 1998, 2002, 2003), have provided an opportunity to begin testing such hypotheses. Here we apply molecular and fossil data to better understand the history of amphi-Atlantic tropical disjuncts in Malpighiaceae.

Malpighiaceae are a lineage of trees, shrubs, and vines distributed widely across the tropical and subtropical forests and savannas of the New and Old Worlds. Their present distribution, with only two species common to both these areas (perhaps recently introduced by humans from the New World into Africa; Anderson 1990), has invited repeated speculation about their origin and diversification (Raven and Axelrod 1974; Anderson 1979, 1990; Vogel 1990). Vogel (1990) proposed the "Gondwanian aborigine" hypothesis, which attributes the current distribution to vicariance of western Gondwana (fig. 1A). It implies that the family is relatively old and originated before western Gondwana divided, as did disjuncts between New and Old World species. Anderson (1981, 1990) and others (Raven and Axelrod 1974) proposed the "American colonist" hypothesis, which suggests
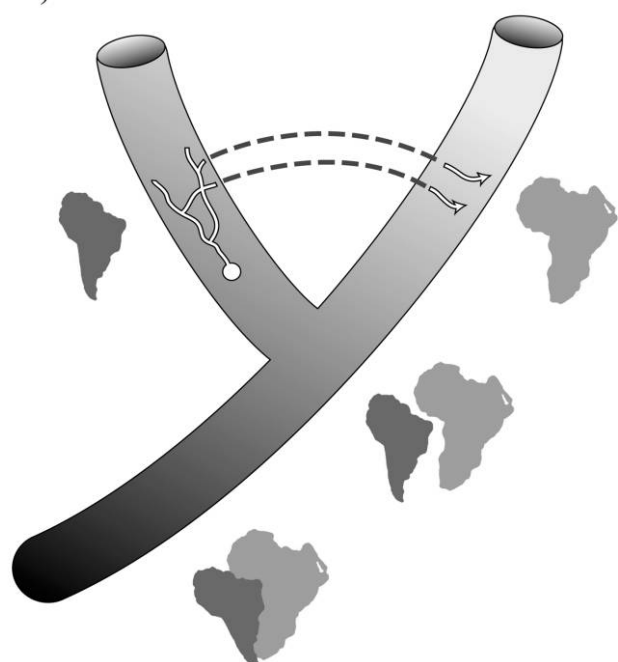
Fig. 1 Gondwanian aborigine hypothesis for Malpighiaceae. *A*, Origin and diversification of intercontinental disjunctions between Africa and South America are ancient (i.e., at least ca. 105 mybp) and attributable to continental breakup. Outer (containing) tree corresponds to the breakup of these landmasses and inner (contained) tree to the origin and diversification of disjunct groups. American colonist hypothesis for Malpighiaceae. *B*, Origin and diversification of intercontinental disjunctions between Africa and South America are attributable to more recent long-distance dispersal from South America across the southern Atlantic Ocean into Africa. Dashed lines indicate transatlantic dispersals. Other disjunct groups for scenario *B* may have had their origins in Africa and instead dispersed westward.

that the family is relatively young and originated in northern South America in isolation from Africa and dispersed eastward across the southern Atlantic at least twice (fig. 1*B*). This hypothesis implies that Malpighiaceae originated after western Gondwana divided and that the divergence times between New and Old World lineages are younger than the most recent connection between South America and Africa. On the basis of fossil and phylogenetic evidence of Malpighiaceae, Davis et al. (2002*b*) proposed that the family originated in South America, in isolation from Africa, and reached the Old World Tropics via high-latitude North Atlantic land connections during warm climatic intervals, perhaps followed by vicariance through climatic cooling. This North Atlantic corridor may have facilitated the migration of several different lineages of Malpighiaceae throughout the Tertiary (Davis et al. 2002*b*). This scenario (Davis et al. 2002*b*) is similar to Anderson's (1990) hypothesis in that both claim more recent amphi-Atlantic divergence times for Malpighiaceae; Anderson, however, claims long-distance dispersal to explain such disjunctions, whereas Davis et al. (2002*b*) claim Northern Hemisphere migration followed by vicariance.

To evaluate the biogeographical history of Malpighiaceae, we estimated molecular divergence times across the family using ca. 2000 nucleotides of plastid *ndh*F and nuclear *PHYC* coding sequence data from 106 species. This data set is similar to that analyzed by Davis et al. (2002*b*) but includes 35 new taxa and two additional fossil calibration points. One limitation of the study by Davis et al. (2002*b*) was its reliance on minimum divergence estimates to test Gondwanan versus alternative scenarios. This study places a maximum age constraint on lineage divergence based on the origin and distribution of the densely sampled eudicot clade, thus incorporating a reliable lower bound on the origin of the family. Also, we contrast estimates of divergence times using both methods, nonparametric rate smoothing (NPRS; Sanderson 1997) and penalized likelihood (PL; Sanderson 2002). PL has been shown (Sanderson 2002) to outperform both clock (Langley and Fitch 1974) and nonclock NPRS methods whenever data depart significantly from a molecular clock.

Material and Methods

Taxon Sampling

The *PHYC* and *ndh*F data sets contain 103 ingroup taxa and three outgroups; 32 *PHYC* and 28 *ndh*F sequences were newly generated for this study (table 1). These data sets include ca. 12% of the total species diversity of Malpighiaceae, representing 56 of the 66 currently recognized genera (*Banisteriopsis*, *Clonodia*, *Cordobia*, *Dinemagonum*, *Excentradenia*, *Henleophytum*, and *Mezia* from the New World and *Flabellaria*, *Flabellariopsis*, and *Digoniopterys* from the Old World are not included; see also Davis et al. 2001). Members of the family encompass a range of tropical habitats from lowland rain forest to open savannas.

Within the order Malpighiales (APG 2003), Elatinaceae are strongly placed as sister to Malpighiaceae on the basis of plastid (*rbc*L plus *ndh*F) and nuclear (*PHYC*) sequence data

(Davis and Chase 2004) and were included here as outgroups. *Androstachys johnsonnii* (Picrodendraceae) was also included as an additional, more distantly related, outgroup to the Elatinaceae-Malpighiaceae clade (Davis and Chase 2004).

Molecular Methods

Protocols for extracting DNA, PCR amplification of *ndh*F and *PHYC*, cloning (for *PHYC*), and automated sequencing generally followed those reported by Davis et al. (2002*a* and references cited within; but see also 2001 and 2002*b*). Nucleotide and amino acid sequences were aligned manually, and the ends were trimmed from each data set to maintain complementarity among taxa. The *PHYC* and *ndh*F data sets contained 1180 and 810 nucleotides, respectively, before trimming ends.

Phylogenetic Methods

Data sets were analyzed in combination and included 1830 nucleotides. To assess the level of congruence between these data partitions, we employed the incongruence length difference test (ILD; Farris et al. 1994), implemented in PAUP* version 4.0b10 (Swofford 2002), as the partition-homogeneity test. We used simple taxon addition (saving 10 trees per replicate) with all uninformative characters excluded, tree bisection-reconnection (TBR) branch swapping, and heuristic searches with 999 repartitions of the data and MulTrees in effect. Gap positions were treated as missing, all characters were weighted equally, and character states were unordered (Fitch parsimony; Fitch 1971). Bootstrap percentages (Felsenstein 1985) for each clade were estimated from 100 heuristic search replicates as above but with simple taxon addition in effect.

A series of hierarchical likelihood ratio tests (Felsenstein 1981; Huelsenbeck and Rannala 1997) was performed with Modeltest version 3.06 (Posada and Crandall 1998) to determine which model of sequence evolution best fit the data. Bayesian analyses were carried out under the preferred model of sequence evolution with Metropolis-coupled Markov chain Monte Carlo (MC^3) methods implemented in MrBayes version 2.01 (Huelsenbeck and Ronquist 2001). The chain was run for 40 million generations, initiated with a random starting tree, and sampled every 1000 generations; 40,000 trees were sampled from the posterior distribution, which were used to calculate posterior clade probabilities (sample points collected before stationarity, i.e., "burn-in," were eliminated). The incremental heating scheme for each MC^3 search used the default settings in MrBayes (three "heated" chains and one "cold" chain). We also used the defaults for the priors on the rate matrix (0–100), branch lengths (0–10), gamma shape parameter (0–10), and the proportion of invariable sites (0–1). A Dirichlet distribution was used for the base frequency parameters, and an uninformative prior was used for the tree topology.

Dating Methods

We used the single fixed Bayesian tree topology with the lowest likelihood score to test for rate constancy between

Table 1

Taxa Sequenced with Distribution, Voucher Information, and GenBank (GBAN) Accession Numbers

Taxon	Distribution	Voucher	Plastid ndhF	Nuclear PHYC
Elatinaceae[a]:				
Bergia texana Seub. ex Walp.	NW	Sanders et al. 13525 (MICH)	GBAN-AY425033[b]	GBAN-AY425091[b]
Elatine triandra Schkuhr	NW	Burton et al. 13384 (MICH)	GBAN-AY425049[b]	GBAN-AY425104[b]
Picrodendraceae[a]:				
Androstachys johnsonii Prain	OW	Chase 1904 (K)	GBAN-AF500495[c]	GBAN-AF500522[c]
Malpighiaceae:				
Acmanthera latifolia (Adr. Juss.) Griseb. in Mart.	NW	Anderson 13771 (MICH)	GBAN-AF351013[d]	GBAN-AF500528[c]
Acridocarpus adenophorus Adr. Juss.	OW	SMG 3399	GBAN-AY137243[e]	GBAN-AY499049
Acridocarpus chevalieri Sprague	OW	Davis 99-15 (A)	GBAN-AY137247[e]	GBAN-AY499050
Acridocarpus excelsus Adr. Juss.	OW	Rakotomalaza et al. 378 (MO)	GBAN-AY137248[e]	GBAN-AY499051
Acridocarpus macrocalyx Engl.	OW	Davis 99-09 (A)	GBAN-AF351017[d]	GBAN-AF500532[c]
Acridocarpus natalitius Adr. Juss.	OW	Goldblatt s.n. (PRE)	GBAN-AF351016[d]	GBAN-AF500531[c]
Acridocarpus orientalis Adr. Juss.	OW	Popov 85 (MO)	GBAN-AY137255[e]	GBAN-AY499052
Acridocarpus smeathmannii (DC.) Guill. & Perr. in Guill. et al.	OW	Davis 99-13 (A)	GBAN-AY137261[e]	GBAN-AY499053
Acridocarpus zanzibaricus Adr. Juss.	OW	Davis 99-23 (A)	GBAN-AY137264[e]	GBAN-AY499054
Aspicarpa brevipes (DC.) W. R. Anderson	NW	Cházaro 6295 (MICH)	GBAN-AF351082[d]	GBAN-AF500581[c]
Aspicarpa hirtella Rich.	NW	Anderson 13525 (MICH)	GBAN-AF351033[d]	GBAN-AF500541[c]
Aspidopterys elliptica (Blume) Adr. Juss.	OW	XVI.G.110 (BO)	GBAN-AF351019[d]	GBAN-AF436796[f]
Barnebya dispar (Griseb. in Mart.) W. R. Anderson & B. Gates	NW	Leoni 1473 (MICH)	GBAN-AF351073[d]	GBAN-AF500574[c]
Blepharandra heteropetala W. R. Anderson	NW	Anderson 13782 (MICH)	GBAN-AF351008[d]	GBAN-AF500523[c]
Brachylophon curtisii Oliv.	OW	Middleton et al. 387 (A)	GBAN-AF351018[d]	GBAN-AY137337[e]
Bunchosia armeniaca (Cav.) DC.	NW	FTG77-999C (FTG)	GBAN-AF351045[d]	GBAN-AF500550[c]
Burdachia sphaerocarpa Adr. Juss.	NW	Anderson 13774 (MICH)	GBAN-AF351071[d]	GBAN-AF500572[c]
Byrsonima crassifolia (L.) H. B. K.	NW	FTG81-680A (MICH)	GBAN-AF351011[d]	GBAN-AF500526[c]
Callaeum septentrionale (Adr. Juss.) D. M. Johnson	NW	Anderson 13491 (MICH)	GBAN-AF351058[d]	GBAN-AF500562[c]
Camarea axillaris A. St.-Hil.	NW	Amorim 3659 (CEPEC)	GBAN-AY499081	GBAN-AY499055
Caucanthus auriculatus (Radlk.) Nied.	OW	Knox 2128 (MICH)	GBAN-AF351020[d]	GBAN-AF436797[f]
Coleostachys genipifolia Adr. Juss.	NW	Anderson 13752 (MICH)	GBAN-AF351012[d]	GBAN-AF500527[c]
Diacidia ferruginea (Maguire & K. D. Phelps) W. R. Anderson	NW	Berry et al. 4987 (MICH)	GBAN-AF351010[d]	GBAN-AF500525[c]
Dicella nucifera Chodat	NW	Anderson 13607 (MICH)	GBAN-AF351048[d]	GBAN-AF500553[c]
Dinemandra ericoides Adr. Juss.	NW	Dillon & Teillier 5103 (MICH)	GBAN-AF351069[d]	GBAN-AF500570[c]
Diplopterys cabrerana (Cuatrec.) B. Gates	NW	Burnham 1774 (MICH)	GBAN-AF351039[d]	GBAN-AF500582[c]
Echinopterys eglandulosa (Adr. Juss.) Small	NW	Van Devender 98-178 (MICH)	GBAN-AF351047[d]	GBAN-AF500552[c]
Ectopopterys soejartoi W. R. Anderson	NW	Callejas 11806 (MICH)	GBAN-AF351064[d]	GBAN-AF500565[c]
Gallardoa fischeri Hicken	NW	Anderson 13580 (MICH)	GBAN-AF351035[d]	GBAN-AF500543[c]
Galphimia gracilis Bartl.	NW	FTG79-235 (FTG)	GBAN-AF351015[d]	GBAN-AF500530[c]
Gaudichaudia albida Schlechtend. & Cham.	NW	Anderson 13309A (MICH)	GBAN-AF351034[d]	GBAN-AF500542[c]
Gaudichaudia mcvaughii W. R. Anderson	NW	Anderson 12699C (MICH)	GBAN-AF351032[d]	GBAN-AF500540[c]
Glandonia macrocarpa Griseb. in Mart.	NW	Anderson 13776 (MICH)	GBAN-AF351072[d]	GBAN-AF500573[c]

Table 1

(*Continued*)

Taxon	Distribution	Voucher	Plastid ndhF	Nuclear PHYC
Heladena multiflora (Hook & Arn.) Nied.	NW	Anderson 13599 (MICH)	GBAN-AF351044[d]	GBAN-AF500549[c]
Heteropterys aureosericea Cuatrec.	NW	Burnham 3344 (MICH)	GBAN-AY499082	GBAN-AY499056
Heteropterys bahiensis Nied.	NW	Amorim 3664 (CEPEC)	GBAN-AY499083	GBAN-AY499057
Heteropterys bicolor Adr. Juss. in A. St.-Hil.	NW	Amorim 2710 (CEPEC)	GBAN-AY499084	GBAN-AY499058
Heteropterys byrsonimifolia Adr. Juss.	NW	Amorim 3663 (CEPEC)	GBAN-AY499085	GBAN-AY499059
Heteropterys capixaba A. Amorim	NW	Amorim 3317 (CEPEC)	GBAN-AY499086	GBAN-AY499060
Heteropterys catingarum Adr. Juss.	NW	Souza 455 (CEPEC)	GBAN-AY499087	GBAN-AY499061
Heteropterys chrysophylla (Lam.) DC.	NW	Amorim 3097 (CEPEC)	GBAN-AY499088	GBAN-AY499062
Heteropterys ciliata Nied.	NW	Anderson 13778 (MICH)	GBAN-AF351049[d]	GBAN-AF500554[c]
Heteropterys leona (Cav.) Exell	NW & OW	Davis 99-5 (A)	GBAN-AF351050[d]	GBAN-AF500555[c]
Heteropterys lindleyana Adr. Juss.	NW	Amorim 3375 (CEPEC)	GBAN-AY499089	GBAN-AY499063
Heteropterys megaptera Adr. Juss.	NW	Amorim 3667 (CEPEC)	GBAN-AY499090	GBAN-AY499064
Heteropterys nitida (Lam.) DC.	NW	Amorim 3327 (CEPEC)	GBAN-AY499091	GBAN-AY499065
Heteropterys pauciflora (Adr. Juss. in A. St.-Hil.) Adr. Juss.	NW	Amorim 3623 (CEPEC)	GBAN-AY499092	GBAN-AY499066
Heteropterys rhopalifolia Adr. Juss.	NW	Amorim 2879 (CEPEC)	GBAN-AY499093	GBAN-AY499067
Heteropterys sanctorum W. R. Anderson	NW	Amorim 3653 (CEPEC)	GBAN-AY499094	GBAN-AY499068
Heteropterys sericea (Cav.) Adr. Juss. in A. St.-Hil.	NW	Amorim 3342 (CEPEC)	GBAN-AY499095	GBAN-AY499069
Heteropterys sincorensis W. R. Anderson	NW	Queiroz 7145 (CEPEC)	GBAN-AY499096	GBAN-AY499070
Heteropterys steyermarkii W. R. Anderson	NW	Maguire & Politi 27524 (MICH)	GBAN-AY499097	GBAN-AY499071
Heteropterys ternstroemiifolia Adr. Juss.	NW	Amorim 3619 (CEPEC)	GBAN-AY499098	GBAN-AY499072
Heteropterys trichanthera Adr. Juss.	NW	Amorim 3019 (CEPEC)	GBAN-AY499099	GBAN-AY499073
Hiptage benghalensis (L.) Kurz	OW	Herbst 9221 (MICH)	GBAN-AF351057[d]	GBAN-AF500561[c]
Hiraea fagifolia (DC.) Adr. Juss.	NW	Anderson 13593 (MICH)	GBAN-AF351060[d]	GBAN-AF500564[c]
Janusia anisandra (Adr. Juss.) Griseb. in Mart.	NW	Anderson 13694 (MICH)	GBAN-AF351028[d]	GBAN-AF500536[c]
Janusia californica Benth.	NW	Anderson 12539 (MICH)	GBAN-AF351031[d]	GBAN-AF500539[c]
Janusia linearis Wiggins	NW	Anderson 12540 (MICH)	GBAN-AF351030[d]	GBAN-AF500538[c]
Janusia mediterranea (Vell.) W. R. Anderson	NW	Anderson 13686 (MICH)	GBAN-AF351029[d]	GBAN-AF500537[c]
Jubelina wilburii W. R. Anderson	NW	Anderson 13789 (MICH)	GBAN-AY499100	GBAN-AY499074
Lasiocarpus sp.	NW	Anderson 13834 (MICH)	GBAN-AF351066[d]	GBAN-AF500567[c]
Lophanthera lactescens Ducke	NW	Anderson 13781 (MICH)	GBAN-AF351009[d]	GBAN-AF500524[c]
Lophopterys floribunda W. R. Anderson & C. Cav. Davis	NW	Anderson 13754 (MICH)	GBAN-AF351078[d]	GBAN-AF500579[c]
Madagasikaria andersonii C. Cav. Davis	OW	Davis et al. 20-01 (A)	GBAN-AF436790[f]	GBAN-AF436800[f]
Malpighia emarginata DC.	NW	Anderson 13621 (MICH)	GBAN-AF351023[d]	GBAN-AF436799[f]
Malpighia stevensii W. R. Anderson	NW	Davis 1019 (MICH)	GBAN-AF351022[d]	GBAN-AF436798[f]
Mascagnia anisopetala (Adr. Juss. in A. St.-Hil.) Griseb. in Mart.	NW	Anderson 13598 (MICH)	GBAN-AF351053[d]	GBAN-AF500557[c]
Mascagnia bracteosa Griseb. in Mart.	NW	Anderson 13777 (MICH)	GBAN-AF351055[d]	GBAN-AF500559[c]
Mascagnia chasei W. R. Anderson	NW	Anderson 13710 (MICH)	GBAN-AF351054[d]	GBAN-AF500558[c]
Mascagnia dipholiphylla (Small) Bullock	NW	Anderson 13816 (MICH)	GBAN-AF351063[d]	GBAN-AF436795[f]
Mascagnia hippocrateoides (Triana & Planch.) Nied.	NW	Anderson 13802 (MICH)	GBAN-AF351059[d]	GBAN-AF500563[c]
Mascagnia rigida (Adr. Juss. in A. St.-Hil.) Griseb. in Mart.	NW	Anderson 13691 (MICH)	GBAN-AY499101	GBAN-AY499075

Table 1

(*Continued*)

Taxon	Distribution	Voucher	Plastid ndhF	Nuclear PHYC
Mascagnia sepium (Adr. Juss. in A. St.-Hil.) Griseb. in Mart.	NW	Chase 90160 (MICH)	GBAN-AF351025[d]	GBAN-AF436804[f]
Mascagnia stannea (Griseb.) Nied.	NW	Anderson 13804 (MICH)	GBAN-AF351056[d]	GBAN-AF500560[c]
Mcvaughia bahiana W. R. Anderson	NW	Anderson 13690 (MICH)	GBAN-AF351070[d]	GBAN-AF500571[c]
Microsteira sp.	OW	Davis et al. 38-01 (A)	GBAN-AF436791[f]	GBAN-AF436803[f]
Mionandra camareoides Griseb.	NW	Anderson 13585 (MICH)	GBAN-AF351080[d]	GBAN-AF500580[c]
Peixotoa glabra Adr. Juss. in A. St.-Hil.	NW	Anderson 13636 (MICH)	GBAN-AF351036[d]	GBAN-AF500544[c]
Peregrina linearifolia (A. St.-Hil.) W. R. Anderson	NW	Krapovickas & Cristóbal 46451 (MICH)	GBAN-AY499102	GBAN-AF500535[c]
Philgamia glabrifolia Arènes	OW	Davis 40-01 (A)	GBAN-AY499103	GBAN-AY499076
Pterandra arborea Ducke	NW	Anderson 13766 (MICH)	GBAN-AF351014[d]	GBAN-AF500529[c]
Ptilochaeta bahiensis Turcz.	NW	Anderson 13725 (MICH)	GBAN-AF351068[d]	GBAN-AF500569[c]
Ptilochaeta nudipes Griseb.	NW	Anderson 13588 (MICH)	GBAN-AF351067[d]	GBAN-AF500568[c]
Rhynchophora phillipsonii W. R. Anderson	OW	Davis et al. 23b-01 (A)	GBAN-AF436793[f]	GBAN-AF436802[f]
Ryssopterys timoriensis (DC.) Adr. Juss. in Deless.	OW	XVIII.F.172 (BO)	GBAN-AF351040[d]	GBAN-AF500545[c]
Spachea correae Cuatrec. & Croat	NW	Hammel 17746 (MO)	GBAN-AF351074[d]	GBAN-AF500575[c]
Sphedamnocarpus sp. (accession a)	OW	Davis 03-01 (A)	GBAN-AY499104	GBAN-AF500546[c]
Sphedamnocarpus sp. (accession b)	OW	Davis 39-01 (A)	GBAN-AY499105	GBAN-AY499077
Stigmaphyllon paralias Adr. Juss. in A. St.-Hil.	NW	Anderson 13693 (MICH)	GBAN-AF351065[d]	GBAN-AF500566[c]
Stigmaphyllon puberum (Rich.) Adr. Juss.	NW	Anderson 13793 (MICH)	GBAN-AF351038[d]	GBAN-AF436794[f]
Stigmaphyllon sagraeanum Adr. Juss.	NW	FTGX-1-6 (FTG)	GBAN-AF351077[d]	GBAN-AF500578[c]
Tetrapterys discolor (G. Mey.) DC.	NW	Chase 90158 (MICH)	GBAN-AF351076[d]	GBAN-AF500577[c]
Tetrapterys microphylla (Adr. Juss. in A. St.-Hil.) Nied.	NW	Anderson 13644 (MICH)	GBAN-AF351052[d]	GBAN-AF500556[c]
Thryallis longifolia Mart.	NW	Anderson 13657 (MICH)	GBAN-AF351046[d]	GBAN-AF500551[c]
Triaspis hypericoides Burch.	OW	Immelman 650 (PRE)	GBAN-AF351021[d]	GBAN-AF500533[c]
Tricomaria usillo Hook. & Arn.	NW	Anderson 13581 (MICH)	GBAN-AF351075[d]	GBAN-AF500576[c]
Triopterys rigida Sw.	NW	Hammel 17816 (MICH)	GBAN-AF351024[d]	GBAN-AF500534[c]
Tristellateia africana S. Moore	OW	Davis 99-25 (A)	GBAN-AF351043[d]	GBAN-AF500548[c]
Tristellateia madagascariensis Poir. in Lam.	OW	McPherson 14398 (MICH)	GBAN-AF351042[d]	GBAN-AF500547[c]
Tristellateia sp. (accession a)	OW	Davis 19-01 (A)	GBAN-AY499106	GBAN-AY499078
Tristellateia sp. (accession b)	OW	Davis 29-01 (A)	GBAN-AY499107	GBAN-AY499079
Verrucularia glaucophylla Adr. Juss.	NW	Amorim 3662 (CEPEC)	GBAN-AY499108	GBAN-AY499080

Note.   Herbarium acronyms follow Holmgren et al. (1990). Distribution: NW = New World; OW = Old World.

[a] Outgroups.

[b] Previously sampled from Davis and Chase (2004).

[c] Previously sampled from Davis et al. (2002*b*).

[d] Previously sampled from Davis et al. (2001).

[e] Previously sampled from Davis et al. (2002*a*).

[f] Previously sampled from Davis (2002).

clock versus nonclock trees using $2(\ln L_1 - \ln L_0)$ as a test statistic. This was compared to a χ^2 distribution to assess significance (with $n - 2$ degrees of freedom, where $n =$ number of taxa). Because rate constancy was rejected ($P < 0.001$, $-\ln L$ unconstrained $= 22,500.89$ vs. constrained $= 22,677.55$; df $= 104$), we used clock-independent NPRS (Sanderson 1997) and PL (Sanderson 2002) methods implemented in r8s version 1.6 (Sanderson 2003; http://ginger.ucdavis.edu/r8s) to estimate absolute ages. These methods relax the assumptions of global or local molecular clocks by smoothing changes of nucleotide substitution across the tree. NPRS is a nonparametric method that estimates rates and times by using a least square criterion, which penalizes rapid rate changes across branches in a phylogeny (Sanderson 1997). PL is a semiparametric method that combines the statistical power of parametric methods (models of molecular evolution) with the robustness of nonparametric methods by assigning penalties to limit rate changes between adjacent branches on a phylogeny. Like NPRS, PL assumes that there is an autocorrelation of substitution rates and attempts to

minimize rate changes between ancestral/descendant branches on a tree (i.e., at the nodes). Branches are allowed to change rates of molecular evolution but are penalized when rates change from ancestral to descendant branches. The crux of the penalized likelihood method is determining the optimal smoothing parameter. The smoothing parameter can vary from very small, in which each branch of the phylogeny has a different substitution rate (saturated model), to very large, in which parameters are essentially clocklike. r8s implements a data-driven cross-validation procedure that systematically prunes terminals from the tree and then estimates parameters from the submatrix under a given smoothing value. It then tries to predict the data for the pruned taxa by using the estimated parameters. Last, it calculates a χ^2 error associated with the difference between the predicted and observed data. The optimal smoothing value corresponds to the lowest χ^2 error (Sanderson 2002).

NPRS and PL analyses were performed on the single unconstrained Bayesian tree topology mentioned above ($-\ln L = 22,500.89$; tree not shown). Branch lengths were estimated for the data set with its best-fitting model. *Androstachys* was used as the rooting outgroup and was included in the dating analyses. A maximum age of 125 mybp was enforced for the clade (*Androstachys*, (Elatinaceae, Malpighiaceae)), which corresponds with the probable origin of the densely sampled, and palynologically distinctive, eudicot clade (Magallón et al. 1999) to which Malpighiaceae belong. Our sampling does not correspond directly with all eudicots (Soltis et al. 2003) but rather to the more derived eudicot clade Malpighiales (APG 2003). Malpighiales appear to be very old and began to diversify during the mid-Cretaceous (116–111 million years ago [mya]; C. Davis, unpublished data). The Malpighiales clade should be no older than the first appearance of the distinctive eudicot pollen type. All zero-lengths branches were collapsed before analysis. For the PL analysis, the optimal smoothing parameter, ranging between 0.001 and 10,000 (Sanderson 2003; M. Sanderson, personal communication), was selected before the dating analysis by performing the cross-validation procedure in r8s.

Absolute age estimates were obtained for nodes 0–6 (fig. 2) by using several calibration points (fig. 2; see details below). These nodes represent the crown age of Malpighiaceae (node 0) and the six disjuncts (nodes 1–6) between New and Old World Malpighiaceae (see also Davis et al. 2002b). All age estimates were restarted 10 times to minimize the chance of converging onto a suboptimal solution.

To estimate the 95% confidence intervals around our age estimates, we used the method developed by Cutler (2000) as implemented in r8s (Sanderson 2003). This procedure uses the curvature of the likelihood surface around the parameter estimate to find the endpoints of optimal age estimates. These values are determined from the decline in log likelihood units around this surface, which is specified in r8s by the cutoff value. Under a normal distribution, a drop in two log likelihood units (cutoff value = 2) corresponds to the 95% confidence interval (Sanderson 2003). However, as previously noted (Sanderson 2003), there is little reason to believe that this should be the case with real data, and simulation studies (Cutler 2000; Sanderson 2003) have shown that values twice that (i.e., cutoff value = 4) may be necessary. We used a cut-off of four based on these studies. Age estimates for determining confidence intervals were restarted three times to avoid suboptimal solutions.

Fossil Calibration

A fossil species of *Tetrapterys* from the early Oligocene (33 mybp; Hably and Manchester 2000) of Hungary and Slovenia provides a reliable minimum age estimate for the stem (see Doyle and Donoghue 1993; Magallón and Sanderson 2001 for stem vs. crown groups) *Tetrapterys* clade (Davis et al. 2002b; fig. 2, node A). In addition, we have included two additional fossil calibration points that have not previously been included in any dating analysis of Malpighiaceae.

Eoglandulosa warmanensis Taylor and Crepet was described on the basis of extraordinarily preserved flowering material from the Eocene Claiborne formation of northwestern Tennessee (Taylor and Crepet 1987). This unmistakable malpigh fossil has all of the distinctive features of New World Malpighiaceae flowers, including clawed (or paddle-shaped) petals and glandular sepals. Taylor and Crepet (1987) placed this fossil taxon as a member of the New World subfamily Byrsonimoideae (Anderson 1978; Davis et al. 2001, "byrsonimoid" clade) on the basis of the presence of 10 paired and enlarged sepal glands and tricolporate pollen; both are characteristics found in combination only among extant Byrsonimoideae (Anderson 1978; Davis et al. 2001; W. Anderson, personal communication).

There are three major tribes of Byrsonimoideae (Anderson 1978) to which *Eoglandulosa* may belong: Galphimieae, Byrsonimeae *sensu stricto* (Davis et al. 2001, i.e., excluding *Burdachia*, *Glandonia*, and *Mcvaughia*), and Acmantherae. With the exception of *Galphimia*, which has diversified in Mexico, the overwhelming majority of Byrsonimoideae are restricted to South America (Anderson 1978, 1981). It is unlikely that *Eoglandulosa* belongs with *Galphimia* (or to other Galphimieae) because most Galphimieae have either very reduced sepal glands (in total number and size) or more often none at all (Anderson 1978). Of the remaining byrsonimoid genera, *Byrsonima* has a distribution (Anderson 1981) that is most consistent with the distribution (Anderson 1981) and paleoclimate (Dilcher 1973; Frederiksen 1980; Taylor and Crepet 1987) of the *Eoglandulosa* type locality (Potter and Dilcher 1980; Taylor and Crepet 1987). Species of *Byrsonima* occur as far north as Florida today (Anderson 1981). In addition, it is the only genus in Byrsonimoideae whose species have an obvious adaptation for widespread migration (Anderson 1978); they have fleshy bird-dispersed fruits, which may have aided their movement out of South America, their likely center of origin (Raven and Axelrod 1974; Anderson 1981, 1990; Davis et al. 2002a). Other possible byrsonimoids have no obvious adaptation for long-distance dispersal; none have winged, setose, or fleshy fruits (Anderson 1978, 1981).

Given the proximity and climatic similarity of *Eoglandulosa* to modern species of *Byrsonima* and the relative vagility of *Byrsonima* species, we have placed this fossil taxon as a member of the stem lineage that gave rise to the *Byrsonima* clade (fig. 2; node B). Biostratigraphic analyses of the Upper Claiborne formation where *Eoglandulosa* was collected are
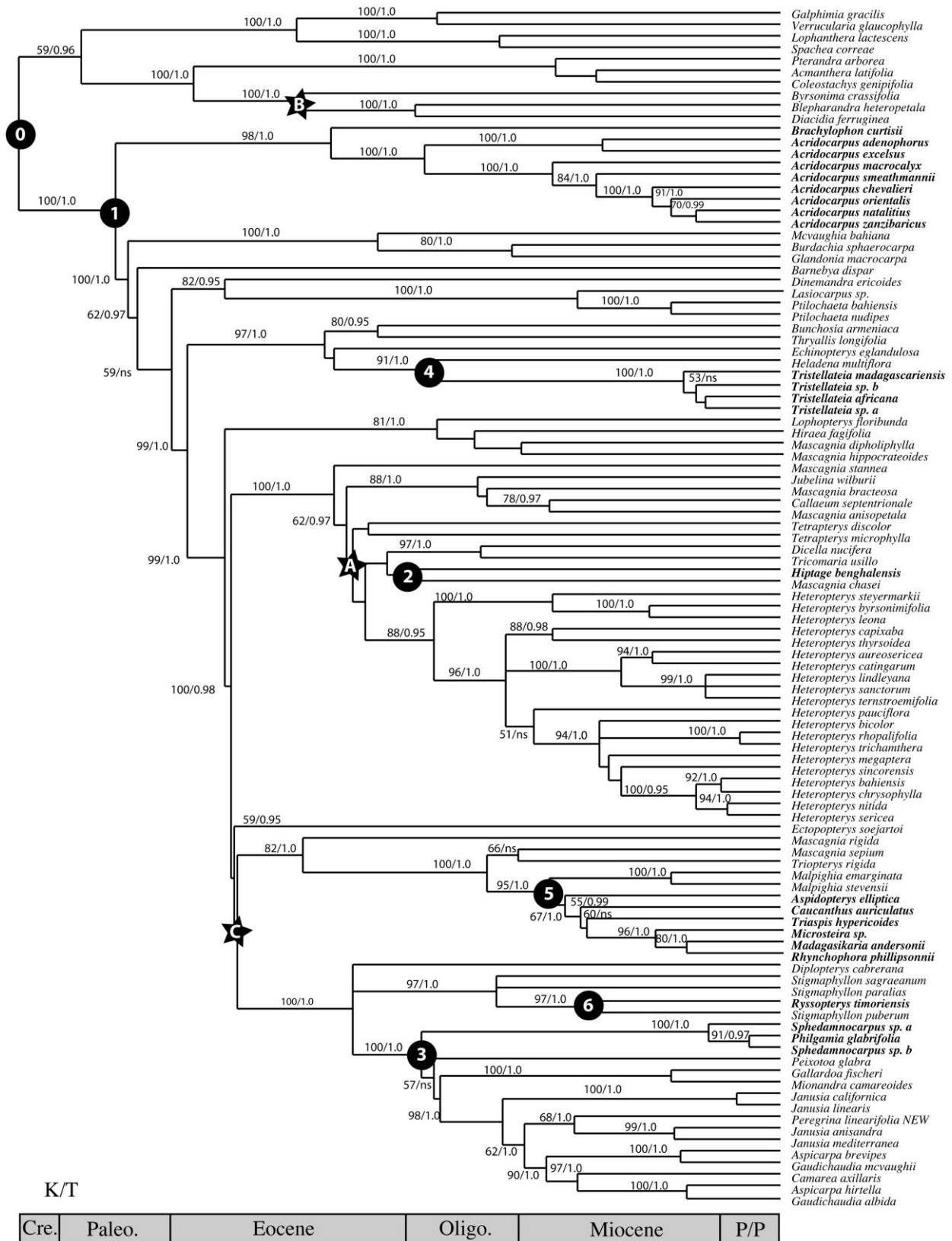
Fig. 2 Penalized likelihood chronogram based on combined *ndh*F and *PHYC* data. Fossil calibration points *A*, *B*, and *C* are starred, and the seven circled nodes (0–6) correspond to the origin of Malpighiaceae (node 0) and to the six disjunctions between New and Old World clades (nodes 1–6). Old World taxa are shown in boldface. Numbers near nodes are parsimony bootstrap percentages and Bayesian posterior clade probabilities, respectively. See table 2 for confidence intervals around relevant nodes. P/P = Pliocene/Pleistocene.

43–40 mybp in age (Potter and Dilcher 1980; D. Dilcher, personal communication). Because the Warman Pit is one of the oldest beds from this deposit (Potter and Dilcher 1980), we have placed a minimum age on the stem *Byrsonima* clade (fig. 2; node *B*) at 43 mybp.

Perisyncolporites pokornyi Germeraad et al. (1968) has a distinctive and mostly hexaporate 12-rugate pollen grain in which the pores form the apices of an octahedron and the rugae are arranged at the edges of a cube ("banisterioid" type, *sensu* Lowrie 1982, p. 28, his fig. 3.1). The pores are in or near the ruga, and usually only six of them are porate. The other rugae, which lack pores, connect to those with pores and occur along the equator of the grain. This pollen type is unique among angiosperms (Germeraad et al. 1968) and within Malpighiaceae is synapomorphic for the stigmaphylloid clade (Lowrie 1982; Davis et al. 2001; fig. 2, node *C*).

Perisyncolporites pokornyi has been widely collected across the tropics by petroleum corporations because it is an important indicator of Paleogene strata, which are rich in hydrocarbon reservoirs (Jaramillo and Dilcher 2001). It has been documented from all major tropical regions from the Eocene, including the Caribbean (Germeraad et al. 1968), South and Central America (Regali et al. 1974; Muller 1981; Rull 1997, 1998; Jaramillo and Dilcher 2001; Jaramillo 2002), Africa (Germeraad et al. 1968; Salard-Cheboldaeff 1991), and Australia (Martin 2002). We fixed the minimum age of the stem stigmaphylloid clade (fig. 2, node *C*) at ca. 49 mybp (Cenozoic time scale *sensu* Berggren et al. 1995) on the basis of the oldest reliably dated samples (i.e., outcrop and core) of *P. pokornyi* from the latest early Eocene of Colombia (Jaramillo and Dilcher 2001; Jaramillo 2002; C. Jaramillo, personal communication). Rull (1997) reported earlier late Paleocene samples of *P. pokornyi* from Venezuela, but his data are presented as an undistinguished mixture of less reliably dated well-type cuttings and more reliable core samples. Moreover, his data (Rull 1997, his fig. 5) show several other fossil pollen types within the same Paleocene time frame as *P. pokornyi* that are much older than their known occurrences (C. Jaramillo, Instituto Colombiano del Petroleo, personal communication).

We performed the NPRS analyses using several different fossil calibration points, three with each fossil calibration point enforced independently and one where all calibration points were enforced in a single analysis. Age estimates based on single fossil calibration points were performed to assess the degree to which estimated ages corroborate other clade ages for which fossil calibration points were available but not enforced. In the case of the PL analysis, all three calibration points were enforced in a single analysis to estimate absolute ages.

Results

Phylogenetic Analyses

The *ndh*F and *PHYC* data sets were not significantly different, as determined by the ILD test ($P = 0.20$), and were analyzed in combination. A general time-reversible model (Rodríguez et al. 1990) including parameters for invariant sites and rate variation ($GTR + I + \Gamma$) best fit the data and was used to conduct maximum likelihood analyses in MrBayes. The optimal likelihood tree from the combined data analyses in MrBayes had a log-likelihood score of $-\ln L = 22,500.89$ (tree not shown). This tree was topologically similar to previous less densely sampled analyses (Davis et al. 2002*b*). Six disjunctions were identified between New and Old World lineages (nodes 1–6; fig. 2).

Molecular Dating

The results of our molecular dating analyses are summarized in table 2. When fossil calibration points for nodes A and B were enforced independently by using NPRS (table 2*A*), the optimal age estimates were younger than expected. For example, when node A was constrained to be at least 33 mybp, the optimal ages of (the uncalibrated) nodes B and C were ca. 39 and 35 mybp, respectively. On the basis of fossil data for nodes B and C, they should be at least 43 and 49 mybp, respectively. Similarly, when node B was constrained to be at least 43 mybp, nodes A and C were inferred to be 32 and 34 mybp, respectively, which should be at least 33 and 49 mybp, respectively. We interpret this to mean that the best age estimates for the family should be based on all three calibration points (table 2*B*, 2*C*). Results of age estimates from NPRS and PL are compared in figure 3, and the chronogram for PL with all calibration points enforced is shown in figure 2. The optimal smoothing value for the PL analyses (table 2*C*) was 316.23.

NPRS and PL analyses (table 2*B*, 2*C*, respectively) indicate that Malpighiaceae originated during the latest Cretaceous (ca. 80–74 mybp, NPRS; 73–65 mybp, PL; Cretaceous time scale *sensu* Gradstein et al. 1995), which is consistent with previous age estimates based on NPRS (63.6 ± 5.8 mybp; Davis et al. 2002*b*). There are a total of six disjunctions between New and Old World Malpighiaceae (fig. 2, nodes 1–6; table 2). The first disjunction occurred during the Maastrichtian (ca. 72–66 mybp, NPRS) or Paleocene (63–57 mybp, PL), the second from middle Eocene to Oligocene (44–31 mybp, NPRS; 41–26 mybp, PL), the third during the late Eocene to earliest Miocene (34–24 mybp, NPRS) or late Eocene to late Oligocene (37–28 mybp, PL), the fourth during the middle Eocene to late Oligocene (46–26 mybp, NPRS; 40–25 mybp, PL), the fifth during the Oligocene to middle Miocene (29–11 mybp, NPRS; 26–16 mybp, PL), and the sixth during the late Oligocene to middle Miocene (26–11 mybp, NPRS) or earliest to middle Miocene (24–12 mybp, PL).

Discussion

Dating Analyses

Age estimates from NPRS and PL mostly overlapped (fig. 3), the exception being for the two deepest nodes in the tree (nodes 0 and 1). In these two cases, the age estimates from NPRS were older than those from PL. NPRS tends to overfit the data (Sanderson 2002), resulting in high levels of rate variation despite small changes in the data. Sanderson (2002) found that PL outperformed both the clock (Langley and Fitch 1974) and the nonclock method NPRS whenever data depart from a molecular clock. Thus, because our combined

Table 2

Molecular Divergence Time Estimates based on NPRS (*A*, *B*) and PL (*C*)

Fossil calibration points			Malpigh origin	New World–Old World disjuncts					
A	B	C	0	1	2	3	4	5	6
A. NPRS (individual calibration points)									
33	*38.73* (27.54, 48.08)	*34.73* (33.14, 39.04)	66.57 (62.05, 73.31)	56.83 (52.89, 62.25)	28.69 (25.10, 33.00)	20.64 (17.45, 24.42)	29.19 (21.89, 35.38)	13.54 (9.19, 18.84)	12.92 (9.20, 17.23)
32.24 (25.63, 37.76)	**43**	*34.12* (29.39, 39.48)	67 (62.36, 73.76)	57.05 (52.05, 62.66)	28.01 (23.16, 33.42)	20.25 (16.58, 24.74)	28.93 (21.41, 35.83)	13.31 (9.05, 19.73)	12.68 (8.98, 17.48)
46.64 (41.60, 48.90)	47.30 (34.17, 65.18)	**49**	76.88 (74.33, 79.64)	68.74 (65.99, 71.85)	40.56 (29.85, 44.16)	29.39 (23.61, 34.10)	39.84 (26.73, 46.48)	19.37 (12.31, 28.91)	18.45 (12.15, 25.10)
B. NPRS (all calibration points included)									
33	**43**	**49**	76.90 (74.02, 80.31)	68.76 (66.09, 71.79)	40.59 (31.43, 44.16)	29.39 (23.60, 34.10)	39.82 (26.24, 46.46)	19.49 (11.42, 28.80)	18.45 (11.22, 25.92)
C. PL (all calibration points included)									
33	**43**	**49**	68.58 (64.82, 72.69)	59.85 (56.88, 63.33)	33.78 (26.47, 41.25)	32.37 (27.88, 36.93)	31.42 (24.73, 39.61)	20.90 (16.32, 26.06)	17.40 (11.83, 23.54)

Note. Confidence intervals shown in parentheses following optimal ages estimates. Italicized ages in section *A* indicate optimal age estimates that are younger than expected based on unenforced calibration points. Fossil calibration points (shown in bold) provide minimum age constraints for starred nodes labeled *A*, *B*, and *C* in figure 2 (from Hably and Manchester 2000 [*A*], Taylor and Crepet 1987 [*B*], Jaramillo and Dilcher 2001 [*C*]). NPRS = nonparametric rate smoothing; PL = penalized likelihood.

*ndh*F and *PHYC* data depart from a molecular clock, we based our reconstruction of the biogeographic history of Malpighiaceae on age estimates from PL (table 2*C*; fig. 2).

Historical Biogeography

Gondwanian aborigines and American colonists. Paleogeographic reconstructions of the breakup of western Gondwana suggest that direct land connections between Africa and South America were lost by the Upper Middle Cretaceous (ca. 105 mybp, *sensu* McLoughlin 2001), and by ca. 84 mybp, all plant migration between the remnants of western Gondwana likely ceased except through chance long-distance dispersal (Raven and Axelrod 1974). If transatlantic connections between New and Old World Malpighiaceae were consistent with western Gondwanan vicariance, we would expect the origin of the family, as well as relevant disjunctions, to have occurred before 84 mybp. Our Late Cretaceous age estimate (73–65 mybp; table 2*C*) for the origin of Malpighiaceae is more recent than this. Moreover, all of the disjunctions between New and Old World clades (table 2*C*; 63–12 mybp) are even younger, rendering the Gondwanian aborigine hypothesis (Vogel 1990; fig. 1*A*) untenable as an explanation of extant Malpighiaceae distribution.

Our age estimates are potentially consistent with a series of episodic long-distance dispersal events across the southern Atlantic (American colonist scenario; fig. 1*B*; Raven and Axelrod 1974; Anderson 1981, 1990). Under a strict dispersalist scenario, however, we would need to invoke at least six over-water dispersal events to explain the distribution of Malpighiaceae. Furthermore, these dispersals would have to be postulated for (1) times starting in the Paleocene (ca. 60 mybp), when the distance between Africa and South America was already substantial (Scotese et al. 1988), and (2) later in the Tertiary, when the continents were even further apart. Moreover, the American colonist scenario does not account for well-preserved Eocene and Oligocene fossils of Malpighiaceae from Hungary and Slovenia (*Tetrapterys*) and Tennessee (*Eoglandulosa warmanensis*), both of which suggest a role for Northern Hemisphere high-latitude intercontinental migration of at least some lineages of Malpighiaceae (see below).

It is possible that some of the six disjuncts do result from long-distance dispersal. The chance of long-distance dispersal increases dramatically over time (Simpson 1952), and the undeniable importance of this mode is illustrated by the terrestrial biota of the Hawaiian Islands (Carlquist 1966, 1974). The phylogenetic distribution of fruit types, however, suggests that long-distance transport in Malpighiaceae is rare. Fleshy bird-dispersed fruits have evolved in at least three New World Malpighiaceae (Anderson 1978; Davis et al. 2001), but none of these has become established in the Old World, despite their high diversity and widespread distribution (Anderson 1978). Rather, only Malpighiaceae with winged wind-dispersed fruits have become established in the Old World. In contrast to fleshy bird-dispersed fruits, wind-dispersed taxa constitute a very small percentage of Hawaiian Island seed plant immigrants (ca. 40% vs. <1.5%;

NPRS vs PL
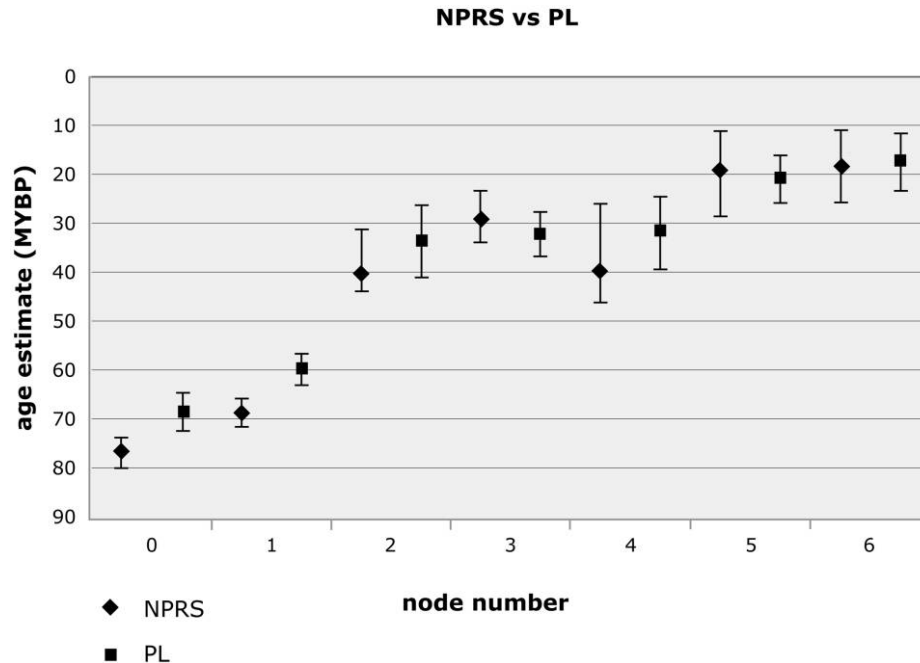
Fig. 3 Nonparametric rate smoothing (NPRS) versus penalized likelihood (PL). Optimal age estimates for nodes 0–6 shown with a diamond (NPRS) or square (PL). Confidence intervals around optimal ages estimated with the method of Cutler (2000) as implemented in r8s (Sanderson 2003).

Carlquist 1974, p. 77, table 2.1), suggesting that these fruits do not easily travel for long distances over water. Taken together, these data indicate that winged fruits might have facilitated travel across short oceanic barriers, such as those in the nascent Caribbean and across the North Atlantic but not across the distances that separated South America from Africa.

Northern Hemisphere migration. Migration across Northern Hemisphere land bridges has been considered a viable scenario for the intercontinental migration of thermophilic evergreen flowering plants that today inhabit tropical regions (Raven and Axelrod 1974; Wolfe 1975). Two Northern Hemisphere land connections, one spanning Beringia, the other spanning the North Atlantic, existed in the Tertiary. Beringia has played an important role for plant migrations throughout the Tertiary for temperate and boreal groups distributed across the Northern Hemisphere (Wolfe 1975; Tiffney 1985a, 1985b; Manchester 1999; Donoghue et al. 2001; Tiffney and Manchester 2001). Although our estimates of divergence times are compatible with overland migration via Beringia, its high latitude (between 69° and 75°N; Tiffney 1985b), limited light availability, and lower temperatures (Tiffney and Manchester 2001) probably restricted its use by broad-leaved evergreen thermophilic lineages for most, if not all, of the Tertiary. Furthermore, the geographic distribution of neither fossils nor extant Malphighiaceae supports this route for the dispersal of the family. Fossils are distributed between eastern North America, northern Europe, the Neotropics, Africa, and Australia. Extant Old World Malpighiaceae are almost entirely restricted to Africa and Madagascar, with a few, mostly minor, incursions into Asia

(Arènes 1957). If Malpighiaceae had utilized Beringia, we would expect fossil localities from eastern Asia or western North America (or both) and more family diversity in tropical Asia today.

The more likely Northern Hemisphere route for Malpighiaceae during the Tertiary is via the North Atlantic. The warmest climates in the Northern Hemisphere occurred in the late Paleocene/Eocene (Zachos et al. 2001), and midlatitude fossil floras from this time all contain a large percentage of thermophilic evergreen taxa (Wolfe 1978; Tiffney 1985a, 1985b, 2000; Manchester 1999; Tiffney and Manchester 2001; Jaramillo 2002). This period coincides with the presence of a land bridge spanning the North Atlantic during a time when the ocean was much narrower. This bridge extended south to roughly 45°N and is thought to have maintained sufficient warmth, light, and humidity for thermophilic broad-leaved evergreen plants to flourish (Tiffney and Manchester 2001). Beginning in the late Eocene, climates progressively cooled, and the potential for thermophilic evergreen elements across the North Atlantic diminished accordingly. The early Miocene warming period (Zachos et al. 2001) apparently supported mainly temperate and warm-temperate vegetation in the North Atlantic, giving way to cool-temperate and boreal vegetation by the middle Miocene. Although direct land connections were apparently severed by the middle Eocene, there was probably ample opportunity throughout the Tertiary for island hopping in the region (Tiffney and Manchester 2001).

The optimal estimates for the six disjunctions between New and Old World Malpighiaceae (table 2C) indicate transatlantic migration of the family during three major time

intervals: late Paleocene (ca. 60 mybp; fig. 2, node 1), latest Eocene–earliest Oligocene (ca. 34–31 mybp; fig. 2, nodes 2–4), and early Miocene (ca. 21–17 mybp; fig. 2, nodes 5, 6). The time of disjunction at node 1 coincides with the dominance of the boreotropical flora and the North Atlantic Land Bridge; it can easily be accommodated by the North Atlantic corridor. Despite somewhat cooler climates in the Oligocene across the Northern Hemisphere, the occurrence of fossil *Tetrapterys* (a genus that today is exclusively New World) in the Oligocene of northern Europe strongly suggests that the North Atlantic remained a viable corridor for intercontinental migration of Malpighiaceae until at least this time; thus, nodes 2, 3, and 4 can also be accommodated by a North Atlantic migration. The times of disjunction of nodes 5 and 6 correspond to the early Miocene warming period. This period primarily supported mixed-mesophytic vegetation throughout the middle latitudes in the Northern Hemisphere, and it is unclear whether the North Atlantic could support thermophilic broad-leaved evergreen elements such as Malpighiaceae (Tiffney and Manchester 2001). The few post-Eocene floras that are known from the vicinity of the North Atlantic suggest an early Miocene warm-temperate vegetation and later cool-temperate and boreal vegetation. Thus, whether a North Atlantic migration or long-distance dispersal best accounts for these Miocene disjuncts remains an open question. A clearer picture of the boreotropical flora during the Miocene is needed before northern migration is ruled out entirely for these more recent disjuncts.

Based on the above, we offer the following scenario for the historical biogeography of Malpighiaceae. The Neotropical subfamily Byrsonimoideae (*sensu* Davis et al. 2001) is sister to all Malpighiaceae. Their phylogenetic placement and high diversity in northern South America indicates that Malpighiaceae may have originated in South America during the latest Cretaceous (ca. 69 mybp; table 2C) in isolation from Africa (see also Raven and Axelrod 1974; Anderson 1981, 1990; Davis et al. 2002b). From South America, these groups migrated into present-day North America across the Caribbean Basin, which consisted of scattered continental and volcanic islands (Iturralde-Vinent and MacPhee 1999). These connections appear to have been fairly direct between North and South America, starting during the late Eocene (ca. 35 mybp; MacPhee and Iturralde-Vinent 1995; Iturralde-Vinent and MacPhee 1999) and perhaps extended into the Miocene. Our data suggest that Malpighiaceae may have migrated into North America via the proto-Caribbean even earlier in the Tertiary, starting during the Paleocene (node 1; see also Davis et al. 2002a).

Once Malpighiaceae became established in North America, they were able to move across North Atlantic land routes (Tiffney 1985a, 1985b, 2000) during periods of global warming (Zachos et al. 2001). The subsequent movement of Malpighiaceae into Africa (and later into Madagascar) with minor incursions into Asia may be attributable to cooling during the Oligocene (Berggren and Prothero 1992; Tiffney and Manchester 2001; Zachos et al. 2001) that initiated the southward retreat and ultimately vicariance of thermophilic lineages (Collinson 1992; Wolfe 1992; Manchester 1999; Davis et al. 2002a, 2002b). Subsequent warming during the Miocene (Tiffney 1985b; Tiffney and Manchester 2001;

Zachos et al. 2001) may have resulted in further intercontinental migration across the North Atlantic, but long-distance dispersal of these Miocene disjuncts remains a viable alternative. More knowledge of North Atlantic paleoecology would help clarify the significance of divergence times for both thermophilic and mixed-mesophytic plant lineages that may be too recent for Northern Atlantic land bridges to accommodate (Xiang et al. 1998; Wen 1999; Donoghue et al. 2001; Tiffney and Manchester 2001).

Neotropical oil-bee pollinators. One potential problem with our hypothesis is that the primary pollinators of Malpighiaceae have not made it to the Old World, as would be expected if Northern Hemisphere migration (vs. long-distance dispersal) were a major factor in the amphi-Atlantic distribution of Malpighiaceae. Neotropical Malpighiaceae appear to have coevolved with their centridine (and tapinotaspidine) pollinators (Vogel 1974, 1990; Anderson 1979, 1990; Neff and Simpson 1981; Taylor and Crepet 1987). One might thus expect that the migration of Malpighiaceae would be limited by the distribution of their primary pollinators. However, unlike Malpighiaceae, these bees have not made it into the Old World (Vogel 1974, 1990; Michener 2000). Paleotropical Malpighiaceae instead exhibit a diverse array of floral morphologies and appear to be pollinated by a host of insects whose primary reward is pollen rather than oil (Vogel 1990; C. Davis, unpublished data). Unfortunately, there are no reliable fossils for these bees (M. Engel and C. Michener, personal communication), from which their ability to disperse along with Malpighiaceae might be inferred. However, several phylogenetically diverse Neotropical Malpighiaceae, along with most of the Old World taxa, have lost many (in some cases all) of the floral characteristics associated with oil-bee pollination (Anderson 1979; Vogel 1990; W. Anderson, personal communication; C. Davis, unpublished data). That they are apparently capable of existing outside of this selective regime, in both the New and Old Worlds, indicates that the migration of Malpighiaceae was not limited by the distribution of their primary pollinators. It may be that various ecological factors restricted the coincident migration of oil-pollinating bees that visit New World Malpighiaceae. An investigation of floral evolution in Malpighiaceae is ongoing by one of us (C. Davis) and may shed light on their association with these bees.

Conclusions

Our results, and those from several other studies, indicate that North Atlantic land connections may have played an important role not only in the development of the temperate biota for plants (Tiffney 1985a, 1985b; Wen 1999; Donoghue et al. 2001; Tiffney and Manchester 2001) and animals (Sanmartín et al. 2001) but also in the migration of tropical lineages no longer present at high latitudes. Dispersion via the North Atlantic may have been possible for Malpighiaceae starting in the Paleocene and extending into the early Oligocene, during periods when northern latitudes supported tropical forests. Our data also indicate, however, that the most recent disjunctions in Malpighiaceae occurred during the Miocene, when North Atlantic land connections may have been unavailable and cooler climates existed. Whether these

Miocene disjuncts arose via Northern Hemisphere migration or long-distance dispersal awaits further paleontological and phylogenetic investigation.

Acknowledgments

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