

HISTORICAL BIOGEOGRAPHY OF MELASTOMATACEAE: THE ROLES OF TERTIARY MIGRATION AND LONG-DISTANCE DISPERSAL¹

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Melastomataceae and Memecylaceae are pantropically distributed sister groups for which an *ndhF* gene phylogeny for 91 species in 59 genera is here linked with Eurasian and North American fossils in a molecular clock approach to biogeographical reconstruction. Nine species from the eight next-closest families are used to root phylogenetic trees obtained under maximum likelihood criteria. Melastomataceae comprise ~3000 species in the neotropics, ~1000 in tropical Asia, 240 in Africa, and 225 in Madagascar in 150–166 genera, and the taxa sampled come from throughout this geographic range. Based on fossils, ranges of closest relatives, tree topology, and calibrated molecular divergences, Melastomataceae initially diversified in Palaeocene/Eocene times in tropical forest north of the Tethys. Their earliest (Eocene) fossils are from northeastern North America, and during the Oligocene and Miocene melastomes occurred in North America as well as throughout Eurasia. They also entered South America, with earliest (Oligocene) South American fossils representing Merianieae. One clade (Melastomeae) reached Africa from the neotropics 14–12 million years ago and from there spread to Madagascar, India, and Indochina. Basalmost Melastomataceae (Kibessieae, Astronieae) are species-poor lineages restricted to Southeast Asia. However, a more derived Asian clade (Sonerileae/Dissochaeteae) repeatedly reached Madagascar and Africa during the Miocene and Pliocene. Contradicting earlier hypotheses, the current distribution of Melastomataceae is thus best explained by Neogene long-distance dispersal, not Gondwana fragmentation.

Key words: biogeography; fossil calibration; long-distance dispersal; Melastomataceae; Memecylaceae; molecular clock; *ndhF*.

Difficulties in identifying sister groups and in dating the times of their divergence have characterized biogeographic work on tropical angiosperms. First, the great species richness of many tropical groups and inaccessibility of material make dense molecular phylogenetic sampling problematic. Second, even after major clades and sister groups are reliably identified, dating the times of their divergences is difficult. Previous biogeographic analyses of the World's tropical floras have tended to attribute transtropical disjunctions at higher taxonomic levels to the break-up of Gondwana (Raven and Axelrod, 1974; Gentry, 1982, 1993; Barlow, 1990; Romero, 1993; Burnham and Graham, 1999, their Table 2). However, this implies ages of 100–90 million years (Ma) for divergences among neotropical-African sister clades and even older divergences for taxa also found in Indochina and Southeast Asia. However, fossils supporting a Gondwanan range are available for few of the many pantropical eudicot families. Other workers have taken the absence of Cretaceous fossils at face value and attributed most tropical range disjunctions to long-distance dispersal (Smith, 1973; Thorne, 1973; Brenan, 1978). In the absence of a dense fossil record from key areas, such as South America (Burnham and Graham, 1999), the controversy pit-

ting the break up of Gondwana against more recent long-distance dispersal as major factors shaping today's geographic ranges could not be resolved.

To resolve the problem, absolute age estimates for sister groups are needed. These can come from nucleotide substitution rates if a single rate across a phylogenetic tree can reliably be estimated and calibrated. Much discussion has surrounded both tasks. The assumption of similar substitution accumulation among descendants of a common ancestor must be justified prior to drawing inferences about either rates or times. And fossil or geological evidence must constrain the age of at least one calibration point on the tree in order for rates to be transformed into absolute ages. Doyle and Donoghue (1993; see also Sanderson, 1998) have characterized the kind of time constraint that can be inferred from fossils. To fix the age of a calibration node A, a fossil must exhibit not only the apomorphy of clade A, but also some additional synapomorphy of a subclade of A. Together, these traits indicate that the fossil is indeed part of clade A (thus proving its minimum age), rather than perhaps representing the sister group of A.

We here estimate absolute ages for key divergence events in the history of Melastomataceae from substitution rates estimated for their NADH dehydrogenase subunit F gene (*ndhF*) calibrated with different fossils. Melastomataceae are an important component of today's tropical floras and comprise ~3000 species in the neotropics, ~1000 in tropical Asia, 240 in Africa, and 225 in Madagascar in together 150–166 genera (Renner [1993] for all genera's ranges and species numbers; a few genera have been synonymized since then). Their sister group, Memecylaceae, include ~360 species in four genera in Africa, Madagascar, and Southeast Asia, and ~90 species in two genera in tropical America. Melastomataceae fossil leaves and seeds are known from Eurasia and North America, and these fossils show morphological details that permit their assignment to particular nodes in a phylogeny (below). Meme-

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ylaceae wood is known from the Oligocene of Germany (Gottwald, 1992). The families' closest relatives are species-poor lineages with restricted geographic ranges and poor fossil records, making it difficult to constrain the age of the entire clade. However, Myrtaceae, which are more distant relatives of Melastomataceae and Memecylaceae, have a fossil record that goes back to the Upper Cretaceous (Raven and Axelrod, 1974; Manchester, 1999).

Melastomataceae have been seen as having originated either in West Gondwana (South America + Africa) (Raven and Axelrod, 1974; Gentry, 1982: Table 5, 1993; Jacques-Félix, 1994) or East Gondwana (Madagascar, India, Australia, Antarctica) (Renner, 1993). Earliest fossils are Eocene leaves from northwestern North America (Hickey, 1977; Wehr and Hopkins, 1994), an Oligocene leaf from Andean Colombia (Huertas, 1977), and Miocene seeds from throughout Eurasia (Dorofeev, 1960, 1963, 1988; Collinson and Pinggen, 1992; Dyjor et al., 1992; Fairon-Demaret, 1994; Mai, 1995, 2000). Pollen records are much younger. These fossils suggest that the family is too young to have reached its present pantropical distribution via overland dispersal. Nevertheless, the above-cited biogeographic analyses preferred the assumption of "missing older fossils" over the assumption of long-distance dispersal between South America and Africa, and Africa, Madagascar, and tropical Asia.

As will be presented, branch lengths in the *ndhF* tree can be calibrated by using two fossil-constrained calibration points. The resulting estimated times for the spread of Melastomataceae lineages across the tropics imply repeated long-distance dispersal events during the Neogene.

MATERIALS AND METHODS

DNA isolation and amplification and sequence alignment—Total cellular DNA was extracted from fresh or silica-dried leaves following standard procedures. Extractions or amplifications often had to be repeated several times because Melastomataceae leaves contain secondary products that make their DNA extremely difficult to work with. The *ndhF* gene was amplified by conventional PCR, using the primers developed by Olmstead and Sweere (1994; primer sets used are specified in Clausing and Renner, 2001a). For purification, PCR products were run on a low melting point agarose gel and then recovered with the help of QIAquick gel extraction kits (QIAGEN) or by using the QIAquick purification columns directly. Cycle sequencing of the amplified double-stranded products used the ABI Prism Dye Terminator ready reaction kit (Perkin Elmer, Norwalk, Connecticut, USA), the dye was removed by ethanol precipitation, and samples were run on an ABI 373 automated sequencer at the University of Mainz. Consensus sequences were constructed using Sequencher version 3.1 (GeneCodes Corporation, Ann Arbor, Michigan, USA) and SeqPup version 0.9 (D. Gilbert, Indiana University, Bloomington).

Taxon sampling, phylogenetic analysis, and rate and age estimation—A phylogenetic hypothesis for 45 representatives of Melastomataceae and Memecylaceae is available based on sequences from two chloroplast DNA genes and one intron (Clausing and Renner, 2001a). For a biogeographic analysis, denser taxon sampling was desirable to substantiate unexpected groupings, such as the nesting of African, Madagascan, and Southeast Asian Melastomeae within a clade of neotropical Melastomeae and the nesting of Madagascan and African Sonerileae among Southeast Asian Dissochaeteae/Sonerileae. Second, to assess possible substitution rate constancy between sister groups, it was necessary to concentrate on one genome region. This is because the evolution of combined gene and intron sequences, the latter with large insertions and deletions, is less likely to be captured by a model of nucleotide substitution. Of the molecular data sets begun, the *ndhF* data appeared most suited for a molecular clock approach because of intermediate levels of divergence. We sequenced *ndhF* for 102 species from 59 genera of Melasto-

mataceae and Memecylaceae of which 91 are included here. (A few congeners differed little from each other and were therefore excluded.) Table 1 lists all species with their geographical ranges, vouchers, and GenBank accession numbers. Trees were rooted with representatives of Alzateaceae, Crypteroniaceae, Oliniaceae, Penaeaceae, Rhynchoalycaceae, Myrtaceae, Onagraceae, and Lythraceae. While *ndhF* alone is used for age estimation, the biogeographic discussion is restricted to clades that have strong bootstrap support in the two genes/one intron analysis with the exception of the Madagascan *Medinilla* clade of which but one species had been sampled.

Phylogenetic analyses of the aligned sequences were conducted with test version 4.0b.4a of PAUP* (Swofford, 2000).

Maximum likelihood analyses were performed using the general time-reversible model (Yang, 1994), which estimates independent probabilities for the six possible nucleotide substitutions in a symmetric rate matrix and also allows unequal base frequencies. This model had been found to fit the data significantly better than less parameter-rich models (data not shown). To compensate for among-site rate heterogeneity some proportion of nucleotide sites (P_{inv}) was modeled as completely resistant to change while substitution in the remainder was assumed to follow a gamma distribution with shape parameter α . The rate matrix, P_{inv} , and α were estimated simultaneously, using the discrete approximation of Yang (1994; implemented in PAUP*) with four rate categories and empirically observed base frequencies. All searches were heuristic, with the "multiple trees" and "steepest descent" options in effect, and tree-bisection-reconnection (TBR) swapping. The initial search for model estimation used a minimum evolution (ME) starting tree (Rzhetsky and Nei, 1992a, b; implemented in PAUP*) and log-determinant genetic distances (Lockhart et al., 1994). The dependence of model parameters on tree topology is minor as long as strongly supported groups are maintained (Yang and Kumar, 1996; Sullivan, Swofford, and Naylor, 1999), and we therefore aborted parameter estimation after 400 TBR rearrangements (36 h). The estimated parameters were used in searches with ~20 000 TBR rearrangements that used different starting trees, namely an ME tree, a neighbor-joining tree, and a randomly chosen parsimony tree. Nonparametric bootstrap frequencies were obtained with PAUP's "fast bootstrap" option under the ME optimality criterion and using ML genetic distances with the same ML settings as used before.

Likelihood ratio testing was used to assess whether substitution rates in sister groups can justifiably be modeled as clock-like. Likelihood ratio tests are extremely powerful at detecting differences in rates (Sanderson, 1998), and in large data sets they usually reject the null hypothesis of rate constancy between sisters. This is the case here. The number of branches significantly shortened or lengthened in the clock tree compared to the nonclock tree was assessed by a Student's *t* test. Since there were few differences in topology and branch lengths between the two trees (Results), genetic distances (branch lengths) in the clock tree were calibrated by assigning fossils to two calibration points. We used binomial probability theory to estimate the standard deviation (SD) of the distance from a fixed calibration node to the tips and then used this value to obtain the SDs of the estimated ages. The number of nucleotide substitutions (S) is equal to the product of the total number of nucleotides in a sequence (N) times the proportion of nucleotides substituted (p). Thus, $S = Np$. The SD of this value is the square root of $Np(1 - p)$, or $SD(S) = \sqrt{Np(1 - p)}$. The SD of the number of nucleotides substituted divided by the total number of nucleotides is the SD of the proportion of nucleotide substitutions. Thus, $SD(p) = \sqrt{p(1 - p)/N}$.

RESULTS

Sequence data and phylogenetic analysis—The aligned *ndhF* sequences had a length of 1057 nucleotide positions after one region of four nucleotides had been eliminated because of base call ambiguities. The matrix contained 140 autapomorphic variable sites and 358 parsimony-informative sites for the 91 taxa. For the general topology found in all nonclock searches, the estimated proportion of invariable sites was 0.34 and α was 1.30, indicating that most sites have intermediate sub-

TABLE 1. Representatives of Melastomataceae, Memecylaceae, and outgroup included in the biogeographic analysis, with their geographic ranges, voucher information, and GenBank accession numbers. Outgroup taxa are listed at the end. BG stands for Botanical Garden, and herbarium acronyms are AAU = Aarhus University; BONN = University of Bonn; CAS = California Academy of Sciences; CAY = Cayenne; COL = Colombian National Herbarium; K = Royal Botanic Gardens, Kew; MICH = Michigan University; MJG = University of Mainz; MO = Missouri Botanical Garden; QCNE = Ecuadorean National Herbarium, Quito.

Species	Species range	Voucher	GenBank accession no. ^a
ALZATEACEAE			
<i>Alzatea verticillata</i> Ruiz & Pavón	Costa Rica to Bolivia	Jiménez 1111 (MO)	GBAN-AF215591
CRYPTERONIACEAE			
<i>Crypteronia paniculata</i> Bl.	Indochina and Malaysia	Tange s.n. (AAU)	Partial sequence
LYTHRACEAE			
<i>Heimia myrtifolia</i> Cham. & Schldl.	Southeast Brazil, Uruguay	Cultv. BG Mainz; Meyer s.n. (Kent State University herbarium)	GBAN-AF294837
MELASTOMATACEAE			
<i>Aciotis purpurascens</i> (Aubl.) Triana	South America	Renner 2154b (QCNE)	GBAN-AF215561
<i>Amphiblemma cymosum</i> (Schr. & Wendl.) Naudin	West Africa	Cultv. BG Mainz	GBAN-AF215588
<i>Anerincleistus macrophyllus</i> Bakh. f.	Borneo	Clausing 248 (MJG)	GBAN-AF289366
<i>Arthrostemma ciliatum</i> Pavón ex D. Don	Mexico to Andes; Greater Antilles	Cultv. BG Mainz	GBAN-AF215562
<i>Astronia macrophylla</i> Bl.	Sumatra, Java, Borneo, Celebes, Moluccas	Clausing 208 (MJG)	GBAN-AF215548
<i>Astronia smilacifolia</i> Triana ex C.B. Clarke	Malay Peninsula	Clausing 189 (MJG)	GBAN-AF215549
<i>Bertolonia maculata</i> DC.	Brazil	Cultv. BG Mainz	GBAN-AF215550
<i>Blakea trinervia</i> L.	Jamaica	Cultv. BG Mainz	GBAN-AF215555
<i>Blastus borneensis</i> Cogn.	Indochina and Malaysia	Clausing 163 (MJG)	GBAN-AF215585
<i>Calvoa orientalis</i> Taub.	East Africa, but genus centered in West Africa	Cultv. BG Amani, Tanzania, voucher Orava 1 (MJG)	GBAN-AF215589
<i>Catanthera pilosa</i> M. P. Nayar	Borneo	Clausing 258 (MJG)	GBAN-AF289367
<i>Catanthera quintuplinervis</i> (Cogn.) M. P. Nayar	Borneo, Sumatra	Clausing 196 (MJG)	GBAN-AF289368
<i>Centradenia inaequilateralis</i> (Schlechtld. & Cham.) G. Don	Central America	Cultv. BG Mainz	GBAN-AF215563
<i>Clidemia rubra</i> (Aubl.) Mart.	South America	Cultv. BG Bonn	GBAN-AF215579
<i>Comolia coriacea</i> Gleason	Venezuela	Cultv. BG Munich	GBAN-AF272799
<i>Dichaetanthera aborea</i> Baker	Madagascar	Clausing 281 (MJG)	GBAN-AF272800
<i>Dichaetanthera asperrima</i> Cogn.	Madagascar	Clausing 280 (MJG)	GBAN-AF215564
<i>Dionycha bojerii</i> Naudin	Madagascar	Clausing 300 (MJG)	GBAN-AF272801
<i>Diplectria divaricata</i> (Willd.) O. Ktze. (<i>Dissochaeta divaricata</i> (Willd.) G. Don)	Throughout tropical Southeast Asia	Clausing 236 (MJG)	GBAN-AF215556
<i>Diplectria viminalis</i> (Jack) O. Ktze. (<i>Dissochaeta viminalis</i> (Jack) Clausing, ined.)	Malay Peninsula, Sumatra, Java, Borneo, New Guinea	Clausing 233 (MJG)	GBAN-AF322236
<i>Dissochaeta annulata</i> Hook.f. ex Triana	Malay Peninsula and Borneo	Clausing 243 (MJG)	GBAN-AF322237
<i>Dissochaeta bracteata</i> (Jack) Blume	Malay Peninsula, Borneo, Sumatra, Java, Philippines	Clausing 183 (MJG)	GBAN-AF289369
<i>Dissotis fruticosa</i> (Brenan) Brenan & Keay	Nigeria	Cultv. BG Mainz	GBAN-AF272802
<i>Dissotis grandiflora</i> (Sm.) Benth. (Type of <i>Dissotis</i> subgen. <i>Dissotis</i>)	Widespread in tropical Africa	Porembski 41 (BONN)	GBAN-AF272803
<i>Dissotis rotundifolia</i> (Sm.) Triana See under <i>Heterotis</i>			
<i>Driessenia glanduligera</i> Stapf	Borneo	Clausing 254 (MJG)	GBAN-AF215586
<i>Graffenrieda rotundifolia</i> (Bonpl.) DC.	South America	Cultv. BG Munich, acc. no. 94/3113	GBAN-AF215576
<i>Gravesia guttata</i> (Hook.) Triana	Madagascar	Cultv. BG Mainz	GBAN-AF270755
<i>Gravesia rutenbergiana</i> Cogn.	Madagascar	Clausing 287 (MJG)	GBAN-AF289370
<i>Heterocentron elegans</i> (Schldl.) Kuntze	Central America	Cultv. BG Mainz	GBAN-AF272804
<i>Heterocentron subtriplinervium</i> (Link & Otto) A. Brown & Bouché	Central America	Cultv. BG Mainz	GBAN-AF215566
<i>Heterotis rotundifolia</i> (Sm.) Jacq.-Félix	Widespread in tropical Africa, naturalized in Brazil, Indonesia, and Hawaii	Cultv. BG Mainz	GBAN-AF215565
<i>Kendrickia walkeri</i> (Wight ex Gardn.) Triana	Ceylon, southern India	Cultv. BG Stockholm	GBAN-AF289371
<i>Lavoisiera cordata</i> Cogn.	Brazil	Almeda 7798 (CAS)	GBAN-AF215582
<i>Leandra mexicana</i> (Naud.) Cogn.	Mexico	Cultv. BG Bonn	GBAN-AF215580
<i>Macrocentrum repens</i> (Gleason) Wurdack	Venezuela	Berry et al. 6587 (MO)	GBAN-AF324498

TABLE 1. Continued.

Species	Species range	Voucher	GenBank accession no. ^a
<i>Macrolenes nemorosa</i> (Jack) Bakh.f. (<i>Dissochaeta affinis</i> (Korth.) Clausing, ined.)	Malay Peninsula, Sumatra, and Borneo	Clausing 174 (MJG)	GBAN-AF289372
<i>Macrolenes stellulata</i> (Jack) Bakh.f. (<i>Dissochaeta reformata</i> Blume)	Malay Peninsula, Sumatra, Java, and Borneo	Clausing 182 (MJG)	GBAN-AF289373
<i>Maieta guianensis</i> Aubl.	South America	Cultv. BG Mainz	GBAN-AF215581
<i>Medinilla alternifolia</i> Blume	Malay Peninsula, Sumatra, Borneo	Clausing 184 (MJG)	GBAN-AF289374
<i>Medinilla humbertiana</i> H. Perrier	Madagascar	Cultv. BG Mainz, voucher Clausing 289 (MJG)	GBAN-AF215557
<i>Medinilla humblotii</i> Cogn.	Madagascar	Cultv. BG Mainz Claus- ing 296 (MJG)	GBAN-AF322235
<i>Medinilla rubrifrons</i> Regalado	East Kalimantan, Sabah	Clausing 211 (MJG)	GBAN-AF289375
<i>Medinilla serpens</i> Stapf	Sarawak	Clausing 268 (MJG)	GBAN-AF289376
<i>Medinilla stephanostegia</i> Stapf	Mount Kinabalu (Borneo)	Clausing 257 (MJG)	GBAN-AF289378
<i>Melastoma cyanoides</i> sm. See under <i>Otanthera</i>			
<i>Melastoma orientale</i> Guillaumin	Thailand, Laos, Vietnam	Cultv. BG Mainz; Meyer 9617 (MJG)	GBAN-AF272811
<i>Melastomastrum capitatum</i> (Vahl) A. & R. Fern. (<i>Dissotis capitata</i> (Vahl) Hook.)	Centered in West Africa	Kayombo 1158 (MO)	GBAN-AF272814
<i>Meriania nobilis</i> Triana	Colombia	Barriga 21192 (COL)	GBAN-AF215577
<i>Microlepis oleaeifolia</i> (DC.) Triana	Brazil	Almeda 7746 (CAS)	GBAN-AF272815
<i>Microlicia fasciculata</i> Cogn.	Brazil	Almeda 7717 (CAS)	GBAN-AF215583
<i>Monochaetum calcaratum</i> (DC.) Triana	Mexico to Central America	Cultv. BG Munich	GBAN-AF215568
<i>Monolena primuliflora</i> J.D. Hooker	Central and South America	Cultv. BG Mainz	GBAN-AF215553
<i>Nepsera aquatica</i> (Aubl.) Naud.	Tropical America and Antilles	Miller & Morello 8853 (MO)	GBAN-AF215569
<i>Osbeckia aurata</i> H. Perr. See under <i>Rousseauxia</i>			
<i>Osbeckia chinensis</i> L.	India, Indochina to tropical Australia and Japan	Meyer 9643 (MJG)	GBAN-215570
<i>Osbeckia nepalensis</i> Hook.	India to Indochina	Cultv. BG Mainz	GBAN-AF272817
<i>Osbeckia stellata</i> Ham. ex Ker-Gawl.	India to Indochina	Meyer 9602 (MJG)	GBAN-AF272818
<i>Otanthera cyanoides</i> (Sm.) Triana (<i>Melastoma cyanoides</i> Sm.)	Southeast Asia, Philippines, Australia	Halford Q786, K	GBAN-AF272807
<i>Oxyspora beccarii</i> (Cogn.) Maxw. (<i>Anerincleistus beccarii</i> Cogn.)	Borneo	Clausing 186 (MJG)	GBAN-AF289380
<i>Pachycentria constricta</i> (Blume) Blume	Throughout tropical South- east Asia	Clausing 263 (MJG)	GBAN-AF289381
<i>Pogonanthera pulverulenta</i> (Jack) Blume (<i>Pachycentria pulverulenta</i> (Jack) Clausing)	Malaysia, Philippines, New Guinea	Clausing 230 (MJG)	GBAN-AF289383
<i>Phyllagathis gymnantha</i> Korth.	Borneo	clausing 209 (MJG)	GBAN-AF215590
<i>Plethiandra cuneata</i> Stapf	Borneo	Clausing 129 (MJG)	GBAN-AF289384
<i>Plethiandra hookeri</i> Stapf	Borneo	Clausing 219 (MJG)	GBAN-AF289385
<i>Pternandra caerulea</i> Jack	Throughout tropical South- east Asia to Australia	Clausing 175 (MJG)	GBAN-AF215558
<i>Pternandra echinata</i> Jack	Thailand, West Malaysia, Borneo	Clausing 75 (MJG)	GBAN-AF215559
<i>Pternandra multiflora</i> Cogn.	Borneo (Sarawak)	Clausing 142 (MJG)	GBAN-AF215560
<i>Pterolepis glomerata</i> (Rottb.) Miq.	South America	Miller & Morello 8845 (MO)	GBAN-AF215571
<i>Rhexia mariana</i> L.	Eastern North America	Cultv. J. J. Wurdack;	GBAN-AF272819
<i>Rhexia virginica</i> L.	Eastern North America	Cultv. BG Mainz	GBAN-AF215587
<i>Rhynchanthera grandiflora</i> (Aubl.) DC.	Central and South America	Cultv. BG Mainz, voucher Prévost 3281, CAY	GBAN-AF215584
<i>Rousseauxia aurata</i> (H. Perr.) Jacq.-Félix (<i>Osbeckia aurata</i> H. Perr.)	Madagascar	Clausing 324 (MJG)	GBAN-AF272816
<i>Sonerila obliqua</i> Korth.	Malaysia to Philippines	Clausing 170 (MJG)	GBAN-AF289388
<i>Tetrazygia urbanii</i> Cogn.	Puerto Rico	Skean 3799 (MICH)	GBAN-AF270753
<i>Tibouchina longifolia</i> (Vahl) Baillon ex Cogn.	Central and South America	Cultv. BG Bonn	GBAN-AF215572
<i>Tibouchina urvilleana</i> (DC.) Cogn.	Brazil	Cultv. BG Mainz	GBAN-AF272820
<i>Topobea brenesii</i> Standley	Central America	Almeda & Daniel 7185 (CAS)	GBAN-AF271665
<i>Triolena obliqua</i> (Triana) Wurdack	Colombia to Peru	Renner 2173 (QCNE)	GBAN-AF215554
<i>Tristemma mauritanium</i> J.-F. Gmelin	Genus centered in West Af- rica; this species in Mad- agascar and São Tomé	Clausing 292 (MJG)	GBAN-AF272821

TABLE 1. Continued.

Species	Species range	Voucher	GenBank accession no. ^a
<i>Warneckea membranifolia</i> (Hook.f.) Jacq.Fél.	Tropical Africa	Jongking et al. 1786 (MO)	GBAN-AF331711
MEMECYLACEAE			
<i>Memecylon bakerianum</i> Cogn.	Madagascar	Clausing 318 (MJG)	GBAN-AF215573
<i>Memecylon cogniauxii</i> Gilg	East Africa	Orava 6 (MO)	Partially sequenced
<i>Memecylon edule</i> Roxb.	Throughout tropical South-east Asia	Cultv. BG Munich	GBAN-AF215574
<i>Mouriri guianensis</i> Aubl.	South America	Cultv. BG Munich	GBAN-AF215575
<i>Mouriri helleri</i> Britton	Puerto Rico	Skean 3809 (MICH)	GBAN-AF322230
MYRTACEAE			
<i>Eugenia uniflora</i> L.	Pantropical	Cultv. BG Mainz	GBAN-AF215592
<i>Myrtus communis</i> L.	Mediterranean	Cultv. BG Mainz	GBAN-AF215593
OLINIACEAE			
<i>Olinia ventosa</i> (L.) Cufod. (<i>O. cymosa</i> Thunb.)	East and South Africa	Phillipson 3680 (MO)	GBAN-AF215594
ONAGRACEAE			
<i>Ludwigia suffruticosa</i> Walter	Argentina	Cultv. BG Mainz	GBAN-AF215595
PENAEACEAE			
<i>Penaea mucronata</i> L.	South Africa	J. Manning s.n. (MO)	GBAN-AF270756
RHYNCHOCALYCACEAE			
<i>Rhynchocalyx lawsonioides</i> Oliv.	South Africa	Cultv. BG Sydney	GBAN-AF270757

^a The prefix GBAN- has been added to each GenBank accession to link the online version of *American Journal of Botany* to GenBank but is not part of the actual accession number.

stitution rates, while few sites have very high or low rates (Yang and Kumar, 1996).

The midpoint-rooted highest likelihood tree (Fig. 1) obtained under the GTR + P_{inv} + Γ model shows Melastomataceae, Memecylaceae, and the Southeast Asian genus *Pternandra* (Kibessieae) as a strongly supported (100% bootstrap support) clade that is sister to a clade comprising Crypteroniaceae, Alzateaceae, Rhynchocalycaceae, Oliniaceae, and Penaeaceae. Within Melastomataceae, eight major groups (marked in Fig. 1) can be discerned that traditionally have been recognized at the tribal level (Cogniaux, 1891; Clausing and Renner, 2001a). They are (1) *Astronia* (Astronieae), (2) Merianieae, (3) Miconieae, (4) Blakeeae, (5) a complex formed by all Dissochaeteae and Sonerileae, (6) Bertolonieae, (7) Melastomeae, and (8) Microlicieae.

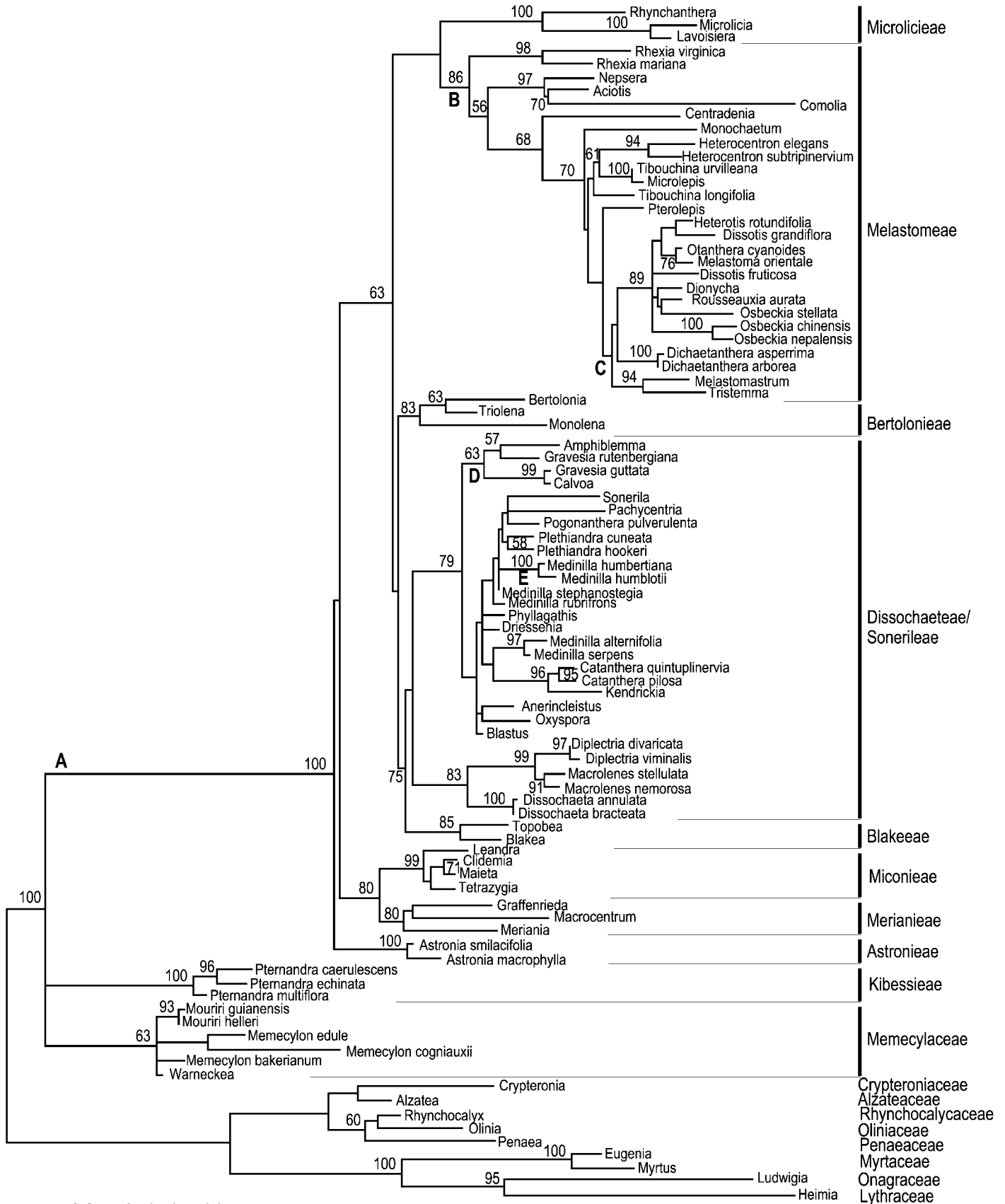
Substitution rate estimation and calibration—Likelihood ratio testing rejected the assumption of clock-like substitution between sister groups ($\chi^2 = 2(10072.09 - 9886.45) = 371.28$; $P < 0.001$; 89 df). The highest likelihood topology found under the nonclock model (after 21 864 rearrangements when TBR swapping on two trees was aborted) and the topology found under the clock model (after 1400 rearrangements when swapping on two trees was aborted) differed in minor rearrangements (compare Figs. 1 and 2). (Searches were run for the same time but searching under the clock model took much longer.) Thus, relationships within Memecylaceae and within neotropical Melastomeae differ. A Student's *t* test showed that of 163 matched branches in the two trees, 25 (15%) significantly changed in length ($P < 0.05$) when the data were modeled under the clock. (Four of the 168 branches in the nonclock tree were so short that standard errors on them

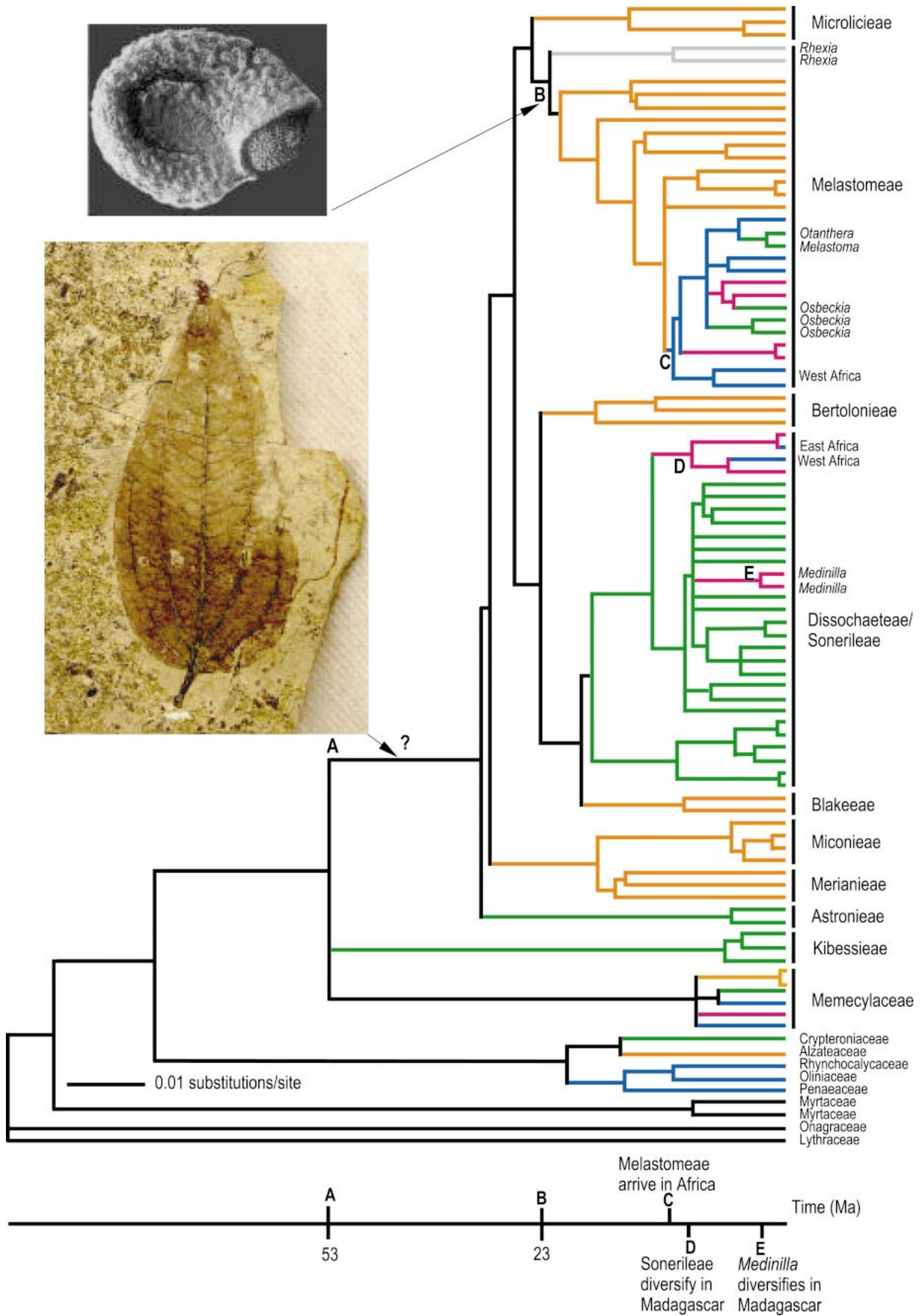
were undefined; one branch was not seen in the clock tree and could therefore not be matched; and 11 branches involved polytomies.) Note that 5% of branch lengths are expected to differ by chance alone. Since most branch lengths remained virtually unchanged (compare Figs. 1 and 2), including the ones of interest for the biogeographic analysis (nodes A through E), the use of branch length as a proxy for age is justified.

Branch length was calibrated in two ways, once with fossil seeds, once with leaves. Melastome seeds are known from Miocene deposits in Siberia, the Tambov region, Belorussia, Poland, several sites in Germany, and Belgium (Dorofeev, 1960, 1963, 1988; Collinson and Pinget, 1992; Dyjor et al., 1992; Fairon-Demaret, 1994; Mai, 1995, 2000). They are 0.8–1.5 mm long and strongly curved (cochleate) with a round operculum (Fig. 2, inset). The testa is tuberculate and carries a secondary ornamentation. Such seeds characterize Melastomeae (including Rhexieae) (Whiffin and Tomb, 1972; Renner, 1989, 1994; F. Almeda, California Academy of Science, unpublished data). All other Melastomataceae have straight or cuneate seeds that lack round operculi and have different testas. The seed fossils thus constrain the age of node B in Figs. 1 and 2, making it minimally 23 Ma old (Berggren et al., 1995). Fixing node B at 23 Ma yields a substitution rate of 0.0012 substitutions·site⁻¹·Ma⁻¹ (the distance from node B to the tips divided by 22 is 0.0012). Table 2 shows age estimates and standard deviations obtained for divergence events C, D, and E under this rate.

Melastomataceae are also known from fossil leaves that show the family's unusual venation pattern (Fig. 2, inset). Fossil leaves come from the Early Eocene of North Dakota (53 Ma; Hickey, 1977), the Early Middle Eocene of Washington State (50–48 Ma; Wehr and Hopkins, 1994), and the Oligo-

Fig. 1. The midpoint-rooted highest likelihood tree obtained for 91 *ndhF* gene sequences of Melastomataceae and their closest relatives under the GTR + P_{inv} + Γ model. Bootstrap frequencies (>50%) at nodes were obtained under minimum evolution criteria, using ML distances and 7500 fast bootstrap replicates. Epithets are given for species with congeners in the analysis; for all species names see Table 1.





cene of northern Colombia (~30 Ma; Huertas, 1977). Mid-Miocene leaves are known from the Latah formation near Spokane (18–16 Ma; J. Wolfe, personal communication, March 2000), Late Miocene leaves from Sumatra (Kräusel, 1929), and Pliocene leaves from Brazil (Duarte, 1956). A presumed Paleocene leaf from Antarctica (Dusén, 1908) does not belong to the family (Birkenmajer and Zastawniak, 1989) nor do Paleocene leaves from the Fort Union formation in Montana and the Ferris formation in Wyoming (Brown, 1962) whose leaf surfaces have glandular dots.

The Early Middle Eocene leaves from Washington State (of which 20 were received on loan by S. S. Renner and one is depicted in Fig. 2) show numerous densely spaced pairs of tertiary veins running in strictly parallel rows between the midrib and pairs of secondary veins that run from the base to the leaf tip. A further faint pair of secondaries can sometimes be discerned very close to the margin. The leaves are entire-margined, have weakly developed drip tips, and are of medium size (between 5–9 cm long and 2.5–5 cm wide). The single Early Eocene leaf from North Dakota is very similar in shape and size, but shows the tertiary venation less clearly. While these fossils document that Melastomataceae with leaves resembling those of modern Miconieae and Merianieae were present in North America 53 Ma ago, it is difficult to assign them to a node in the phylogeny. Most conservatively, they constrain the age of node A in Fig. 2 because all Melastomataceae and Kibessieae (*Pternandra*) have the basic kind of venation seen in the fossils, while none of the outgroups do.

Fixing node A at 53 Ma yields a rate of 0.0011 substitutions·site⁻¹·Ma⁻¹ (the distance from node A to the tips divided by 53). Table 2 shows the age estimates obtained under this second rate for events C, D, and E.

DISCUSSION

Hypotheses of a Gondwanan origin of Melastomataceae (Raven and Axelrod, 1974; Gentry, 1982: Table 5, 1993; Renner, 1993; Jacques-Félix, 1994) are rejected by the *ndhF*-based age estimates. While the fossil record of Melastomataceae and their relatives may be biased, undiscovered fossils would have to be nine times older than current oldest fossils to push back the estimates for entry into Africa and Madagascar to 90 or 100 Ma. Also, while unaccounted-for rate heterogeneity among sister groups must introduce error into the age estimates, the magnitude of such error in this data set may be small, judging from visual comparison of the clock and non-clock trees. Further error could stem from the tenuous links between calibration nodes and fossils assigned to them and from uncertainties in the dating of fossils. However, all three types of error are likely random with respect to under- or over-estimation of rates and ages. Reduction of estimation error—and rejection of wrong biogeographic hypotheses—may come from additional fossils that can add calibration points or prove hypothesized ancient ranges.

The color-coding in Fig. 2 indicates current geographic

ranges occupied by the respective taxa (with very limited back-extrapolation), while the tree's backbone is left black to indicate past ranges. From the Eocene through the Miocene both Melastomataceae and Memecylaceae occurred in tropical Laurasia, and the tree's black spine could be seen as symbolizing that region. Of their sister families, Crypteroniaceae (3 genera, 10 species) are endemic in Southeast Asia, where they are considered a Laurasian element (Raven and Axelrod, 1974; their range is mapped in Zhu, 1997). Alzateaceae (1 species) are neotropical (see Table 1 for detailed ranges), and Rhycolalycaceae (1 species), Oliniaceae (8 species), and Penaeaceae (7 genera, 20 species) South African. Memecylaceae themselves have their greatest morphological diversity in tropical East Africa (Jacques-Félix, 1978a, b, 1994), and two of the African genera extend into Malaysia (Bremer, 1982). More data are needed to resolve whether the neotropical genera of Memecylaceae are nested among paleotropical memecylons, which is indicated by preliminary combined gene and intron data (S. S. Renner and G. Clausing, unpublished data). The family's only fossil record is Oligocene (40 Ma) *Memecylon* wood from Germany (Gottwald, 1992).

First-branching Melastomataceae occur in Southeast Asia. This refers to Astronieae and Kibessieae, which based on morphological and sequence data from three genome regions belong in Melastomataceae (Clausing and Renner, 2001a). Astronieae are endemic in Southeast Asia, with most of their ~150 species occurring in Borneo; Kibessieae comprise 15 species in the Malay Archipelago, with three reaching Thailand (Renner et al., in press). Since basal Melastomataceae and all Memecylaceae are rain forest trees or treelets and since their earliest fossils are from the Eocene and Oligocene of tropical Laurasia, their common ancestor likely lived under humid tropical conditions. In combination, three lines of evidence thus point to an origin of Melastomataceae in the tropical belt that bordered the northern Tethys margin: (1) earliest fossil record restricted to Laurasia; (2) occurrence in Southeast Asia of oldest surviving lineages; and (3) likely humid forest habitat of stem lineage. If melastomes indeed originated somewhere to the north of the Tethys, they could readily have spread into North America (explaining their Early Eocene presence in Dakota) as well as tectonically more labile Southeast Asia (Hall, 1996). Going back further in time, the reconstruction of ancestral ranges based purely on topology (without fossils) becomes dubious.

Following initial radiation (viz. the divergence of Kibessieae and Astronieae), higher Melastomataceae spread into Eurasia and North America as documented by fossils. By the end of the Early Eocene, temperatures reached a global high, and many warm-humid-adapted groups reached North America via Beringia and/or the North Atlantic land bridge (Manchester, 1999; Tiffney, 2000). Malaysian genera become prominent among Alaskan fossils at that time (Graham, 1993), and melastomes with leaves similar to the relatively basal Miconieae and Merianieae reached northern Dakota and northeastern

←

Fig. 2. The tree obtained for the taxa of Fig. 1 under the GTR + P_{inv} + Γ + clock model. For taxon names see Fig. 1. The tree's black backbone denotes the ancestral Laurasian distribution suggested by the fossil record. Modern distributions (with conservative back extrapolation) are in color. Gray denotes North America, orange the Neotropics; blue tropical Africa, purple Madagascar, and green tropical Asia. Insets show fossils similar to the oldest fossils used to calibrate the molecular clock. Inset A shows a 50–48-Ma-old leaf from the Republic flora in Washington State (Burke 56614 B4242; Wehr and Hopkins, 1994). Inset B shows a Melastomeae seed from Germany (reproduced with permission from Collinson and Pinggen, 1992). Nodes for which ages are estimated in Table 2 are marked C, D, and E.

TABLE 2. Age estimates for key events in the history of Melastomataceae based on the branch lengths observed in a clock tree (Fig. 2) under the GTR + P_{inv} + Γ model. For calibration A, the distance from node A in Fig. 2 to the tips (0.05583 substitutions/site) was divided by 53 Ma, the age of the earliest Melastomataceae fossil. The resulting substitution rate "a" of 0.0011 substitutions \cdot site $^{-1} \cdot$ Ma $^{-1}$ yields the age estimates to the left. For calibration B, the distance from node B to the tips (0.02849 substitutions/site) was divided by 23 Ma, the age of the earliest Melastomeae fossils. The resulting rate "b" of 0.0012 substitutions \cdot site $^{-1} \cdot$ Ma $^{-1}$ yields the age estimates to the right. Standard deviation (SD) was calculated as explained in the METHODS.

Node	Distances from nodes to tips	Time (Ma) \pm SD using rate "a"	Time (Ma) \pm SD using rate "b"
C Melastomeae arrive in Africa	0.01483 \pm 0.0037	14 \pm 4	12 \pm 3
D Sonerileae diversify in Madagascar	0.01220 \pm 0.0034	11 \pm 3	10 \pm 3
E <i>Medinilla</i> diversifies in Madagascar	0.00190 \pm 0.0013	2 \pm 1	1.6 \pm 1

Washington. The younger seed fossils from Eurasia represent the phylogenetically younger Melastomeae. However, carpofloras in North America are limited to a few sites, and with the exception of the Brandon Lignite, are not the same kind of environment as the more thoroughly studied Oligocene/Miocene Browncoals of Europe (S. Manchester, personal communication, April 2000). While this may explain the absence of melastome seeds from North America, the absence of leaves from Eurasia may have to do with the disintegration during sieving of samples being prepared for paleocarpological investigations (F. Velichkevich, personal communication, September 2000).

Merianieae/Miconieae spread from North America into South America sometime in the Oligocene, as indicated by an Oligocene *Meriania*-like leaf from northwestern Colombia (Huertas, 1977). This is the oldest securely identified melastome fossil from South America. In North America, melastomes persisted at least until the Mid-Miocene based on fossil leaves found near the Washington/Idaho border (J. Wolfe, unpublished data, personal communication, March 2000). Among their most widespread groups may have been the open habitat-adapted Melastomeae whose seeds are known from the Miocene of Siberia, the Tambov region, Belorussia, Poland, Belgium, and several sites in Germany. Modern Melastomeae are the most cold-tolerant Melastomataceae, occurring at high altitudes in the Andes and the Himalayas, and the tribe also includes the family's only temperate zone endemic, the Eastern North American *Rhexia* with 11 species. The earliest South American records of Melastomeae are Pliocene leaves from Brazil (Duarte, 1956).

Paleotropical Melastomeae form a clade (node C in Figs. 1 and 2) that is deeply embedded in neotropical Melastomeae and between 14 and 12 Ma old (see Table 2 for standard deviations on all estimates). West African genera branch off first, which together with the estimated age of this divergence implies that West Africa was reached from the neotropics via long-distance dispersal. The only two Asian genera of Melastomeae, *Osbeckia* and *Melastoma*, likely derive from African or Madagascan ancestors (Figs. 1, 2). In another analysis, *Melastoma* is sampled more densely (Renner and Meyer, in press), and those data suggest that the radiation of *Melastoma* began during the Pleistocene.

Junction of the Australian continent with the Philippine Sea plate arc in the Miocene (Hall, 1996) and the resulting tectonic reconfiguration of Southeast Asia provided the opportunity for diversification of another large clade, Dissochaeteae/Sonerileae (Figs. 1, 2). Based on the clock tree (Fig. 2), Dissochaeteae/Sonerileae began to diversify during the Miocene. They are confined to rain forest habitat and comprise woody climbers, herbs, and terrestrial and epiphytic shrubs (Clausing and

Renner, 2001b). Two of their sublineages reached Madagascar, one wind dispersed, the other bird dispersed. The wind-dispersed group (node D in Figs. 1 and 2) may have arrived in the Late Miocene, 11 Ma ago (Table 2). Today, it has 107 species in one genus in Madagascar (Perrier de la Bâthie, 1951) and 50 species in seven genera in tropical Africa (Jacques-Félix, 1994). The later-arriving bird-dispersed genus *Medinilla* (node E in Figs. 1 and 2) today comprises \sim 70 species in Madagascar and three in Africa.

This and other studies of the history of major components of tropical biota (Lavin and Luckow, 1993; Chanderbali, van der Werff, and Renner, 2001) have implications for our understanding of the build-up of tropical floristic diversity in general. Based on molecular phylogenies and Laurasian fossil floras, it appears that the ancestral floras shared directly among Gondwanan fragments may be smaller than sometimes assumed. Entry of boreotropical taxa into southern continents, beginning in the Oligocene and Miocene, must be seriously considered as an additional means of establishing pantropical distribution patterns. Tertiary floras document tropical forests at high latitudes in Laurasia during the Eocene worldwide climatic optimum, with connections via Beringia or the North Atlantic land bridge between the floras of Indochina, North America, and to a limited extent South America. Examples of families today more or less restricted to Indomalaysia, tropical Africa, and/or the New World tropics but that were widespread in Eocene and Oligocene Laurasia include Actinidiaceae, Bigoniaceae, Lauraceae, Menispermaceae, Musaceae, groups of Myrtaceae, Rubiaceae, palms, and Zingiberaceae (Mai, 1995; Kubitzki and Krutzsch, 1996; Manchester, 1999).

Our analysis also shows that species accumulation in one of the largest families in the three regions of today's tropics occurred over vastly different lengths of time. Especially illustrative is the case of Madagascar, which harbors 225 species of Melastomataceae (Perrier de la Bâthie, 1951) of which 21% stem from successive arrivals of African members of an ultimately neotropical lineage (Melastomeae), 48% from a capsular-fruited Asian immigrant (Sonerileae), and 31% from a berry-fruited Asian immigrant (*Medinilla*). The paucity of African Melastomataceae (240 species) to some extent may reflect the family's relatively recent (14–12 Ma) arrival on that continent from the west and from the east. Other lineages, such as *Osbeckia* and *Melastoma*, dispersed from Africa and/or Madagascar to Indochina and Malesia, adding to the many ties between these floras (Thorne, 1973) and increasing species diversity in Southeast Asia. Like other taxa in the neotropics that derive from Laurasian ancestors (Gentry, 1982), Melastomataceae are most species rich in the Andes, while their morphological diversity (wood, placentation, anther morphol-

ogy, etc.) is greatest in Indochina and Malesia, regions where oldest and youngest lineages now coexist.

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