Missing fossils, molecular clocks, and the origin of the Melastomataceae[1]

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In a recent analysis of the historical biogeography of Melastomataceae, Renner, Clausing, and Meyer (2001; *American Journal of Botany* 88(7): 1290–1300) rejected the hypothesis of a Gondwana origin. Using a fossil-calibrated chloroplast DNA (*ndh*F) phylogeny, they placed the early diversification of Melastomataceae in Laurasia at the Paleocene/Eocene boundary (ca. 55 Ma) and suggested that long-distance oceanic dispersals in the Oligocene and Miocene (34 to 5 Ma) account for its range expansion into South America, Africa, and Madagascar. Their critical assumption—that oldest northern mid-latitude melastome fossils reflect tribal ages and their geographic origins—may be erroneous, however, because of the sparse fossil record in the tropics. We show that rates of synonymous nucleotide substitutions derived by the Renner et al. (2001) model are up to three times faster than most published rates. Under a Gondwana-origin model advocated here, which includes dispersals from Africa to Southeast Asia via the "Indian ark" and emphasizes filter rather than either sweepstakes dispersal or strict vicariance, rates of nucleotide substitution fall within the range of published rates. We suggest that biogeographic reconstructions need to consider the paucity of Gondwanan fossils and that frequently overlooked interplate dispersal routes provide alternatives to vicariance, boreotropical dispersal, and long-distance oceanic dispersal as explanations for the amphi-oceanic disjunctions of many tropical rain forest plants.

Key words: chloroplast DNA; Melastomataceae; palynology; plate tectonics; synonymous substitution rates; tropical rain forests.

In a recent global evaluation of the biogeography and fossil record of tropical plants within a plate tectonic framework, Morley (2000; pp. 260–262) described three main centers of tropical (megathermal) flowering plant diversification during the Late Cretaceous and earliest Tertiary: (1) one across the northern mid-latitudes (Laurasia), characterized by such families as Actinidiaceae, Icacinaceae, Rutaceae, Menispermaceae, Theaceae, and Zingiberaceae; (2) an equatorial center (West Gondwana) with, among others, Annonaceae, Leguminosae, Myrtaceae, and Arecaceae; and (3) a southern mid-latitude center (Southern Gondwana) that harbored very old families such as Chloranthaceae and Winteraceae and became a center of radiation for such families as Proteaceae. The Northern Hemisphere center is particularly noteworthy because many of its modern taxa display amphi-Pacific distributions (being confined to the Neotropics and Southeast Asia, but absent from Africa) or are relict to Southeast Asia. These distributions reflect the different dispersal opportunities of Boreotropical (Laurasian) rain forest taxa to find refuge in the low latitudes as global climates deteriorated during the mid-Tertiary (Morley, 2001).

Melastomataceae is an important rain forest family, but was excluded from the Morley (2000) evaluation because of its very limited macrofossil record at low latitudes in the older Tertiary and because its pollen is difficult to distinguish from that of Combretaceae (cf. Muller, 1981). Melastomataceae exhibits its greatest diversity in the Neotropics (ca. 3000 species), followed by Southeast Asia (~1000), with moderate di-

versities in Africa (=240) and Madagascar (=225) (Renner, 1993). Its sister family, Memecylaceae, is also pantropical. The biogeographic patterns of Melastomataceae are typical of a Gondwana-derived lineage (Raven and Axelrod, 1974; Gentry, 1982; Jacques-Félix, 1994), which has become the established view.

In a recent molecular systematic interpretation Renner et al. (2001) provided a radically different hypothesis on the biogeographic history of the Melastomataceae. With reference to a fossil-calibrated molecular clock, they placed the initial diversification of the family in Laurasia in the Paleocene/Eocene (ca. 55 million years [Ma]; Tertiary epoch boundaries follow Berggren et al. [1995], Cretaceous stage boundaries follow Harland et al. [1989]), and its pantropical distribution was attributed to long-distance dispersal during the Oligo-Miocene (34 to 5 Ma). This conclusion, subsequently expanded by Renner and Meyer (2001), is remarkable since it implicates trans-oceanic dispersal (possibly by winds) as the primary mode of interplate range expansion, and it implies that much of the species diversity of Melastomataceae is younger than previously thought.

The assumption that the earliest fossil records of particular clades of Melastomataceae reflect their age and geographic origin may be erroneous, however, due to regional biases in the angiosperm fossil record.

Regional bias in the angiosperm macrofossil record—The Tertiary plant macrofossil record is strongly biased to North America, Europe, and northern Asia, where studies of angiosperm leaf and seed fossils have a long tradition. In comparison, other regions, especially the Southern Hemisphere, have provided little data (Collinson, 1990). This bias must be taken into account when reviewing fossil evidence for angiosperms. The macrofossil record for virtually each Tertiary epoch of North America and Europe is particularly prolific, with only the North American Pliocene being poorly

studied (Manchester, 1999), but even here, strong bias is seen in the fossil melastome record. Seeds (Melastomeae) are known only from the Eurasian Miocene (e.g., Collinson and Pingen, 1982; Mai, 2000). There are no records from North America, despite the common occurrence in wetlands from Southeastern USA to Ontario of the temperate swamp herb *Rhexia*, which is a likely candidate for the Eurasian seeds. Similarly, although numerous leaf fossils are known from North America (e.g., Hickey, 1977; Wehr and Hopkins, 1994), probably referable to Miconieae/Merianieae, no leaves referable to the family are known from Eurasia. The macrofossil bias may be due to differences in the ecology and taphonomy of melastomes in these regions.

In tropical regions, the fossil record is strongly biased with respect to collecting intensity. In South America, numerous macrofossil studies have focused on the Mio-Pliocene with more than 50 papers dealing with Neogene macrofloras. These have yielded melastome fossils approximately in proportion to the present-day diversity of the family (Burnham and Graham, 1999). However, Neotropical Palaeogene and Late Cretaceous macrofloras are poorly described with only a scattering of references for the Eocene (many dealing with single fossils rather than floras) and hardly any from the critical Paleocene and Late Cretaceous. There is one melastome record from the "Oligo-Miocene" of Panama (Duarte, 1956), and Huertas (1977) discussed one leaf fossil from the Eocene of Colombia (considered Oligocene, ca. 30 Ma, by Renner et al. [2001]).

There are no melastome fossils from Africa, where most macrofossil studies are based on fossil woods, but there is a single reference to *Memecylon* leaves (Memecylaceae) from the Indian Oligocene (Awasthi and Mehrota, 1995). The paucity of plant macrofossils from the Neotropical and African Tertiary are likely due to lack of study and limited accessibility of appropriate outcrops.

In Southeast Asia and Indochina, the rock record is highly biased toward the Neogene, and this bias is reflected in the plant macrofossil record (Bande and Prakash, 1986). Eocene plant macrofossil-bearing sediments are of extremely limited occurrence, and Paleocene outcrops are virtually nonexistent, except perhaps in Myanmar; no plant macrofossils are known from the Late Cretaceous. The only fossils referable to Melastomataceae are of leaves and have been attributed to *Astronia*. These have been recorded from the Miocene of Sabah (Geyler, 1887) and Sumatra (Krausel, 1929).

The pollen record of Melastomataceae—The pollen of Melastomataceae, Memecylaceae, Oliniaceae, Penaeaceae, and Rhynchocalycaceae is uniformly heterocolpate. Crypteroniaceae includes heterocolpate (*Axinandra*, *Dactylocladus*) and bisyncolpate (*Crypteronia*) pollen, whereas that of Alzateaceae is tricolporate (Muller, 1975). It is difficult to differentiate the heterocolpate pollen of Melastomataceae sensu lato from that of Combretaceae (also Myrtales). The most distinctive difference is pollen size, with many melastome genera having smaller pollen. In South America, palynologists have been confident in referring very small heterocolpate pollen from the Plio-Pleistocene to *Miconia* (van der Hammen and Gonzaléz Guzman, 1963) and in Southeast Asia, small grains are generally referred to the *Medinilla* type (R. J. Morley, unpublished data) and occur back to the Early Miocene. The oldest published heterocolpate pollen is from the Paleocene of Colombia (*Heterocolpites palaeocenica*, van der Hammen and Garcia de Mutís, 1966; attributed by

the authors to probable Melastomataceae), and recently this species has been recorded as a rare element from the latest Maastrichtian (70–65 Ma) of the same area by K. Richards (KRA International, personal communication). Elsewhere, the oldest published records are from the Late Eocene of West Africa (Salard-Chebaldaeff, 1981). Muller (1981) refers the latter to Combretaceae, but affinity with Melastomataceae is an equal possibility. The oldest heterocolpate pollen records from Southeast Asia are also of Late Eocene age, from the Mankalihat Peninsula in Borneo (P. Waton, Corelab, personal communication). The oldest Indian records are from the Early Miocene (Rao and Ramanujam, 1982). The fossil pollen record, although not conclusively indicating the presence of Melastomataceae, is consistent with an origin in Western Gondwana followed by Eocene dispersal to Southeast Asia via the "Indian ark" (see later).

Gondwana origins revisited—The first appearance of Melastomataceae leaves in the Eocene of North America and Melastomeae seeds in the early Miocene of Europe and Asia may reflect colonization from Gondwanan lineages for which there is no fossil record (the "missing fossils" scenario). In order to evaluate this hypothesis it was first necessary to assess the strength of the Renner et al. (2001) molecular data in falsifying the Gondwana model. We did this by calibrating the synonymous nucleotide substitution rates of the *ndh*F data set, based on (1) minimum ages of dispersal corridors among the Gondwana fragments (Fig. 1) and (2) age of earliest Melastomataceae and Melastomeae fossils, as in Renner et al. (2001). We compare these silent substitution rates to a range of published estimates. We then provide an alternative biogeographic hypothesis for the pantropical expansion of the family.

MATERIALS AND METHODS

Gondwana dispersal model—In our model, we dated the ages of key nodes of the Melastomataceae phylogeny (Renner, 2001) through reference to the fossil record and tectonic plate separations. Key dates were positioned on the basis of the oldest record of Myrtaceae pollen at 88 Ma (node B in Fig. 1) and the separation of Madagascar and the Indian Plate at about 68 Ma (nodes L and K). Other divergences were positioned using the relative branching order of the *ndh*F phylogeny (Renner et al., 2001). Using this approach, we estimated the origin of the tribe Melastomeae at 76 Ma.

Molecular analysis—We focused our molecular analysis on the Melastomeae tribe, whose 23 Ma seed fossils were used by Renner et al. (2001) to calibrate the *ndh*F molecular clock. Melastomeae is pantropical, with representatives in North and South America, Africa, India, and Madagascar. The Renner et al. (2001) analysis included 27 species, representing 17 genera. The North American genus *Rhexia* (*R. mariana* and *R. virginica*) was basal in their analysis. The genera *Nepsera*, *Comolia*, and *Aciotis* formed another relatively basal group. We downloaded the *ndh*F sequences of the Melastomeae from Genbank (accession numbers in Renner et al., 2001; alignments available from C. W. Dick) and for generic representatives of other Melastomataceae. The sequences were aligned manually using the program Sequence Alignment Editor v. 2.0 (A. Rambaut, Oxford University, UK).

Our genetic analysis focused on synonymous (silent) nucleotide substitutions, those that do not result in the replacement of an amino acid. We focused on silent rather than total nucleotide substitutions because silent rates are not constrained by natural selection to maintain protein function and are therefore comparable across different protein-coding chloroplast genes (Muse and Gaut, 1997). Gaut et al. (1997), for example, found no significant differences in silent substitution rates in *rbc*L and *ndh*F in the Poaceae. We calculated the synonymous distances (number of synonymous substitutions per synonymous
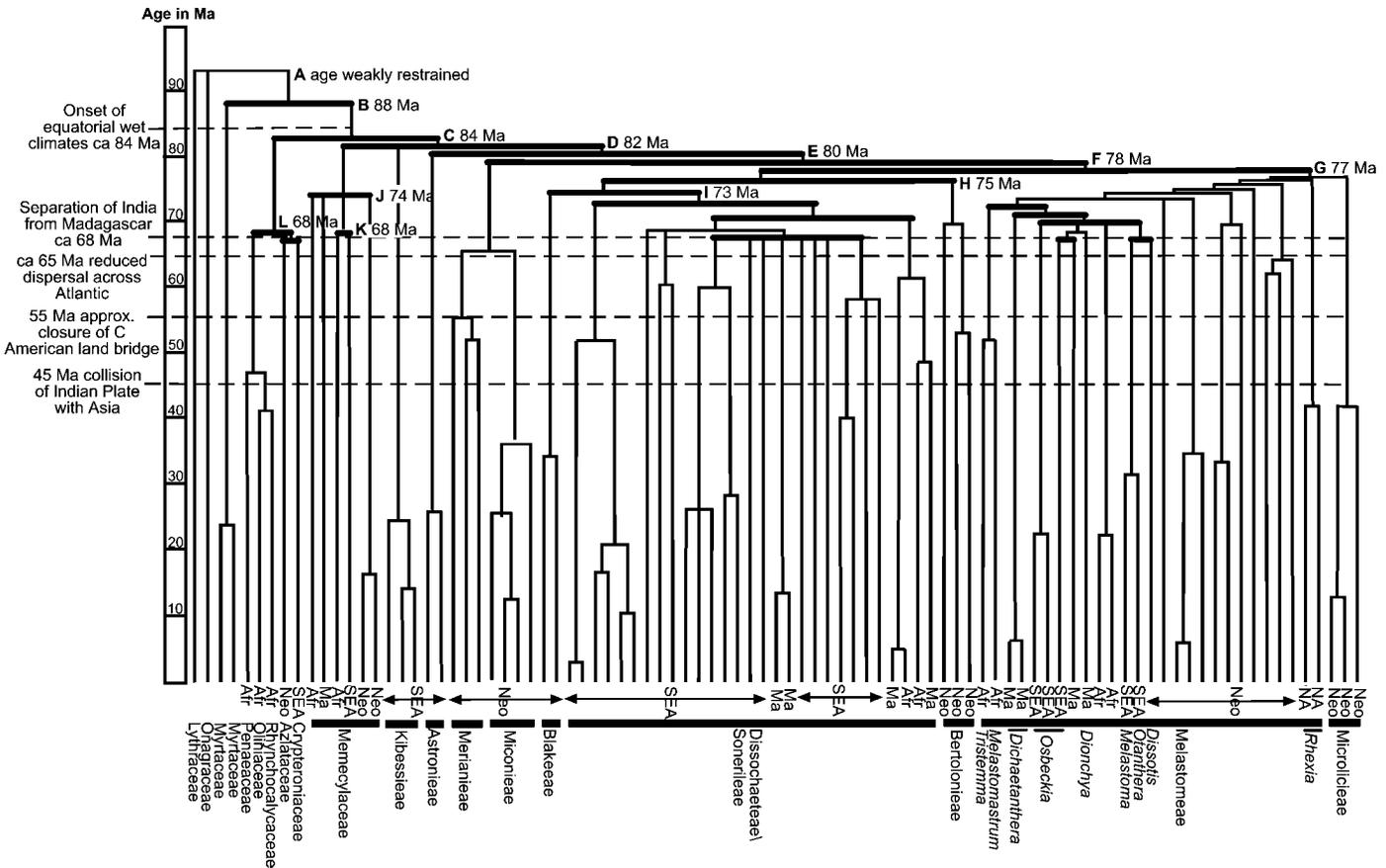
Fig. 1.   Phylogenetic hypothesis for Melastomataceae. Branching patterns are based on Fig. 1 of Renner et al. (2001), but divergence times are based on known dispersal corridors between the post-Gondwana land masses and are indicated by heavy horizontal lines. (A) No direct restraints from fossil record; (B) oldest Myrtaceae pollen in Africa, at about 88 Ma; (C) small sister families separate from Melastomataceae/Memecylaceae in Africa at about 84 Ma; (D) Memecylaceae and Kibessieae separate from mainstream Melastomataceae at about 82 Ma; (E) Astronieae separate from mainstream Melastomataceae at about 80 Ma; (F) South American Miconieae/Meraniaeae separate from pantropical Melastomataceae at about 78 Ma; (G) differentiation of Microlicieae/Melastomeae from Dissochaeteae/Sonerileae/Bertolonieae at about 77 Ma; (H) differentiation of South American Bertolonieae from Blakeeae/Dissochaeteae/Sonerileae at about 75 Ma; (I) South American Blakeeae differentiate from Dissochaeteae/Sonerileae at about 73 Ma; (J) *Memecylon* in Africa, Madagascar, and India at about 74 Ma; (K) *Memecylon* in Madagascar and India at about 68 Ma; (L) ancestor to sister families in South America, Africa, and/or India at about 68 Ma. Afr = Africa; Ma = Madagascar; NA = North America; Neo = Neotropics; SEA = Southeast Asia.

site, denoted K_s) in the program MEGA 2.1 (Kumar et al., 2001). We employed the method of Li-Wu-Luo (Li et al., 1985), in which one-third of the two-fold and all of the four-fold degenerate sites are considered synonymous sites. The Li-Wu-Luo method also factors the different frequencies of transitions and transversions. We coded ambiguous sites as missing data and analyzed gaps through the pairwise deletion option. Confidence limits were computed through bootstrap resampling with 500 replicates.

Silent substitution rates (R_S) were calculated using the formula $R_S = K_S/2T$, where T is the time of divergence of the clade. Renner et al. (2001) used 23 Ma fossil Melastomeae seeds to mark the age of divergence of the Melastomeae, whereas as noted above, we applied a divergence time of 76 Ma based on ages of plate tectonic separations (Fig. 1). We compared estimates to a range of values published for other flowering plants: Wolfe et al. (1987) estimated a range of 1.0 to 3.0 × 10⁻⁹ substitutions per silent site per year for angiosperms based on a comparison of eight chloroplast genes from monocots and dicots ($T = 140$ Ma) and wheat and maize ($T = 20$–40 Ma). Zurawski and Clegg (1987) calculated an R_S of 1.3 × 10⁻⁹ based on chloroplast DNA divergences between spinach and tobacco. Xiang et al. (2000), using a detailed northern latitude fossil record of *Cornus*, calculated R_S of 1.02–1.42 × 10⁻⁹ for *rbc*L and then obtained similar values from 10 sister taxa pairs (from 10 families) that display an East Asian and eastern North American disjunction.

RESULTS

The mean synonymous distance (K_s) among the Melastomeae genera was 0.109 ± 0.013 (means ± 1 SE) and was based on 330 synonymous sites. The synonymous distance involving *Rhexia* and all other Melastomeae was 0.137 ± 0.021, while the mean for the *Nepsera/Aciotis/Comolia* vs. all other Melastomeae was 0.156 ± 0.021. Under the Gondwana model ($T = 76$ Ma), these divergences correspond to rates of 0.9 ± 0.014 × 10⁻⁹ and 1.03 ± 0.14 × 10⁻⁹ synonymous substitutions per synonymous site per year. Applying the seed fossil-based $T = 23$ Ma to the same nodes produces estimates of R_s of 2.978 ± 0.457 × 10⁻⁹ and 3.391 ± 0.457 × 10⁻⁹.

Estimates of R_s under the Gondwana scenario are roughly three times slower than those of the Renner et al. (2001) analysis; yet our estimates fall closer to most of the published synonymous rate estimates for chloroplast genes. Our analysis of synonymous distances shows that the *ndh*F data have not falsified the "missing fossils" or Gondwana hypothesis; in fact the data appear to support Late Cretaceous models of diversification.
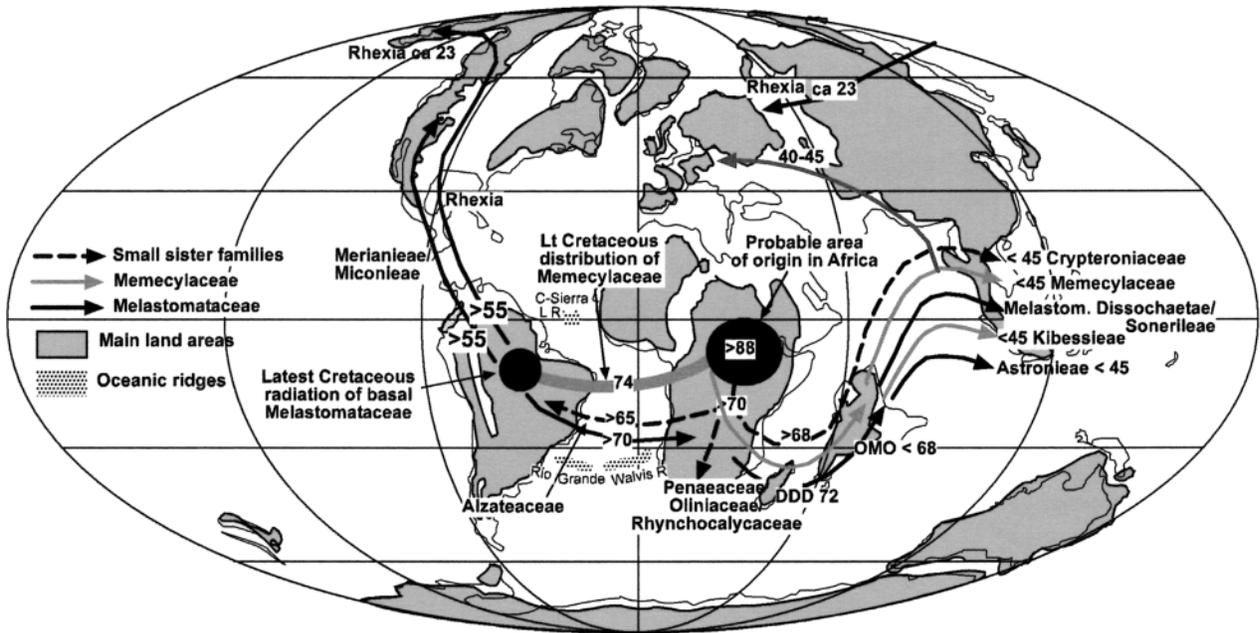
Fig. 2. Origin and dispersal of Melastomataceae. Only ''preferred'' routes discussed in text are shown. Base map for latest Cretaceous (Maastrichtian, 74–65 Ma) from Smith et al. (1994), with main land areas shaded; projection type is Mollweide's equal area. DDD = differentiation of Madagascan *Dichaetanthera*, *Dionychia*, and *Dissotis* from African *Melastomastrum/Tristemma* at about 72 Ma, whereas OMO indicates differentiation of *Osbeckia*, *Melastoma*, and *Otanthera* on the Indian Plate after 68 Ma or in Southeast Asia after 45 Ma. C Sierra L R = Ceara–Sierra Leone Rise.

DISCUSSION

Biogeographical reconstruction—Basal Melastomataceae and sister taxa—Whether we look at its closest relatives or Melastomataceae itself, the cladogram of Renner et al. (2001) provides strong support for a Late Cretaceous West Gondwana center of radiation for the Melastomataceae. The sister taxa to Melastomataceae consist of five small families, with representatives in South America (Alzateaceae), southern Africa (Rhynchocalycaceae, Olineaceae, Penaeaceae) and Southeast Asia (Crypteroniaceae) and the pantropical Memecylaceae. Crypteroniaceae (*Dactylocladus*, a peat swamp tree), has a possible Middle Miocene fossil pollen record in Borneo (Anderson and Muller, 1975; age revised by Morley, 2000 and Morley, in press), whereas fossil leaves of *Memecylon* are described from the Oligocene of India (Awasthi and Mehrota, 1995) and fossil wood is reported from the Late Eocene of Germany (Gottwald, 1992).

Two ''out of Gondwana'' dispersal scenarios need to be considered for the Melastomataceae and its sister families:

1) *Origin in South America*—Under this scenario, the ancestor to South American Alzateaceae/Crypteroniaceae split off from the South African Penaeaceae/Oliniaceae/Rhynchocalycaceae ancestor prior to termination of Late Cretaceous/Paleocene South American–North American land bridge (minimum 55 Ma) (Bonaparte, 1984; Pindall et al., 1988; Hallam, 1994) and prior to termination of trans-oceanic dispersal routes between equatorial Africa and South America (84–65 Ma) (McDougal and Douglas, 1988; Morley, 2000, p. 256) at a time between the Campanian (approximate time of onset of rain forest climates in equatorial South America [ca. 84 Ma, but possibly earlier; Morley, 2000]) and the Paleocene (termination of Central American land bridge). The Alzateaceae/Crypteroniaceae ancestors were able to disperse across the Central American land bridge in Maastrichtian/Paleocene and become part of the Paleocene/Eocene Boreotropical (North America + Eurasia) flora. Crypteroniaceae would have found refuge subsequently in Southeast Asia in Yunnan (*Crypteronia*) and as an element of Bornean peat swamp floras (*Dactylocladus*); Alzateaceae found refuge in South America.

2) *Origin in Africa*—Under this scenario (Fig. 2), the immediate ancestor to Crypteroniaceae/Alzateaceae was in Africa in the latest Late Cretaceous (84–68 Ma) and dispersed to the Indian Plate (before 68 Ma) and subsequently to Southeast Asia after 45 Ma (via the Indian ark) and is now relict as Crypteroniaceae in Southeast Asia, similarly dispersing from Africa to South America before approximately 65 Ma, where it is now relict as Alzateaceae. The ancestral group became extinct in Africa. This scenario is strongly supported by a recent molecular evaluation of Crypteroniaceae by Conti et al. (2002). It is also the simplest, and no fossils of Crypteroniaceae have been recorded from the intensively studied North American/Eurasian Boreotropical floras. Melastomataceae and its sister families therefore are likely to have originated in Africa.

Origin of Memecylaceae—The greatest morphological diversity of Memecylaceae lies in tropical Africa, with *Mouriri* in South America, and *Memecylon* having representatives in Africa, Madagascar, and Southeast Asia. This strongly suggests that Memecylaceae had an African–South American distribution in the latest Cretaceous (ca. 74 Ma), but *Memecylon* subsequently dispersed via the Indian Plate to Southeast Asia (Fig. 2). The Late Eocene record of *Memecylon* wood from Germany postdates the collision of the Indian Plate with Asia, and for such Eurasian occurrences, dispersal from the Indian Plate is the simplest explanation.

By tying the cladogram of Melastomataceae + sister families to the timing of dispersal corridors, the sister families

appear to represent a complex of relict groups that differentiated at an early stage, shortly after the time of domination of angiosperms over other plant groups. The presence of tricolporate pollen in Alzateaceae may be seen as testimony to this initial stage of differentiation, prior to the latest Cretaceous appearance of heterocolpate pollen in the fossil record. The strong representation of sister families in South Africa strongly suggests Africa as an early area of differentiation with subsequent dispersal to Asia via India and to South America. Such an origin would fit well with the history of the related family Myrtaceae, which has its oldest fossils (pollen) in Africa.

Biogeography of the Melastomataceae—Kibessieae (which includes *Pternandra*) appears from the cladogram to be a sister group to Memecylaceae and is found only in Southeast Asia, suggesting that it differentiated on the Indian Plate after separation from Madagascar (68–45 Ma) or in Southeast Asia after 45 Ma.

With respect to subsequent branching, which takes into account the major part of Melastomataceae excluding Kibessieae; most of the basal groups are South American with subsequent branching relating to differentiation in Africa, Madagascar, and Southeast Asia. This suggests that the primary radiation of Melastomataceae may have been in South America during the latest Cretaceous. The Southeast Asian group Astronieae, on the other hand, appears to have had the same history as Memecylaceae, with differentiation on the Indian Plate (68–45 Ma). Such a dispersal pattern would be consistent with *Astronia* leaf fossils from the Southeast Asian Neogene (Geyler, 1887; Krausel, 1929).

The South American Merianieae/Miconiaeae need to have been well established by the Paleocene, before the closure of the Central American land bridge (55 Ma) in order for members of this group to disperse to North America, thus accounting for North American leaf fossils that compare with this group. Such a dispersal would fit admirably with the Early Eocene appearance of leaves of this type in the western interior of the USA. There is no evidence to suggest that this group dispersed into Eurasia.

Subsequent dichotomies within Melastomeae and Dissochaeteae/Sonerileae can be explained, with the exception of *Rhexia*, by dispersals from South America via Africa and Madagascar to Southeast Asia. Under this scenario, basal groups must have been in place in South America between about 78 and 74 Ma. In Melastomeae, dichotomies occur in geographical sequence suggesting dispersal to Africa prior to about 74 Ma, with subsequent differentiation of Madagascan *Dichaetanthera*, *Dionycha*, and *Dissotis* (about 72 Ma) from African *Melastomastrum*/*Tristemma* followed by *Osbeckia*/*Melastoma*/*Otanthera* on the Indian Plate (68–45 Ma) or in Southeast Asia (after 45 Ma). Such a pattern fits admirably with dispersal and differentiation on the Indian Plate prior to collision with Asia in the Middle Eocene.

The widespread occurrence of Melastomeae seeds in Miocene sites from Belgium to Siberia can be explained in two possible dispersal scenarios: (1) Dispersal of a member of Melastomeae to North America via the Central American land bridge (prior to 55 Ma), which subsequently dispersed either across the short-lived Late Paleocene/Early Eocene southern Greenland land bridge (ca. 56 Ma) or via Beringia into Eurasia (Fig. 2). The ecology of this group may have been different from that of the Miconieae/Merianieae members, with the result that it has left its fossil record in the form of seeds rather than leaves. This Boreotropical-derived element may still be extant in North America, where *Rhexia* forms the only temperate-adapted member of the family. Surprisingly, no Melastomeae seed fossils have been reported from the intensively studied European Eocene, possibly giving strength to a mid-Tertiary dispersal of temperate-adapted taxa via Beringia. (2) Because all Melastomeae fossils are Miocene, postdating the collision of India with Asia by 20 Ma, this group could simply have dispersed from Southeast Asia or the Indian Plate and may never have been an element of the early Tertiary Boreotropical flora. If this scenario is correct, *Rhexia* would have dispersed to North America either with ancestral Merenieae/Miconieae toward the end of the Paleocene, and is now relict to the warm temperate forests of southeastern USA (but has left no fossil record), or dispersed across the Isthmus of Panama during the Pliocene, in which case it is currently undergoing a phase of range expansion. We prefer scenario 1, with dispersal to Eurasia via Beringia, in view of the temperate adaptation of *Rhexia*.

The Dissochaeteae/Sonerileae lineage could be explained in a similar manner to low latitude Melastomeae with dispersal from South America via Africa (between 76 Ma and 70 Ma) and the Indian Plate (68–50 Ma) to Southeast Asia (after 45 Ma), but to understand their cladogram it must be borne in mind that this group (and other rain forest lianas, epiphytes, and ground flora elements) is poorly represented today in Africa, possibly because of African late Tertiary extinction as a result of intermittent dry climates and geological factors (Morley, 2000). With descendants of African contributors to this evolutionary lineage without any representatives, Madagascan and Southeast Asian lines link directly with the South American Blakeeae. An anomaly in this cladogram is the apparent late differentiation of *Medinilla* into Southeast Asian and Madagascan clades. If this reflects dispersal of *Medinilla* from the former area of Southeast Asian members of this genus (which may have included the Indian Plate), this dispersal could have taken place any time after about 68 Ma.

We wish to stress that the times of separation of continents as accepted by geologists are not necessarily the times of cessation of interplate plant dispersal. Although geological evidence clearly points to "separation" of South America and Africa by the end of the Albian, many new angiosperm pollen types appeared at approximately the same time in both continents throughout the Late Cretaceous (Morley, 2000, p. 88) suggesting continued trans-Atlantic dispersal, possibly via island chains such as the Rio-Grande Rise–Walvis Ridge (McDougal and Douglas, 1988) and Ceara-Sierra Leone Rise (Hallam, 1994). The proportion of simultaneous appearances either side of the Atlantic dropped off from the Maastrichtian onward, as the Atlantic widened, although dispersals continued on a regular basis until the Middle Eocene (Morley, 2000, p. 255). Similarly, for Africa, Madagascar, and the Indian Plate, the pollen record suggests that plant dispersals continued on a regular basis, presumably via island chains, until the "mid"-Maastrichtian, when they suddenly ceased. The "time window" for dispersal of wet climate plants between South America, Africa, Madagascar, and India was thus from 84 Ma or thereabouts, up to the mid-Maastrichtian (68 Ma). The suggestion by Renner et al. (2001) that undiscovered fossils need to be nine times older than current oldest fossils to push back estimates to 90–100 Ma "for entry into Africa and Madagascar" (p. 1297) is puzzling, for these dates

are only twice the age of the oldest North American fossils and three times the age of the oldest South American ones.

According to our interpretation of the Renner et al. (2001) data, taking into account the fossil record on the one hand and calibrating the molecular clock by placing divergences in relation to the pattern of well-established and dated dispersal corridors/paths on the other, the Melastomataceae, with its great concentration of diversity in South America, is a family that has had a history essentially within the equatorial zone, with occasional episodes of expansion into the Northern Hemisphere Boreotropical province at times of globally warm climates, especially during the Late Paleocene/Early Eocene thermal maximum. This is a pattern followed by other families that radiated from equatorial (Gondwana) rather than mid-latitudes, such as Annonaceae and Myristicaceae (Morley, 2001). Dispersals were primarily along well-established dispersal paths, perhaps with ''island hopping'' for taxa that are dispersed by birds or wind. Our analysis indicates that these dispersal routes and the paucity of Gondwana plant fossils should be key considerations in reconstructing biogeographic history of pantropical rain forest taxa.

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